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Systematics of the snake-eyed skink genus *Cryptoblepharus*

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Front cover: Top, *Cryptoblepharus egeriae*, Christmas Island, Indian Ocean. Photograph S. Donnellan. Left, *C. virgatus*, Lions Den Hotel, Bloomfield Track, Qeensland, Australia. Photograph P. Horner. Right, *C. gurrmul* sp. nov., North Goulburn Island, Northern Territory, Australia. Photograph P. Horner.

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A molecular-systematic assessment of species boundaries in Australian *Cryptoblepharus* (Reptilia: Squamata: Scincidae) – a case study for the combined use of allozymes and morphology to explore cryptic biodiversity

by

PAUL HORNER and MARK ADAMS

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A molecular systematic assessment of species boundaries in Australian *Cryptoblepharus* (Reptilia: Squamata: Scincidae) – a case study for the combined use of allozymes and morphology to explore cryptic biodiversity

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ABSTRACT

The scincid genus *Cryptoblepharus* (snake-eyed skinks) has endured a problematic taxonomic history, both in Australia and throughout the remainder of its extensive geographic range. The present study combines detailed allozyme analyses of 45 putative loci with a preliminary morphological assessment to diagnose operational taxonomic units (OTUs) among 398 specimens of *Cryptoblepharus* from mainland Australia, Christmas Island and New Caledonia. Stepwise Principal Co-ordinates Analysis revealed a total of 27 diagnosable OTUs plus two instances of putative hybridisation among the six species currently recognised from mainland Australia, while both extralimital populations proved to be genetically and phylogenetically unique. The allozyme and morphological profiles of diagnosable OTUs were often discordant, with 10 instances evident in which pairs of OTUs were readily diagnosable based on one dataset but effectively indistinguishable using the other. Despite this complexity, all Australian taxa fell unequivocally into one of two distinctive genetic lineages, only one of which appeared monophyletic. These results have been used by a companion study (Horner 2007) to undertake a thorough morphological revision of Australian *Cryptoblepharus* and determine the taxonomic status of all diagnosable OTUs. Together the two studies provide a model for the successful integration of co-dominant genetic markers and detailed morphological re-appraisals to explore cryptic biodiversity in a taxonomically difficult group.

KEYWORDS: Reptilia, Scincidae, Cryptoblepharus, Australia, cryptic biodiversity, species boundaries, allozymes, morphology.

INTRODUCTION

The family Scincidae is the most species rich, morphologically diverse and geographically widespread of all lizard groups. Containing about 1200 species in 127 genera (Uetz *et al.* 2000), the family is found in most tropical and temperate regions of the world, though its major centres of diversity are the Australia/New Guinea and South-east Asian regions (Greer 1970).

The most geographically widespread scincid taxon is the genus *Cryptoblepharus* Wiegmann. Comprised of small (<55 mm snout-vent length), arboreal or saxicoline species, *Cryptoblepharus* ranges from the east central coast of Africa, through islands of the Mozambique Channel, the Seychelles, Madagascar, Mauritius, Christmas Island, southern Indonesia, New Guinea, Australia, Micronesia, Melanesia, Polynesia and east throughout the Pacific to the west coast of South America. The genus is notable for a pronounced degree of morphological conservatism for most meristic and mensural characters but significant diversity in colouration and back patterning. Indeed, *Cryptoblepharus* species are so alike that Mertens (1931), in a monographic study of the genus, treated all taxa as geographical races of a single species (as *Ablepharus boutonii* Wiegmann), making it (at that time) the world's most widespread lizard species. Despite general agreement that taxonomic problems beset the genus (Dunn 1927; Storr 1976; Haacke 1977; Crombie and Steadman 1986), there has been no recent taxonomic revision.

Thirty-nine *Cryptoblepharus* taxa are currently recognised (at either species or subspecies level), including 14 forms in the south-west Indian Ocean (Ethiopian-Malagasy) region; 19 in the Indo-Pacific region and six in the Australian region. Although the genus is a common and abundant human commensal, there exists considerable confusion with identifying taxa. Most original species descriptions are based on colour pattern and geographic distribution, with the few traditional scalation characteristics mentioned being attributable to virtually any member of the genus.

Based on most assessments (Cogger *et al.* 1983; Wilson and Knowles 1988; Greer 1989; Ehmann 1992; Stanger *et al.* 1998; Cogger 2000; Wilson and Swan 2003) there are seven recognised species of Australian *Cryptoblepharus*: *C. carnabyi* Storr, 1976; *C. egeriae* (Boulenger, 1889); *C. fuhni* Covacevich and Ingram, 1978; *C. litoralis* (Mertens, 1958); *C. megastictus* Storr, 1976; *C. plagiocephalus* (Cocteau, 1836) and *C. virgatus* (Garman, 1901). Six of these are from continental Australia (and its fringing islands) and one (*C. egeriae*) occurs on the Australian Territory of Christmas Island in the Indian Ocean which, while politically Australian, is herein considered part of the Indo-Pacific geographic region. Of those from continental Australia, three (*C. fuhni*, *C. litoralis* and *C. megastictus*) have relatively restricted distributions in the north of the continent, one (*C. virgatus*) is widespread in eastern and southern Australia and two (*C. carnabyi* and *C. plagiocephalus*) are widespread over much of the continent. As an indication of the taxonomic uncertainty associated with *Cryptoblepharus*, the two most widespread Australian species each have multiple synonymies.

The routine use of molecular techniques over the past 20 years has revealed that the taxonomic frameworks underpinning many animal groups are inadequate (Richardson *et al.* 1986; Knowlton 1993; Bickford *et al.* 2007). Two situations are commonly observed: (1) the morphological diversity displayed by a single biological species is erroneously taken to indicate two or more species (oversplitting) and (2) supposedly single species harbour cryptic species, i.e. species that were not formally recognised *a priori* using morphological criteria, even where they are morphologically diagnosable once their existence has been established (Richardson *et al.* 1986; Bickford *et al.* 2007). As argued elsewhere (Donnellan *et al.* 1993), geographically widespread and morphologically conservative groups are those most likely to harbour cryptic species. *Cryptoblepharus* clearly qualifies on both these counts as a candidate for cryptic biodiversity, while the existence of so many formally described morphotypic forms suggests oversplitting may also feature in the genus.

Reviews of the prevalence and significance of cryptic species invariably highlight the need to employ molecular genetic data as part of any systematic revision of problem groups (e.g. Knowlton 2000; Bickford *et al.* 2007). In this study we have chosen allozyme electrophoresis as the preferred technique for molecular analysis, because of its common usage in systematic studies, proven record in recognising cryptic species and ability to diagnose hybrids (e.g. Richardson *et al.* 1986; Hutchinson and Donnellan 1992; Allibone *et al.* 1996; Georges and Adams 1996; Bertozzi *et al.* 2000). Allozyme electrophoresis complements morphology in delineating species (Avise 1975; Richardson *et al.* 1986; Hillis 1987), providing characters that are largely independent of each other and usually expressed in all individuals irrespective of age or sex.

A disadvantage of allozyme analysis is that the technique is not applicable to preserved specimens, necessitating acquisition of 'fresh' material for most studies and thereby restricting the numbers of animals examined (and excluding historic type specimens). This is partially compensated by the fact that, unlike quantitative morphological characters, only a few individuals per population are required to adequately characterise the allozyme variation present in that population (Richardson *et al.* 1986; Adams *et al.* 1987). Moreover, the availability of morphological vouchers of known taxonomic identity usually permits successful determination of the taxonomic identity of historic vouchers, including types, where diagnostic morphological characters become evident *post hoc* to differentiate the cryptic species identified using molecular criteria.

The primary aim of this study was to undertake a comprehensive systematic revision of species boundaries in Australian members of the genus *Cryptoblepharus*. Herein we combine a detailed analysis of the allozyme data with a preliminary morphological diagnosis for the same set of specimens to allocate individuals to known species, presumptive taxa, or animals of likely hybrid origin. This is accompanied by an assessment of the genetic and phylogenetic affinities of the taxa thus identified. All other components of the systematic revision of *Cryptoblepharus* are presented and discussed in a companion paper (Horner 2007), including morphology and the taxonomic decisions regarding the status of all taxa.

MATERIAL AND METHODS

Details of specimens used. Allozyme electrophoresis was undertaken on 396 *Cryptoblepharus* liver samples, from 214 Australian localities (including Christmas Island). Although most samples were collected specifically for this study, improved geographic coverage was gained with the addition of *Cryptoblepharus* tissues from the South Australian Museum, Australian Museum and Western Australian Museum tissue collections. Detailed allozyme analysis of material extralimital to Australia was not attempted due to a paucity of tissue samples. However, tissues from two specimens of *C. novocaledonicus* were available (courtesy of the Australian Museum) and these were included in the allozyme study, along with a single specimen of *Carlia munda* (NTM R22894) to act as an outgroup for rooting phylogenetic trees. Details of all animals examined are provided in Appendix 1.

Allozyme electrophoresis. Allozyme electrophoresis of liver homogenates was carried out on cellulose acetate gels (Cellogel™) according to the principles and procedures of Richardson *et al.* (1986). The following enzymes exhibited zymograms of sufficient activity and resolution to permit allozymic interpretation (EC = Enzyme Commission numbers): aconitase hydratase (ACON, EC 4.2.1.3), acid phosphatase (ACP, EC 3.1.3.2), aminoacylase (ACYC, EC 3.5.1.14), adenosine deaminase (ADA, EC 3.5.4.4), alcohol dehydrogenase (ADH, EC 1.1.1.1), albumen (ALB), carbonate dehydratase (CA, EC 4.2.1.1), citrate (si)-synthase (CS, EC 4.1.3.7), diaphorase (DIA, EC 1.6.99.), enolase (ENOL, EC 4.2.1.11), fructose-bisphosphatase (FDP, EC 3.1.3.11), fumarate hydratase (FUM, EC 4.2.1.2), glyceraldehyde-3-phosphate dehydrogenase (GAPD, EC 1.2.1.12), guanine deaminase (GDA, EC 3.5.4.3), glutamate dehydrogenase (GDH, EC 1.4.1.3), lactoylglutathione lyase (GLO, EC 4.4.1.5), aspartate aminotransferase (GOT, EC 2.6.1.1), glycerol-3-phosphate dehyrogenase (GPD, EC 1.1.1.8), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), glutathione peroxidase (GPX, EC 1.11.1.9), guanylate kinase (GUK, EC 2.7.4.8), 3-hydroxybutyrate dehydrogenase (HBDH, EC 1.1.1.30), isocitrate dehydrogenase (IDH, EC 1.1.1.42), cytosol aminopeptidase (LAP, EC 3.4.11.1), L-lactate dehydrogenase (LDH, EC 1.1.1.27), malate dehydrogenase (MDH, EC 1.1.1.37), mannose-6-phosphate isomerase (MPI, EC 5.3.1.8), purine-nucleoside phosphorylase (NP, EC 2.4.2.1), dipeptidase (PEPA, EC 3.4.13.), tripeptide aminopeptidase (PEPB, EC 3.4.11.), proline dipeptidase (PEPD, EC 3.4.13.), phosphoglycerate mutase (PGAM, EC 5.4.2.1), phosphogluconate dehydrogenase (6PGD, EC 1.1.1.44), phosphoglycerate kinase (PGK, EC 2.7.2.3), phosphoglucomutase (PGM, EC 5.4.2.2), superoxide dismutase (SOD, EC 1.15.1.1), L-iditol dehydrogenase (SORDH, EC 1.1.1.14) and triose-phosphate isomerase (TPI, EC 5.3.1.1). The nomenclature used to designate allozymes at a locus and multiple loci follows Adams *et al.* (1987).

Preliminary morphological analysis. Preliminary morphological assessment of specimens from mainland Australia, based on the existing taxonomic framework (Cogger 2000; Wilson and Swan 2003), recognised the following 14 morphotypic forms (Horner 2007): 'carnA' (most *C. carnabyi*); 'carnB' (*C. carnabyi* with very narrow laterodorsal stripes), 'carnC' (*C. carnabyi* with prominent broad laterodorsal stripes), 'carnD' (*C. carnabyi* from central Australia with obtusely pointed plantar scales), 'fuhn' (*C. fuhni*), 'litor' (*C. litoralis*), 'oxley' (*C. litoralis*-like form from Oxley and New Year Islands, NT), 'horn' (form described as *C. horneri* by Wells and Wellington (1985), but placed in the synonomy of *C. litoralis* by Horner (1999), 'megaA' (most *C. megastictus*), 'megaB' (*C. megastictus*-like form from the Pilbara region of WA), 'plagA' (most *C. plagiocephalus*), 'plagB' (form described as *C. swansoni* by Wells and Wellington (1985), but the name was determined to be a *nomen nudum* by Horner (1999), 'virgA' (*C. virgatus virgatus*) *and* 'virgB' (*C. virgatus clarus*). Each form was treated as a putative operational taxonomic unit (OTU) and the genetic integrity of all OTUs except 'oxley' (for which no tissues were available) investigated using Principle Co-ordinates Analysis (PCoA). The two OTUs available for study from outside mainland Australia were *C. egeriae* from Christmas Island (OTU 'eger') and *C. novocaledonicus* from New Caledonia (OTU 'novo').

General procedure for stepwise PCoA. The identification of OTUs among the mainland Australian specimens based on their allozyme profiles involved the stepwise use of Principal Co-ordinates Analysis (PCoA). This approach aims to (1) determine major genetic groups independently of any morphological considerations and (2) ensure that individuals assigned to a group are genetically more closely related to each another than to individuals of any other group. Such an approach avoids the risk that diagnosable hybrids or composite taxa will be missed by the *a priori* assignment of individuals to groups. The advantages of stepwise PCoAs for the delineation of OTUs from first principles are discussed in more detail elsewhere (Georges and Adams 1992; Smith and Adams 2007).

The stepwise PCoA procedure involves conducting a series of PCoAs, starting with the entire dataset (in this case all 394 specimens from mainland Australia) and thereafter sequentially removing those individuals that can be assigned to discrete genetic groups based on the initial PCoA. Importantly, each genetic group is only recognised and the individuals within that group removed from the next analytical step where an examination of individual genotypes reveals the group to be diagnosable from all other putative PCoA clusters by multiple "fixed" allozyme differences (allowing a defined tolerance for shared allozymes). This cycle of genetic group identification followed by a further PCoA on the reduced subset of individuals is repeated until all primary genetic groups have been recognised. A second round of stepwise PCoAs is then undertaken separately for each individual genetic group thus identified, to assess whether any group is itself a composite of two or more diagnosable subgroups. As before, subgroups are only recognised where the raw allozyme data reveal subgroups to be unequivocally diagnosable by fixed allozyme differences. If necessary, further rounds of PCoA are conducted on genetic subgroups until all subgroups are genetically homogeneous i.e. no discrete PCoA clusters are apparent within a genetic subgroup or those present are not diagnosable by any fixed allozyme differences. These homogeneous subgroups are then regarded as the final OTUs for those genetic analyses based on pooling individuals into taxa.

One of the many strengths of the stepwise PCoA approach outlined above is that it allows the detection of individual hybrids and/or populations of hybrid origin. Such individuals (1) occupy positions on PCoA scatterplots which are intermediate between those clusters representing the hybridising taxa, (2) are heterozygous at *all* loci which diagnose these taxa (for an F_1 hybrid) or heterozygous for at least one of the diagnostic loci (for animals of hybrid origin) and (3) should not display genotypes at any other locus which are inconsistent with their proposed hybrid origin. Together these three criteria permit genuine cases of hybridisation to be distinguished from 'normal' within taxon variability, or outliers resulting from an individual displaying 'missing values' at one or more key loci.

It must be stressed that PCoA, when used in the manner advocated here, is a technique for delineating taxa and assessing how diagnosable they are, not determining their overall genetic or phylogenetic affinities. PCoA does not always place sister taxa into the same composite genetic group or position the most genetically or phylogenetically distinctive taxa as outliers. Thus consideration of the evolutionary relationships among taxa require other analytical approaches.

Although stepwise PCoA can be used as a stand-alone procedure independent of any morphological considerations, it is usually instructive to overlay existing morphological diagnoses onto any analyses undertaken, as a means of assessing the relationship between the existing taxonomic framework and the genetic affinities of individuals. This approach has been followed in this study and thus some of the final OTUs identified by stepwise PCoA were recognised primarily on morphotypic criteria, even where they were not diagnosable genetically.

Operational details of stepwise PCoA. Each PCoA was generated using the computer program PATN (DOS version; Belbin 1994) from a pairwise matrix of Rogers genetic distances (Rogers R; Rogers 1972) between individuals. The operational definition of a fixed difference was relaxed slightly to allow taxa/groups to cumulatively share up to 9% of their alleles in common (as compared to the 5% tolerance advocated by Richardson *et al.* 1986). This recognition that a taxonomic character can be diagnostic, despite the taxa involved sharing character states at low frequency, is standard practice in traditional morphological taxonomy.

A PCoA cluster was only recognised as a primary genetic group if it displayed at least two fixed differences from all other groups or clusters, while genetic subgroups were required to display at least one fixed difference from other subgroups. All genetic groups, subgroups and distinct morphotypic forms were treated as final OTUs for subsequent analyses. Final OTUs are underlined to distinguish them from the initial OTUs designated on morphological grounds alone (e.g. plagB versus 'plagB').

Genetic relationships among OTUs. Genetic relationships among the OTUs were explored by tabulating allele frequencies and calculating the percentage fixed differences (%FD; Richardson *et al.* 1986) between OTUs, also allowing a cumulative 9% tolerance for shared alleles. Further investigation was made by calculating Nei's genetic distance (Nei D; Nei 1978) and Rogers R values. Treefiles were created with PHYLIP (Felsenstein 1993) and used by the computer program TREEVIEW (Page 1996) to construct UPGMA (unweighted pair-group method of arithmetic averages) dendrograms and NJ (neighbor joining) phlyograms. A measure of the robustness of clusters and clades was obtained by bootstrapping the allele frequency data using 1000 pseudoreplicates. All allele frequencies, genetic distance measures and bootstrap values were generated using unpublished BASIC computer programs written by M. Adams.

RESULTS

A total of 45 putative allozyme loci were successfully scored for the 399 specimens screened in this study. The allozyme genotypes are not presented due to space considerations, but are available upon request from either co-author. Tables 1 and 2 summarise the allele frequencies for those OTUs recognised following the completion of stepwise PCoA, while Table 3 contains the pairwise %FD and Nei D measures between all final OTUs.

An initial PCoA was undertaken on all 394 specimens from mainland Australia (i.e. all OTUs except 'eger' [n=2], 'novo' [n=2] and the outgroup [n=1]) to assess whether any primary genetic dichotomies could be established among mainland Australian *Cryptoblepharus*. This PCoA revealed that all specimens fell neatly into one of two clusters based on their PCoA score for the first dimension (which explained 38% of the total variability present in 393 dimensions; Fig. 1), with additional minor heterogeneity present in one cluster in the second PCoA dimension. Individuals in one cluster were fully diagnosable at four loci (*Ca, Fum, Pgk* and *Sod*; Tables 1 versus 2) from individuals in the other cluster and effectively diagnosable by near-fixed differences at a further four loci (*Acon-1, Adh-2, Guk* and *Srdh*). This result clearly demonstrates that the two clusters represent real and distinctive genetic lineages. These two lineages are hereinafter referred to as lineage 1 and lineage 2 and each was independently subjected to its own stepwise PCoA.

To keep the presentation of results to a reasonable length, we have included only a selection of the many individual PCoAs undertaken. Thus although a final PCoA was performed for every final OTU represented by at least eight specimens and collected from at least two different sites, none are displayed herein because (by definition) they do not reveal any significant genetic subgroups (as defined in

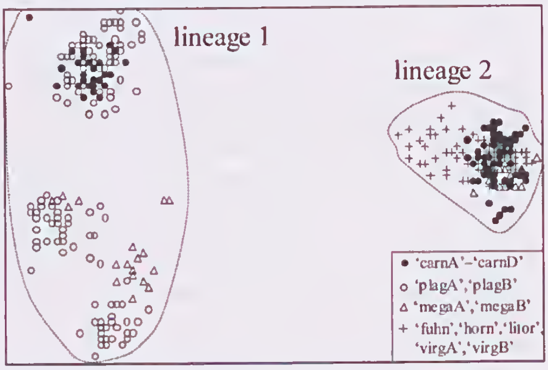

Fig. 1. Principal Co-ordinates Analysis of all 394 mainland Australian specimens, revealing the primary dichotomy between lineage 1 and lineage 2. The relative PCoA scores have been plotted for the first (X-axis) and second (Y-axis) dimensions, which individually explained 38% and 9% respectively of the total multivariate variation. Individuals are represented by symbols which reflect the initial morphological diagnosis. As with any PCoA, the number of points will be less than the total number of individuals where individuals share the same values in the first two dimensions.

Materials and Methods). Furthermore, while we present all five key PCoAs for lineage 1 in order to demonstrate the stepwise PCoA procedure in detail, only two of the many separate PCoAs undertaken on lineage 2 specimens are required to summarise the final outcome of stepwise PCoA on this lineage.

Stepwise PCoA of lineage 1 animals. Eleven separate PCoAs were ultimately undertaken to identify the final OTUs present within lineage 1. The initial PCoA scatterplot of 203 individuals (Fig. 2) revealed six genetic groups, namely OTU plagB, OTU megaA3, three composite groups (designated 1A, 1B and 1C) and a single specimen (NTM R18837). Both plagB and megaA3 were ultimately diagnosable from all other lineage 1 OTUs at multiple allozyme loci (minimum value for megaA3 = 27%FD, equal to 12 fixed differences; minimum value for plagB = 16 %FD, equal to 7 fixed differences), thus confirming their genetic distinctiveness.

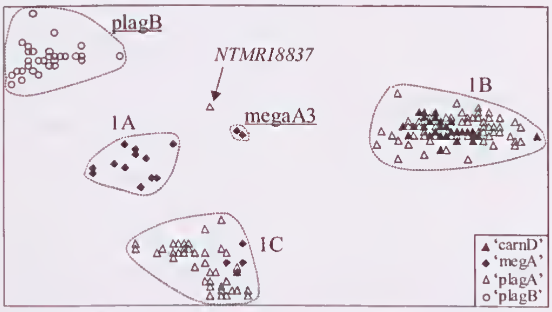

Fig. 2. Initial PCoA scatterplot of the 203 specimens of genetic lineage 1. General presentation as in Fig. 1. The first and second dimensions individually explained 24% and 18% respectively of the total multivariate variation. Individuals are represented by symbols which reflect their initial morphological diagnosis. Primary genetic groups are encircled and labeled according to whether they represent a final OTU (underlined) or a composite of OTUs as revealed by follow-up PCoAs (groups 1A – 1C). The single putative F1 hybrid is indicated by an arrow.

A follow-up PCoA on genetic group 1A revealed the presence of two distinctive genetic subgroups, identified as megaA1 and megaA2 (Fig. 3). These two OTUs were diagnosable at four loci (9 %FD, Table 3) from one another and at a minimum of five loci (equal to 11%FD) from all other lineage 1 OTUs.

Genetic group 1B comprised specimens referable to the morphotypic forms 'plagA' and 'carnD'. A follow-up PCoA on this group revealed a substantial degree of overlap (Fig. 4), indicating that the two forms could not be diagnosed allozymically. As outlined earlier, we nevertheless recognise them as distinct OTUs on morphological grounds (distinctive morphotypes in sympatry). Table 3 demonstrates that although plagA5 and carnD display no fixed differences from one another, they are diagnosable from all other lineage 1 OTUs by a minimum of four fixed differences.

A follow-up PCoA on genetic group 1C (Fig. 5) revealed two genetic subgroups, one corresponding to OTU plagA1 and the other (labelled 1D in Fig. 5) shown by a further PCoA (Fig. 6) to be a composite of four OTUs (plagA2, plagA3, plagA4 and megaA4). These five OTUs are diagnosable from one another either on morphological grounds (megaA4 versus plagA2, distinctive morphotypes in sympatry but 0 %FD) or by fixed allozyme differences

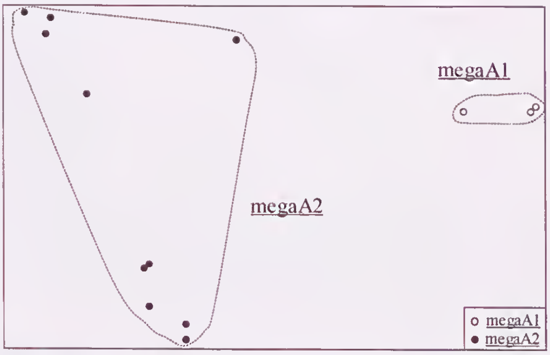

Fig. 3. Follow-up PCoA scatterplot of genetic group 1A in Fig. 2. The first and second dimensions individually explained 42% and 24% respectively of the total multivariate variation. Individuals are represented by symbols which reflect the final OTUs. All other details as per Fig. 2.

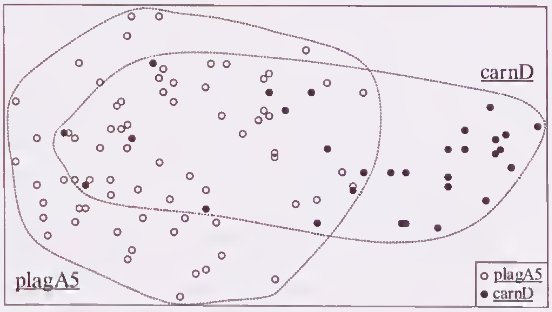

Fig. 4. Follow-up PCoA scatterplot of genetic group 1B in Fig. 2. The first and second dimensions individually explained 13% and 11% respectively of the total multivariate variation. Individuals are represented by symbols which reflect the final OTUs. All other details as per Fig. 2.

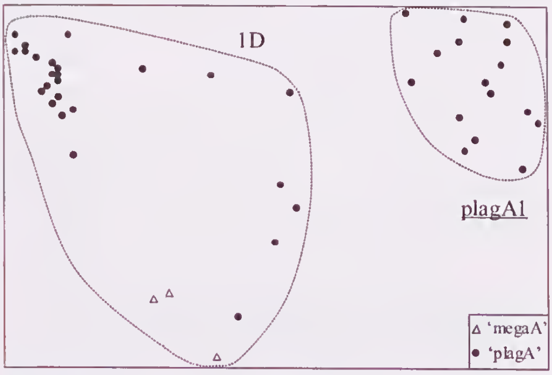

Fig. 5. Follow-up PCoA scatterplot of genetic group 1C in Fig. 2. The first and second dimensions individually explained 34% and 10% respectively of the total multivariate variation. Individuals are represented by symbols which reflect their initial morphological diagnosis. All other details as per Fig. 2.

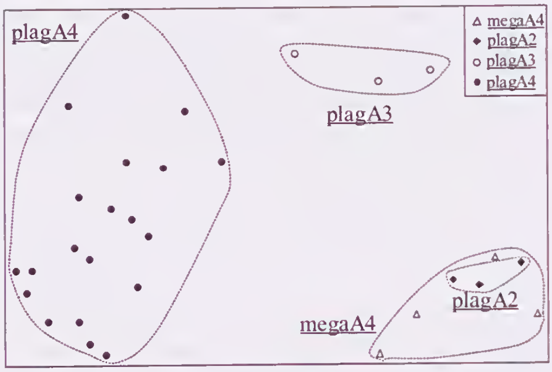

Fig. 6. Follow-up PCoA scatterplot of genetic group 1D in Fig. 5. The first and second dimensions individually explained 23% and 12% respectively of the total multivariate variation. Individuals are represented by symbols which reflect the final OTUs. All other details as per Fig. 2.

(range 2–9 %FD, Table 3). Together they can be diagnosed from all other lineage 1 OTUs by a minimum of four fixed differences (range 9–36 %FD, Table 3).

The geographic locations of all specimens initially contained in genetic group 1C are included in Figure 7. PlagA4 is widespread and obviously allopatric from the other four OTUs, which are restricted to northern and north-western Australia and (with the exception of plagA1) have only been collected at a few localities. Given the generally small sample sizes and a lack of detail regarding the comparative geographic distributions of these northern OTUs, the allozyme data by themselves are unable to unequivocally determine their taxonomic status.

Specimen NTM R18837, the final genetic group evident in the initial PCoA (Fig. 2), displayed an allozyme profile consistent with it being an F_1 hybrid between OTUs plagA5 and plagB. This individual was heterozygous for the appropriate alleles at a suite of loci which distinguish the putative parental OTUs (*Dia*, *Gda*, *Gpi*, *Guk*, *PepB*, *PepD-1* and *Tpi*) and displayed no genotypes which were inconsistent with this hypothesis at any locus surveyed. The position occupied by NTM R18837 on the initial PCoA is also intermediate between the plagA5 and plagB groups (Fig. 2), as would be expected for an F_1 hybrid.

In summary, stepwise PCoA of lineage 1 individuals revealed 11 diagnosable OTUs plus one F_1 hybrid. Of these, six were referable to *C. plagiocephalus* (plagA1, plagA2, plagA3, plagA4, plagA5 and plagB), four to *C. megastictus* (megaA1, megaA2, megaA3 and megaA4) and one to *C. carnabyi* (carnD). Diagnostic allozyme differences were apparent among all OTUs except for the combinations plagA2 versus megaA4 and plagA5 versus carnD.

Stepwise PCoA of lineage 2 animals. Twenty separate PCoAs were ultimately undertaken to identify the final OTUs present within lineage 2. Additional PCoAs were required when compared to lineage 1 because lineage 2 contains more OTUs and hence the genetic groups evident after PCoA were often less well separated (i.e. there is simply less 'free space' available on the PCoA scatterplot). In addition, a putative hybrid zone between two partially overlapping OTUs required several rounds of PCoA to adequately resolve. As a consequence, some of the PCoAs undertaken were based on the most obvious genetic groups present in the initial PCoA, while others combined adjacent genetic groups where these groups contained members of the same morphotypic form (mainly involving 'carnA' and 'virgA' morphotypes).

The initial PCoA scatterplot of 191 individuals revealed five genetic groups (Fig. 8), all but one of which (carnA1) ultimately proved to be a composite of two or more final OTUs. Two of these composite groups involved final OTUs that were recognised solely on morphological grounds, despite the absence of fixed allozyme differences. Group 2A contained a series of individuals displaying the 'virgA' morphotype (OTU virgA1) plus all those displaying the allopatrically distributed 'virgB' morphotype (OTU virgB; Fig. 7). These OTUs never occupied distinct clusters at any level of stepwise PCoA, indicating that are genetically very similar (see also Fig. 9). Group 2D was composed of animals possessing either the 'litor' or 'horn' morphotypes. Despite a lack of fixed differences, OTUs litor and horn did form discrete clusters in a follow-up PCoA, indicating they appear to be genetically distinctive based on allele frequencies.

The majority of final OTUs resided in the two remaining composite groups. Four OTUs (carnA3, carnA4, carnB and megaB) were ultimately recognised by stepwise PCoA in composite group 2C. All were diagnosable from one another by a minimum of two fixed differences except for carnA3 and megaB, which display a single fixed difference (Table 3) plus differ morphologically in allopatry (Pilbara region, WA versus northern SA). Group 2B contained the greatest diversity and comprised individuals with any of four different morphotypes. The final OTUs recognised within 'carnabyi', 'megastictus' and 'fuhni' morphs were carnA2, carnA5, carnC, fuhn and megaA5. All were diagnosable from one another by a minimum of three fixed differences except for the morphologically distinguishable and sympatric megaA5 and carnA5, which displayed a single fixed difference (Table 3). Interestingly, carnA5 was not diagnosable by fixed differences (Table 3) from the morphologically distinctive virgA3 (see next paragraph), although they did form discrete PCoA clusters in one-on-one PCoA and are therefore genetically distinctive based on allele frequencies.

Individuals referable to 'virgatus' (groups 2A and 2B, Fig. 8) were ultimately placed into one of three subgroups, based on a series of stepwise PCoAs. Two of these subgroups corresponded to OTUs virgA2 and virgA3, while the third comprised a series of seven individuals (labelled 'virgA1x3') from three locations at the northern geographical limits of virgA1, in a zone of putative overlap with virgA3 (Fig. 7). As indicated in Figure 9, these individuals occupied a position after PCoA which was intermediate between the clusters representing virgA1 (which included the allozymically indistinguishable virgB) and virgA3. Evi-

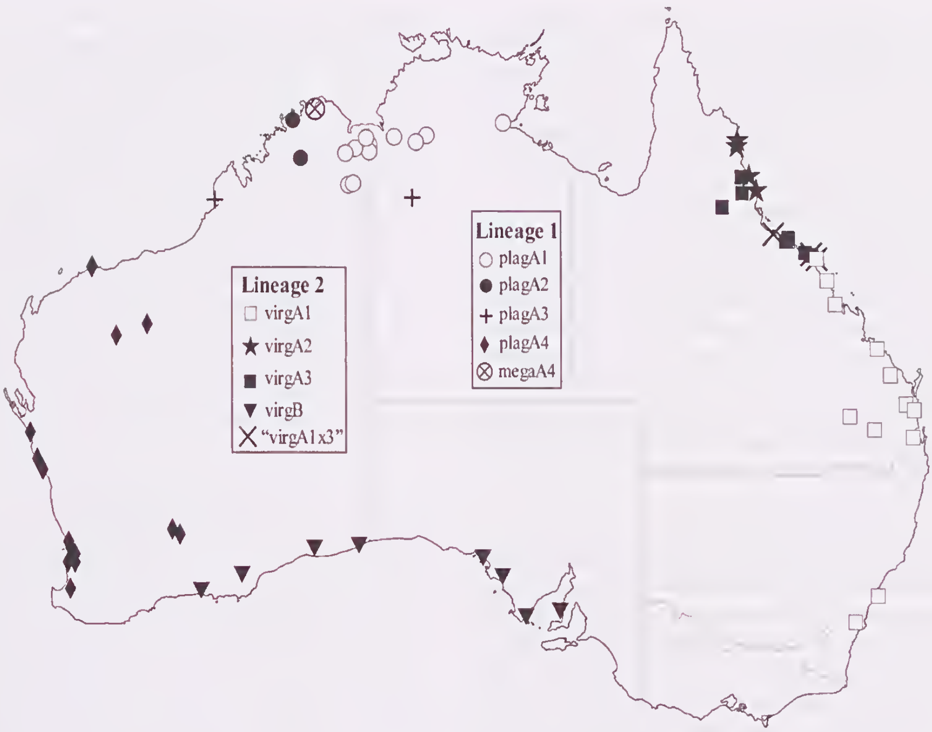

Fig. 7. Map of mainland Australia indicating the location of all collecting sites for two groups of genetically-similar OTUs.

dence that 'virgA1x3' represents individuals with a virgA1 x virgA3 hybrid origin is provided by the allele frequency data, which show 'virgA1x3' to be polymorphic for the appropriate alleles at the two loci found to diagnose virgA1 from virgA3 (*Acyc* and *PepA-2*) and generally displaying intermediate frequencies for those alleles at other loci which most differentiate the putative parental OTUs (Table 2). Additional support comes from the observation that pure virgA1 animals or pure virgA3 animals were collected in close proximity (<6 kilometres) to 'virgA1x3 animals at two of the three sites involved (Horner 2007).

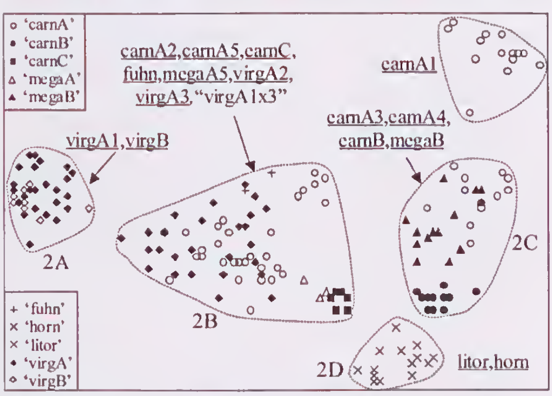

Fig. 8. Initial PCoA scatterplot of the 191 specimens of genetic lineage 2. The first and second dimensions individually explained 19% and 11% respectively of the total multivariate variation. Individuals are represented by symbols which reflect the initial morphological diagnosis. Primary genetic groups are encircled and labeled with the final OTU(s) contained therein, as revealed by follow-up PCoAs. Composite groups are also individually labeled (2A -2D) to allow cross-referencing with the text. All other details as per Fig. 1.

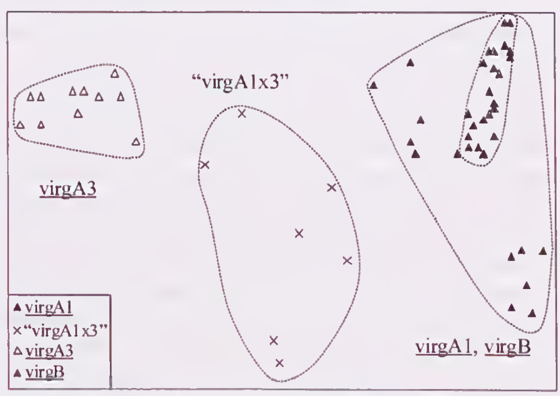

Fig. 9. Follow-up PCoA scatterplot of the virgA1/virgA3/virgB complex. The first and second dimensions individually explained 25% and 10% respectively of the total multivariate variation. Individuals are represented by symbols which reflect the final OTUs or animals of putative hybrid origin (labeled as "virgA1x3"). All other details as per Fig. 2. The heterogeneity present in the second dimension for virgA1 reflects differences in allele frequency at a suite of loci (but no fixed differences) between southern (two sites, n=6) and northern (10 sites, n = 20) subpopulations.

In summary, stepwise PCoA of lineage 2 individuals revealed 16 diagnosable OTUs plus one putative hybrid zone. Of the diagnosable OTUs, seven were referable to *C. carnabyi* (carnA1, carnA2, carnA3, carnA4, carnA5, carnB and carnC), four to *C. virgatus* (virgA1, virgA2, virgA3 and virgB), two to *C. megastictus* (megaA5 and megaB) and one to each of *C. fuhni* (fuhn), *C.* 'horneri '(horn) and *C. litoralis* (litor). Diagnostic allozyme differences were apparent among all OTUs except for the combinations virgA1 versus virgB, carnA5 versus virgA3 and horn versus litor.

Genetic relationships among OTUs. The genetic distance data demonstrate that each of the two extralimital morphotypic forms 'eger' and 'novo' are distinguishable from all of the Australian taxa at a minimum of 14 fixed allelic differences (range 32–73 %FDs; Table 3). Thus the raw allozyme data confirm eger and novo as diagnosable OTUs and indicate they have no close affinities with either of the two Australian lineages.

As discussed elsewhere (Downes and Adams 2001), the widespread presence of within-taxon polymorphism in allozyme datasets usually ensures that only distance-based analyses, rather than the more preferred character-based methods, can be used for phylogenetic analysis. A total of six such analyses were undertaken, involving both UGPMA and NJ trees generated on each of three distance measures (%FD, Nei D and Rogers R). Together these analyses represent the most commonly used tree building algorithms and genetic distance measures and cover a range of differing assumptions about the nature and rate of molecular evolution (Swofford *et al.* 1996; Downes and Adams 2001). Our approach here is to focus only on those phylogenetic relationships which were supported by all analyses.

Figure 10 presents the NJ tree obtained based on the Rogers R values, but incorporating bootstrap values obtained by averaging across all six analyses. Only eight clades were both present in all analyses and supported by mean bootstrap values above 70%. Two of these reflect basal relationships, namely (1) all Australian taxa plus eger and (2) all lineage 2 taxa. The remaining six involve terminal or near-terminal affinities within both lineage 1 (carnD/plagA5 and megaA1/megaA2 both sister pairs; plagA1/plagA2/plagA3/plagA4/megaA4 form a monophyletic clade) and lineage 2 (horn/litor, carnA5/virgA3 and virgA1/virgB all sister pairs). Of these latter six clades, only one (megaA1/megaA2) does not involve the five pairs of OTUs which could not be diagnosed by their alloyme profiles. Thus the phylogenetic analyses provide no support that lineage 1 taxa form a natural clade, nor offer any major insights into the relationships among most taxa within either lineage.

Despite the lack of detailed phylogenetic resolution on offer, one surprising inference from the initial phenetic assessments was nevertheless confirmed. Stepwise PCoA not only demonstrated each of the four most widespread morphotypic species to be a composite of multiple diagnostic OTUs (i.e. eight in *C. carnabyi*, six in *C. megastictus*, six in *C.plagiocephalus* and four in *C. virgatus*), but also suggested there was little correspondence between the genetic affinities of an OTU and its morphotype. The phylogenetic analyses provided a clear indication that all four morphospecies are paraphyletic or polyphyletic with respect to their constituent taxa. This marked disparity between the genetic and morphotypic profiles of most taxa is particularly evident for the diagnosable OTUs within *C. megastictus*, which occurred in both lineages, were scattered throughout the phylogram and exhibited the same range of relatedness levels to other morphotypic forms as was displayed by the entire Australian radiation (Fig. 10).

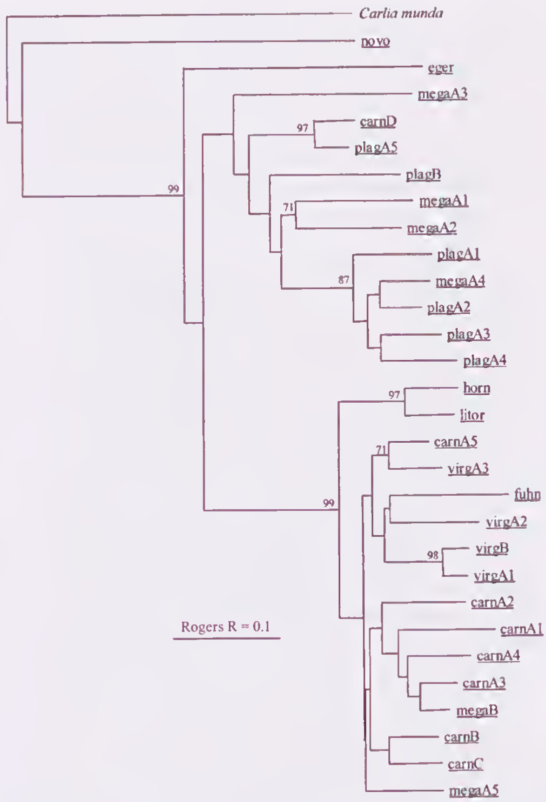

Fig. 10. Neighbor Joining tree depicting the genetic relationships amongst 29 *Cryptoblepharus* taxa, based on Rogers R and rooted using the outgroup *Carlia munda*. The 29 taxa comprise the 27 diagnosable OTUs identified using stepwise PCoA plus the two extra-limital taxa 'eger' and 'novo'. Composite bootstrap values (see text) above 70% are shown for all nodes.

DISCUSSION

The present study has revealed the presence of 27 diagnosable OTUs and two instances of putative hybridisation among the 394 specimens of *Cryptoblepharus* available for allozyme analysis from continental Australia. Twenty-two of these 27 OTUs were distinguishable solely by their allozyme profiles. In stark contrast, each of the remaining five OTUs could only be discriminated from a putative sibling by morphological differences which previously have been regarded as sufficient to justify species level ranking (Cogger 2000). For every morphospecies not displaying a narrow geographic range, the most common morphotypic form (i.e. morphotypes 'carnA', 'megaA', 'plagA' and 'virgA') was shown to harbour a minimum of three and up to five diagnosable OTUs. Moreover, neither the OTUs representing any one of the four composite morphospecies involved (*C. carnabyi*, *C. megastictus*, *C. plagiocephalus* and *C. virgatus*), nor those representing any of the most common morphotypic forms within these morphospecies, were found to be monophyletic assemblages. Thus the genetic affinities of OTUs as assessed by allozyme analysis are regularly discordant with those based on preliminary morphological appraisals, a conclusion that remains fully supported after thorough morphological assessment (Horner 2007).

The companion paper of Horner (2007) examines the taxonomic affinities of all diagnosable OTUs using stepwise Discriminant Function Analysis of a comprehensive morphological dataset obtained from 899 voucher specimens. It also provides detailed discussion of most aspects of the systematics and biology of the *Cryptoblepharus* taxa collectively identified by the two studies, thus obviating the need for any preliminary discussion of many issues herein. Instead we will restrict our comments to those matters which largely relate to molecular systematics or are not fully explored by Horner (2007).

This study has produced unexpected outcomes, several of which can justifiably be labelled remarkable. Included among the latter are the sheer number of taxa (most of which have been diagnosed as full species, with two of these species acknowledged as likely composites (Horner 2007) and the presence of two distinct lineages within the *Cryptoblepharus* of continental Australia. Not only has the number of Australian taxa increased nearly four-fold as a result of this study (from seven to 25), but the levels of genetic diversity encountered (mean = 39 %FDs between lineage 1 and lineage 2 species) indicate that the Australian radiation is likely to be older than perhaps expected. Lineage 1 and lineage 2 species are almost fully diagnosable using one primary morphological feature (Horner 2007), although our phylogenetic analyses only confirm species monophyly for lineage 2, the genetically less heterogeneous of the two lineages.

The other striking outcome of the present study is the great disparity between the taxa identified solely by diagnostic allozyme differences versus those revealed by a combined allozyme plus morphological appraisal. Indeed, the two techniques only agree around 55% of the time (Horner 2007). This discordance manifests itself as one of two types, namely (1) 'type A' - species which are clearly diagnosable by their allozyme profiles but are morphologically too similar for unequivocal diagnosis, or (2) 'type B' - species which are diagnosable by a suite of morphological characters despite the absence of any fixed allozymic differences (see Horner 2007). While discordance between molecular and morphological datasets is common (Hillis 1987; Patterson *et al.* 1993; Avise 2004), one rarely sees such high levels in a single complex (Avise 2004). It is therefore intriguing to speculate as to the reasons underlying this discordance.

In comparison to molecular characters, morphological characters are generally regarded as more prone to stasis, convergence and plasticity, plus are less likely to evolve in a clock-like manner (Baverstock and Adams 1984; Losos 2001; Wiens *et al.* 2003; Bickford *et al.* 2007). Thus it is tempting to conclude that the molecular data more closely reflect the 'true' phylogeny for the group and that the major morphological features used to characterise Australian *Cryptoblepharus* have either remained unaltered during and after speciation events ('type A' discordance) or have been fashioned by rapid evolutionary convergence ('type B' discordance).

Clearly such a conclusion is premature however, for several reasons. Firstly, allozyme data are known to not be particularly informative for phylogenetic reconstruction where too many of the included species share a recent evolutionary past i.e. most lineage 2 species and several clades within lineage 1 (Richardson *et al.* 1986; Avise 2004). Secondly, given two instances of contemporary hybridisation have already been observed between species, it is possible that historic introgression between 'type B' species pairs, plus contrasting selective regimes on the genes affecting morphology versus those encoding molecular markers, have together resulted in similar allozyme profiles whilst maintaining existing morphological differences (Gaubert *et al.* 2005). Finally, it makes sense to defer such speculation until DNA sequence data become available for the group, providing the twin benefits of a robust phylogeny and an independent assessment of species boundaries.

While we are unable to form definitive conclusions regarding the nature of morphological evolution in the Australian *Cryptoblepharus*, the general picture encountered is at first glance remarkably reminiscent of the situation occurring in the iguanid lizard genus *Anolis*. This very speciose genus is found throughout the Caribbean and adjacent mainland landforms, where it is displays numerous instances of morphological convergence in phylogenetically unrelated ecomorphs, sudden morphological evolution following a switch in ecological niche and inferred phenotypic plasticity leading to rapid adaptive evolution (Losos 1994, 2001; Thorpe *et al.* 2004). *Cryptoblepharus* also shares a number of key attributes with *Anolis*, namely (1) a very extensive geographic distribution which includes numerous islands and many distinctive island morphotypes (Horner 2007), (2) a high level of species richness (assuming by extrapolation from the present study that considerable cryptic biodiversity is present throughout that part of its distribution yet to be subjected to detailed collecting or molecular assessment), (3) a range of distinct habitat types, which for *Cryptoblepharus* include arboreal, littoral, saxicoline and human commensal lifestyles (Horner 2007) and (4) a tendency for pronounced, population specific differences in pattern and colouration (Horner 2007; Nicholson *et al.* 2007), possibly indicating the involvement of sexual selection (Gray and McKinnon 2007). Whether these shared attributes are simply coincidental or reflect an underlying similarity in evolutionary trajectory remains to be determined.

With hindsight, the genetic data presented herein for the Australian members of *Cryptoblepharus* demonstrate why morphological appraisals *per se* were unable to determine species boundaries in the genus from first principles. Widespread, little studied and morphologically conservative groups commonly harbour cryptic species (Richardson *et al.* 1986; Donnellan *et al.* 1993) and their detection and diagnosis usually requires an independent molecular dataset (Knowlton 1993; Bickford *et al.* 2007). Once specimens have been independently allocated to individual taxa, Discriminant Function Analysis can then be applied to the entire morphological dataset to identify which characters are diagnostic for the genetic taxa known to be present. As is the case with *Cryptoblepharus*, objectively distinguishing within-taxon polymorphism from between-taxon divergence offers two major advantages, namely (1) it reveals which morphological characters are the most informative taxonomically for the group in question and (2) the selective use of these characters may in turn reveal the presence of taxa which are molecularly cryptic.

Allozyme analysis and morphological re-analysis are ideally suited as companion techniques, since the strengths of one largely complement the weaknesses of the other (Richardson *et al.* 1986; Hillis 1987). Unfortunately, a greater emphasis on alcohol-based tissue collections, plus an ever dwindling number of molecular laboratories which include allozyme analysis in their repertoire, together seem likely to ensure the demise of this technique within a generation. Yet the resolution of species boundaries using DNA sequence data remains problematic for recently diverged species, particularly where mtDNA is the primary marker (Nicholls 2001; Funk and Omland 2003; Moritz and Cicero 2004). In such groups, it may require a dozen or more nuclear DNA gene trees to resolve species boundaries (Machado and Hey 2003), an exercise akin to using a sledgehammer to crack a peanut. We contend that allozymes offer a far quicker, cheaper and equally effective alternative into the foreseeable future.

The data presented herein and the companion dataset of Horner (2007) together represent an ideal case study for demonstrating the analytical power available to any systematic revision when co-dominant genetic markers are used jointly with detailed morphological analyses. From an Australian perspective, previous examples have typically involved one or just a few widespread morphospecies being shown to be composites of multiple biological or evolutionary species, each morphologically diagnosable *post hoc* e.g. the dasyurid marsupial *Sminthopsis* "*murina*" (Richardson *et al.* 1986) and the little brown bat *Eptesicus* (now *Vespadelus*) "*pumilis*" (Adams *et al.* 1987; Kitchener *et al.* 1987). However, none of these other examples displayed the same combination of pronounced morphometric conservatism but diversity of pattern and colouration, a highly confused taxonomy, numerous and often widespread morphospecies and sporadic instances of hybridisation, as is evident within *Cryptoblepharus*.

In principle, PCoA (or the functionally similar multivariate technique Multidimensional Scaling) can be used on any matrix of metric distances (Pielou 1984), whether obtained from one data type as herein, or constructed from a mix of data types. Thus it would be feasible to incorporate into the one analysis distance data derived from allozymes, qualitative morphological characters, microsatellite genotypes, even DNA sequence-based assignment to allele or clade membership, provided each character can be translated into the equivalent of a co-dominant genetic marker. A simpler although perhaps less powerful alternative is to overlay the additional character states directly onto PCoAs based on the primary allozyme dataset (as was the case herein with morphotype). Other examples of this approach are available in the literature for mtDNA profile (Adams *et al.* 2003) and morphotype (Smith and Adams 2007). Regardless of which procedure is adopted, the successful resolution of species boundaries in *Cryptoblepharus* using an integrated stepwise approach should encourage more researchers to employ the same methodology when tackling cryptic biodiversity in other taxonomically complex groups.

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APPENDIX I

List of *Cryptoblepharus* voucher specimens that supplied liver tissues used in the allozyme analysis. Provided are: final diagnosable OTU; museum registration number; tissue sample number; and place of collection.

Final OTU	Reg. No.	Tissue No.	Locality
carnA1	NTMR22070	Y42	Denham, WA
carnA1	NTMR22071	Y43	Denham, WA
carnA1	NTMR22074	Y44	Carnavon, WA
carnA1	NTMR22075	Y45	Carnavon, WA
carnA1	NTMR22076	Y46	Carnarvon, WA
carnA1	NTMR22077	Y47	Carnavon, WA
carnA1	NTMR22078	Y48	Carnavon, WA
carnA1	WAMR113603	R113603	Dirk Hartog Island, WA
carnA1	WAMR115229	R115229	Eurardy Station, WA
carnA1	WAMR120633	R120633	107 km NE of Carnarvon, WA
carnA1	WAMR123920	R123920	Bulong, WA
carnA1	WAMR123935	R123935	Bulong, WA
carnA1	WAMR123936	R123936	Bulong, WA
carnA1	WAMR131780	R131780	12 km WNW of Wandida Hstd, WA
carnA1	WAMR131789	R131789	Hamelin Hstd, WA
carnA1	WAMR135134	R135134	Rosemont, WA
carnA1	WAMR137970	R137970	Yardie Creek, Cape Range, WA
carnA2	NTMR25994	EV5	Coulomb Point, nr Broome, WA
carnA2	NTMR25995	EV6	Coulomb Point, nr Broome, WA
carnA2	WAMR114224	R114224	Cape Leveque, WA
carnA2	WAMR114244	R114244	9 km NE of Broome, WA
carnA2	WAMR114246	R114246	Coulomb Point, nr Broome, WA
carnA3	NTMR22024	Y05	Coward Springs Siding, SA
carnA3	NTMR22025	Y06	Coward Springs Siding, SA
carnA3	SAMAR40234	NP2518	Horse Creek Waterhole, SA
carnA3	SAMAR40537	NP3262	Mt Dean, SA
carnA3	SAMAR43942	GL129	7.1 km N of Yelpawaralinna Water, SA
carnA3	SAMAR46193	LES111	9.5 km SE of Wares Peak, SA
carnA3	SAMAR46208	LES098	10.5 km SE of Wares Peak, SA
carnA4	NTMR22086	Y56	Fitzroy Crossing, 38 km east, WA
carnA4	NTMR22087	Y57	Fitzroy Crossing, 38 km east, WA
carnA4	SAMAR53888	R53888	16 km N of Windjana Gorge, WA
carnA4	SAMAR53889	R53889	17 km N of Windjana Gorge, WA
carnA4	SAMAR53908	R53908	Willare Bridge, 71 km SW of Derby, WA
carnA5	NTMR13773	I03	Lake Eames, Sir Edward Pellew Islands, NT
carnA5	NTMR13774	I04	Lake Eames, Sir Edward Pellew Islands, NT
carnA5	NTMR18846	BV7	Leichhardt Falls, Leichhardt River, Qld
carnA5	NTMR18847	BV8	Leichhardt Falls, Leichhardt River, Qld
carnA5	NTMR18850	BW2	Cumberland, Qld
carnA5	NTMR18851	BW3	Cumberland, Qld
carnA5	NTMR18855	BW7	Georgetown, Qld
carnA5	NTMR18857	BW9	Mount Surprise, Qld
carnA5	NTMR22038	Y17	Sandy Creek, SA
carnA5	NTMR22039	Y18	Sandy Creek, SA
carnA5	NTMR22937	BC1	near mouth, McArthur River, NT
carnA5	NTMR23438	CK5	Roma, Qld
carnA5	NTMR23439	CK6	Roma, Qld
carnA5	NTMR23444	CL2	Augathella, Qld
carnA5	NTMR23445	CL3	Augathella, Qld
carnA5	NTMR24810	DV5	Dubbo, NSW
carnA5	NTMR25701	DV7	Moira, NSW
carnA5	NTMR25765	EH3	12 Mile Creek, Normanton, Qld
carnA5	NTMR25769	EH7	Walkers Creek, Normanton, Qld
carnA5	NTMR25793	EK4	Chillagoe Rd, nr Normanton, Qld
carnA5	NTMR25803	EL5	Smithburne River, Qld

Final OTU	Reg. No.	Tissue No.	Locality
carnA5	NTMR25829	EO3	Flinders River, Normanton, Qld
carnA5	NTMR25843	EP8	Armstrong Creek, Normanton, Qld
carnA5	NTMR25855	ER2	Gregory Downs, 60 km N of, Qld
carnA5	NTMR25873	ET1	Hells Gate, Qld
carnA5	SAMAR34216	M51	Westmoreland Station, Qld
carnA5	SAMAR36612	L075	6 km E of Wemen, VIC
carnA5	SAMAR42877	C29	6 km E of Noonbah Stn, Qld
carnB	NTMR18665	BR3	Mosquito Flat, Bradshaw Station, NT
carnB	NTMR18666	BR4	Mosquito Flat, Bradshaw Station, NT
carnB	NTMR18667	BR5	Mosquito Flat, Bradshaw Station, NT
carnB	NTMR18668	BR6	Mosquito Flat, Bradshaw Station, NT
carnB	NTMR18669	BR7	Mosquito Flat, Bradshaw Station, NT
carnB	NTMR18670	BR8	Mosquito Flat, Bradshaw Station, NT
carnB	NTMR18671	BR9	Mosquito Flat, Bradshaw Station, NT
carnB	NTMR18672	BS1	Mosquito Flat, Bradshaw Station, NT
carnB	NTMR18674	BS3	Mosquito Flat, Bradshaw Station, NT
carnB	NTMR24787	DR3	Mosquito Flat, Bradshaw Station, NT
carnB	NTMR24788	DR4	Mosquito Flat, Bradshaw Station, NT
carnB	NTMR24792	DS8	Mosquito Flat, Bradshaw Station, NT
carnB	WAMR137943	R137943	Spirit Hills Hstd, WA
carnB	WAMR137945	R137945	Spirit Hills Hstd, WA
carnB	WAMR137946	R137946	Spirit Hills Hstd, WA
carnB	WAMR137947	R137947	Spirit Hills Hstd, WA
carnC	NTMR16357	M27	Nathan River Station, NT
carnC	NTMR16359	M29	Nathan River Station, NT
carnC	NTMR16365	M35	Nathan River Station, NT
carnC	NTMR22449	Z68	Wadamunga Lagoon, Roper River, NT
carnC	NTMR22640	Z57	Roper River, NT
carnC	NTMR22644	Z56	Roper River, NT
carnC	NTMR22645	Z58	Roper River, NT
carnC	NTMR22941	BC2	Sherwin Creek, junction with Roper River, NT
carnC	NTMR22942	BC3	Sherwin Creek, junction with Roper River, NT
carnC	NTMR22943	BC4	Sherwin Creek, NT
carnC	NTMR22944	BC5	Sherwin Creek, NT
carnC	NTMR22945	BC6	Sherwin Creek, NT
carnD	ASMSR15617	R151617	Olive Downs Hstd, NSW
carnD	ASMSR15619	R151619	Olive Downs Hstd, NSW
carnD	NTMR18244	BH1	Arltunga, NT
carnD	NTMR18245	BH2	Arltunga, NT
carnD	NTMR18248	BH5	Arltunga, NT
carnD	NTMR18250	BH7	Arltunga, NT
carnD	NTMR18264	BJ1	Trephina Gorge Nat.Pk, NT
carnD	NTMR22030	Y11	Copley, 11 km north, SA
carnD	NTMR22031	Y12	Copley, 11 km north, SA
carnD	NTMR22032	Y13	Leigh Creek, SA
carnD	NTMR22033	Y14	Leigh Creek, SA
carnD	NTMR22035	Y16	Breakfast Time Creek, 44 km S of Leigh Creek, SA
carnD	NTMR22948	BC8	Alice Springs, NT
carnD	NTMR22949	BC9	Alice Springs, NT
carnD	NTMR23447	CL4	Blackall, Qld
carnD	NTMR23448	CL5	Blackall, Qld
carnD	NTMR23454	CM2	Barcaldine, Qld
carnD	NTMR23455	CM3	Barcaldine, Qld
carnD	NTMR23458	CM6	Winton, Qld
carnD	NTMR23463	CN2	Winton, Qld
carnD	NTMR23464	CN3	Winton, Qld
carnD	NTMR23465	CN4	Mckinlay, Qld
carnD	NTMR23466	CN5	Mckinlay, Qld
carnD	NTMR23470	CN9	Mount Isa, Qld
carnD	NTMR23471	CO1	Mount Isa, Qld

Final OTU	Reg. No.	Tissue No.	Locality
carnD	NTMR23472	CO2	Camooweal, Qld
carnD	NTMR23473	CO3	Camooweal, Qld
carnD	NTMR23478	CO8	Barkly Homestead, Barkly Hwy, NT
carnD	WAMR103862	R103862	Comet Vale, WA
carnD	WAMR126585	R126585	Between Carbine Hstd & Rowles Lagoon, WA
eger	SAMAR32509	H526	Christmas I., Indian Ocean
eger	SAMAR32510	H527	Christmas I., Indian Ocean
fuhn	QMJ58845	PC04	Cape Melville, Qld
fuhn	QMJ58846	PC05	Cape Melville, Qld
horn	NTMR19039	W26	Emu Island, NT
horn	NTMR19040	W27	Jensen Island, Jensen Bay, NT
horn	NTMR19041	W28	Rimija Island, NT
horn	NTMR19128	X11	Wessel Islands (Island L), NT
horn	NTMR19129	X12	Wessel Islands (Island L), NT
litor	NTMR18865	BX5	Cooktown, Qld
litor	NTMR18866	BX6	Cooktown, Qld
litor	NTMR18893	BZ7	Flying Fish Point, Innisfail, Qld
litor	NTMR18894	BZ8	Flying Fish Point, Innisfail, Qld
litor	NTMR18896	CA1	Flying Fish Point, Innisfail, Qld
litor	NTMR18897	CA2	Flying Fish Point, Innisfail, Qld
litor	NTMR18906	CB2	Mourilyan, Qld
litor	NTMR18929	CD7	Dingo Beach, Qld
litor	NTMR18945	CE9	Airlie Beach, Qld
litor	NTMR18946	CF1	Airlie Beach, Qld
megaA1	NTMR13614	D03	Victoria River, 7 km S of bridge, NT
megaA1	NTMR13615	D04	Victoria River, 7 km S of bridge, NT
megaA1	NTMR25985	EC5	Jasper Gorge, Gregory National Park, NT
megaA2	NTMR22353	Y87	Jarrnarm Escarpment, Keep River Nat. Pk, NT
megaA2	NTMR22356	Y90	Jarrnarm Escarpment, Keep River Nat. Pk, NT
megaA2	NTMR22357	Y91	Jarrnarm Escarpment, Keep River Nat. Pk, NT
megaA2	NTMR22363	Y97	Jarrnarm Escarpment, Keep River Nat. Pk, NT
megaA2	NTMR22365	Y98	Jarrnarm Campground, Keep River Nat. Pk, NT
megaA2	NTMR24789	DS2	Bradshaw Station, NT
megaA2	NTMR24793	DT8	Lobby Creek, Bradshaw Station, NT
megaA2	NTMR24794	DT9	Lobby Creek, Bradshaw Station, NT
megaA2	NTMR24795	DU1	Lobby Creek, Bradshaw Station, NT
megaA2	NTMR26008	EX1	nr Bellburn Camp, Purnululu Nat. Pk, WA
megaA3	NTMR26056	FE2	Mount Borradaile, NT
megaA3	NTMR26057	FE3	Mount Borradaile, NT
megaA3	NTMR26061	FE7	Mount Borradaile, NT
megaA3	NTMR26062	FE8	Mount Borradaile, NT
megaA4	AMR140118	1018	1 km S of Mcgowens Beach, Kalumburu, WA
megaA4	AMR140119	1019	2 km S of Mcgowens Beach, Kalumburu, WA
megaA4	NTMR22788	Z96	Kalumburu, WA
megaA4	NTMR22789	Z97	Kalumburu, WA
megaA5	NTMR25845	EQ1	Hells Gate, 10 km SE of Roadhouse, Qld
megaA5	SAMAR34251	M88	Lawn Hill, Qld
megaA5	SAMAR34252	M89	Lawn Hill, Qld
megaB	NTMR22079	Y49	Fortesque Falls, WA
megaB	NTMR22080	Y50	Fortesque Falls, WA
megaB	NTMR22081	Y51	Fortesque Falls, WA
megaB	NTMR22082	Y52	Fortesque Falls, WA
megaB	SAMAR29337	R29337	Python Pool, WA
megaB	SAMAR29338	R29338	Python Pool, WA
megaB	SAMAR29340	R29340	Dales Gorge, WA
megaB	WAMR100645	R100645	Woodstock, WA
megaB	WAMR104222	R104222	Woodstock, WA
megaB	WAMR104223	R104223	Woodstock, WA
megaB	WAMR108595	R108595	12 km SW of Pannawonica, WA
megaB	WAMR121998	R121998	Weeli Wolli Spring, WA

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megaB	WAMR125492	R125492	30 km E of Newman, WA
megaB	WAMR125493	R125493	31 km E of Newman, WA
megaB	WAMR132576	R132576	Burrup Peninsula, WA
megaB	WAMR90709	R90709	Cadjeput Rock Hole, WA
novo	AMR148061	R148061	Nord de Prony, New Caledonia
novo	AMR148062	R148062	Nord de Prony, New Caledonia
plagA1	NTMR13616	D05	Victoria River, 7 km S of bridge, NT
plagA1	NTMR13617	D06	Victoria River, 7 km S of bridge, NT
plagA1	NTMR18663	BR1	Mosquito Flat, Bradshaw Station, NT
plagA1	NTMR20841	G58	Keep River, NT
plagA1	NTMR22352	Y86	Cockatoo Lagoon, Keep River Nat. Pk, NT
plagA1	NTMR22358	Y92	Cockatoo Lagoon, Keep River Nat. Pk, NT
plagA1	NTMR22518	Z79	Durack River Station, Jacks Hole, WA
plagA1	NTMR22638	Z55	Roper River, NT
plagA1	NTMR23669	CP8	Brandy Bottle Creek, Victoria Highway, NT
plagA1	NTMR23670	CP9	Brandy Bottle Creek, Victoria Highway, NT
plagA1	SAMAR51102	L85	Pentecost River, El Questro Sation, WA
plagA1	WAMR108694	R108694	15 km SE of Dave Hill, Mabel Downs, WA
plagA1	WAMR108750	R108750	Bream Gorge, Osmond Valley, WA
plagA1	WAMR132727	R132727	5 km E of Point Springs Yard, WA
plagA1	WAMR137944	R137944	Spirit Hills Hstd, WA
plagA1	WAMR137948	R137948	Spirit Hills Hstd, WA
plagA2	NTMR22522	Z83	Mitchell Falls, WA
plagA2	NTMR22528	Z89	Mt Elizabeth Station, WA
plagA2	NTMR22529	Z90	Mt Elizabeth Station, WA
plagA3	NTMR16387	M68	Wave Hill Station, Flora Bore, NT
plagA3	NTMR22083	Y53	Broome, Cable Beach, WA
plagA3	NTMR22084	Y54	Broome, Cable Beach, WA
plagA4	NTMR21678	V14	Perth, WA
plagA4	NTMR22061	Y39	Donnybrook, WA
plagA4	NTMR22062	Y40	Donnybrook, WA
plagA4	NTMR22063	Y41	Donnybrook, WA
plagA4	WAMR103741	R103741	North Dandalup, WA
plagA4	WAMR113692	R113692	15 km SE of Port Gregory, WA
plagA4	WAMR114610	R114610	Spalding Park, Geraldton, WA
plagA4	WAMR114714	R114714	3 km N of Mandurah, WA
plagA4	WAMR117013	R117013	Nanjilgardy Pool, Turee Creek, WA
plagA4	WAMR117368	R117368	3 km SSE of Boorabbin, WA
plagA4	WAMR117369	R117369	28 km SSE of Woolgangie, WA
plagA4	WAMR117370	R117370	29 km SSE of Woolgangie, WA
plagA4	WAMR119234	R119234	Bungendore, Perth, WA
plagA4	WAMR122001	R122001	Weeli Wolli Spring, WA
plagA4	WAMR123513	R123513	50 km N of Kalbarri, WA
plagA4	WAMR126094	R126094	Neerabup National Park, WA
plagA4	WAMR126097	R126097	Neerabup National Park, WA
plagA4	WAMR127636	R127636	Neerabup, WA
plagA4	WAMR132571	R132571	Burrup Peninsula, WA
plagA4	WAMR132631	R132631	Burrup Peninsula, WA
plagA5	NTMR16127	K08	Cadell River Crossing, Arnhem Land, NT
plagA5	NTMR16128	K09	Cadell River Crossing, Arnhem Land, NT
plagA5	NTMR16353	M23	Nathan River Station, NT
plagA5	NTMR16459	N67	Bing Bong Station, NT
plagA5	NTMR18653	BP7	Bradshaw Station, NT
plagA5	NTMR18654	BP8	Bradshaw Station, NT
plagA5	NTMR18662	BQ9	Lobby Creek, Bradshaw Station, NT
plagA5	NTMR18798	BE7	Alice Springs (Town), NT
plagA5	NTMR18802	BE6	Alice Springs (Town), NT
plagA5	NTMR18838	BU8	Hi-Way Inn Roadhouse, Daly Waters, NT
plagA5	NTMR18840	BV1	Woologorang Station, NT
plagA5	NTMR18841	BV2	Woologorang Station, NT

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plagA5	NTMR18843	BV4	Leichhardt Falls, Leichhardt River, Qld
plagA5	NTMR18844	BV5	Leichhardt Falls, Leichhardt River, Qld
plagA5	NTMR18845	BV6	Leichhardt Falls, Leichhardt River, Qld
plagA5	NTMR18848	BV9	Burke & Wills Roadhouse, Matilda Hwy, Qld
plagA5	NTMR18849	BW1	Burke & Wills Roadhouse, Matilda Hwy, Qld
plagA5	NTMR18856	BW8	Mount Surprise, Qld
plagA5	NTMR18908	CB4	Ayr, Qld
plagA5	NTMR18930	CD8	Dingo Beach, Qld
plagA5	NTMR18939	CE8	5.4 km W of Dingo Beach, Qld
plagA5	NTMR18975	CG8	Clairview, Qld
plagA5	NTMR19056	W47	Guluwuru Island, NT
plagA5	NTMR19094	W75	Jirgari Island, NT
plagA5	NTMR19095	W76	Jirgari Island, NT
plagA5	NTMR19125	X10	Raragala Island, NT
plagA5	NTMR21175	S20	Jabiluka Project Area, NT
plagA5	NTMR21333	U67	Musselbrook Reserve, Qld
plagA5	NTMR21334	U89	Musselbrook Reserve, Qld
plagA5	NTMR22017	Y02	Bularriny, Napier Peninsula, NT
plagA5	NTMR22092	Y61	Kununurra, WA
plagA5	NTMR22093	Y62	Kununurra, WA
plagA5	NTMR22094	Y63	Lake Argyle, WA
plagA5	NTMR22095	Y64	Lake Argyle, WA
plagA5	NTMR22096	Y65	Timber Creek, NT
plagA5	NTMR22097	Y66	Timber Creek, NT
plagA5	NTMR22514	Z75	Wyndham, WA
plagA5	NTMR22515	Z76	Wyndham, WA
plagA5	NTMR22519	Z80	Ellenbrae Station, WA
plagA5	NTMR22520	Z81	Drysdale River Station, WA
plagA5	NTMR22521	Z82	Drysdale River Station, WA
plagA5	NTMR22525	Z86	Mt Elizabeth Station, WA
plagA5	NTMR22526	Z87	Mt Elizabeth Station, WA
plagA5	NTMR22633	Z41	Long Billabong, Roper River, NT
plagA5	NTMR22637	Z50	Wadamunga Lagoon, Roper River, NT
plagA5	NTMR22639	Z49	Wadamunga Lagoon, Roper River, NT
plagA5	NTMR22727	AA4	Nhulunbuy, NT
plagA5	NTMR22728	AA5	Nhulunbuy, NT
plagA5	NTMR22732	AA9	English Company Isles, Pobasso Is, NT
plagA5	NTMR22746	AC5	English Company Isles, Pobasso Is, NT
plagA5	NTMR22759	AD9	English Company Isles, Astell Is, NT
plagA5	NTMR22777	AF9	English Company Isles, Astell Is, NT
plagA5	NTMR22906	AY6	Spirit Hills, NT
plagA5	NTMR23479	CO9	Elliot, NT
plagA5	NTMR23480	CP1	Elliot, NT
plagA5	NTMR23483	CP4	Longreach Waterhole, Elliot, NT
plagA5	NTMR23666	CP5	Limestone Gorge, Gregory National Park, NT
plagA5	NTMR23667	CP6	Limestone Gorge, Gregory National Park, NT
plagA5	NTMR23668	CP7	Timber Creek, NT
plagA5	NTMR23770	CT1	Wickham River, Gregory National Park, NT
plagA5	NTMR23797	CV5	Wickham River, Gregory National Park, NT
plagA5	NTMR23919	DB7	Djapididjapin Creek, nr Ramingining, NT
plagA5	NTMR23926	DC5	Djapididjapin Creek, nr Ramingining, NT
plagA5	NTMR24031	CZ2	Mt Lambell, Nitmiluk National Park, NT
plagA5	NTMR24032	CZ3	Mt Lambell, Nitmiluk National Park, NT
plagA5	WAMR108703	R108703	Banana Sprong, 30 km SE of Gordon Downs, WA
plagA5	WAMR126000	R126000	12 km SW of Carlton Hill Hstd, WA
plagA5	WAMR126009	R126009	30 km E of Wyndham, WA
plagA5	WAMR126019	R126019	ca 7 km SW of Point Spring Yard, WA
plagA5	WAMR126048	R126048	ca 5 km S of Carlton Hill Hstd, WA
plagA5	WAMR132760	R132760	Carlton Hill Station, WA
plagA5	WAMR132769	R132769	Ivanhoe Station, WA

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plagA5	WAMR132777	R132777	Carlton Hill Station, WA
plagA5x plagB	NTMR18837	BU7	Hi-Way Inn Roadhouse, Daly Waters, NT
plagB	NTMR13592	H25	Murgenella, NT
plagB	NTMR13593	H26	Murgenella, NT
plagB	NTMR13729	H78	Swim Creek, Point Stuart Station, NT
plagB	NTMR13770	H99	Ja Ja, NT
plagB	NTMR16117	K15	Goomadeer River Crossing, Arnhem Land, NT
plagB	NTMR16118	K16	Goomadeer River Crossing, Arnhem Land, NT
plagB	NTMR18762	BT7	Darwin, Bullocky Point, NT
plagB	NTMR18763	BT8	Darwin, Bullocky Point, NT
plagB	NTMR20888	R42	Murgenella Creek, NT
plagB	NTMR21028	P24	Black Point, NT
plagB	NTMR21047	P55	Black Point, NT
plagB	NTMR21174	S19	Jabiluka Project Area, NT
plagB	NTMR21508	V02	Darwin, Bullocky Point, NT
plagB	NTMR21509	V03	Darwin, Bullocky Point, NT
plagB	NTMR21740	V56	Litchfield Nat Pk, Tjaynera Falls, NT
plagB	NTMR21744	V60	Litchfield Nat Pk, Tjaynera Falls, NT
plagB	NTMR22098	Y67	Adelaide River Town, NT
plagB	NTMR22099	Y68	Adelaide River Town, NT
plagB	NTMR22105	Y71	Howard Springs, NT
plagB	NTMR22451	Z74	Point Guy, Howard Island, NT
plagB	NTMR22854	AH2	Taracumbie Falls, Melville Island, NT
plagB	NTMR22867	AJ4	Taracumbie Falls, Melville Island, NT
plagB	NTMR22881	AL4	Goose Creek, Melville Island, NT
plagB	NTMR22884	AM3	Goose Creek, Melville Island, NT
plagB	NTMR22886	AM5	Goose Creek, Melville Island, NT
plagB	NTMR22887	AM6	Goose Creek, Melville Island, NT
plagB	NTMR22888	AM7	Goose Creek, Melville Island, NT
plagB	NTMR22891	AN1	Goose Creek, Melville Island, NT
plagB	NTMR22892	AN2	Goose Creek, Melville Island, NT
plagB	NTMR22893	AN3	Goose Creek, Melville Island, NT
plagB	NTMR22900	AO4	Goose Creek, Melville Island, NT
plagB	NTMR23025	AX5	Maxwell Creek Airstrip, Melville Island, NT
plagB	NTMR23026	AX6	Maxwell Creek Airstrip, Melville Island, NT
plagB	NTMR23734	Y73	Stuart Park, Darwin, NT
plagB	NTMR23927	DC6	"The Crossing", Arafura Swamp, NT
plagB	NTMR23928	DC7	"The Crossing", Arafura Swamp, NT
virgA1	NTMR18927	CD5	Airlie Beach, Qld
virgA1	NTMR18928	CD6	Airlie Beach, Qld
virgA1	NTMR18951	CF6	Far Beach, Mackay, Qld
virgA1	NTMR18954	CF9	Far Beach, Mackay, Qld
virgA1	NTMR18969	CG2	Clairview, Qld
virgA1	NTMR18973	CG6	Clairview, Qld
virgA1	NTMR18980	CH3	Tannum Sands, Qld
virgA1	NTMR18981	CH4	Tannum Sands, Qld
virgA1	NTMR18985	CH8	Gin Gin, Qld
virgA1	NTMR18987	CI1	Gin Gin, Qld
virgA1	NTMR18990	CI4	Gympie, Qld
virgA1	NTMR18991	CI5	Gympie, Qld
virgA1	NTMR18993	CI7	Tewantin, Qld
virgA1	NTMR18994	CI8	Tewantin, Qld
virgA1	NTMR18997	CJ2	Chappel Hill, Brisbane, Qld
virgA1	NTMR18998	CJ3	Chappel Hill, Brisbane, Qld
virgA1	NTMR18999	CJ4	Chappel Hill, Brisbane, Qld
virgA1	NTMR23433	CK1	Dalby, Qld
virgA1	NTMR23435	CK3	Dalby, Qld
virgA1	NTMR23436	CK4	Miles, Qld
virgA1	NTMR23690	CQ1	Earlwood, Sydney, NSW
virgA1	NTMR23691	CQ2	Earlwood, Sydney, NSW

Final OTU	Reg. No.	Tissue No.	Locality
virgA1	NTMR23746	CQ4	Earlwood, Sydney, NSW
virgA1	NTMR23747	CQ5	Earlwood, Sydney, NSW
virgA1	NTMR23751	CX4	Yalwal, NSW
virgA1	NTMR23753	CX6	Yalwal, NSW
virgA1x3	NTMR18931	CD9	Dingo Beach, Qld
virgA1x3	NTMR18932	CE1	Dingo Beach, Qld
virgA1x3	NTMR18933	CE2	Dingo Beach, Qld
virgA1x3	NTMR18949	CF4	Airlie Beach, Qld
virgA1x3	QMJ48420	K178	Townsville, Qld
virgA1x3	QMJ48421	K179	Townsville, Qld
virgA1x3	QMJ48423	K181	Townsville, Qld
virgA2	NTMR18868	BX8	Cooktown, Qld
virgA2	NTMR18869	BX9	Cooktown, Qld
virgA2	NTMR18872	BY3	Cooktown, Qld
virgA2	NTMR18879	BZ1	Lions Den Hotel, Bloomfield Track, Qld
virgA2	NTMR18880	BZ2	Lions Den Hotel, Bloomfield Track, Qld
virgA2	NTMR18899	CA4	Flying Fish Point, Innisfail, Qld
virgA2	NTMR18900	CA5	Flying Fish Point, Innisfail, Qld
virgA2	SAMAR21131	R21131	Cairns, Qld
virgA3	NTMR18858	BX1	40 km E of Mt Surprise, Qld
virgA3	NTMR18859	BX2	10 km W of Ravenshoe, Qld
virgA3	NTMR18863	BX3	Mareeba, Qld
virgA3	NTMR18864	BX4	Mareeba, Qld
virgA3	NTMR18912	CB8	Ayr, Qld
virgA3	NTMR18920	CC7	Lynch'S Beach, nr Ayr, Qld
virgA3	NTMR18921	CC8	Mt Gordon Rest Area, Bowen, Qld
virgA3	NTMR18922	CC9	Mt Gordon Rest Area, Bowen, Qld
virgA3	NTMR18923	CD1	Mt Gordon Rest Area, Bowen, Qld
virgA3	NTMR18937	CE6	5.4 km W of Dingo Beach, Qld
virgA3	NTMR18938	CE7	5.4 km W of Dingo Beach, Qld
virgB	NTMR22040	Y19	Smokey Bay, 5 km SE, SA
virgB	NTMR22041	Y20	Smokey Bay, 5 km SE, SA
virgB	NTMR22042	Y21	Eyre Hwy, 40 km E of Cocklebiddy, WA
virgB	NTMR22043	Y22	Eyre Hwy, 40 km E of Cocklebiddy, WA
virgB	NTMR22046	Y25	Deralinya Ruins, 89 km S of Balladonia, WA
virgB	NTMR22047	Y26	Deralinya Ruins, 89 km S of Balladonia, WA
virgB	NTMR22050	Y29	Dalyup River, South Coast Hwy bridge, WA
virgB	NTMR22051	Y30	Dalyup River, South Coast Hwy bridge, WA
virgB	NTMR22058	Y37	Dalyup River, South Coast Hwy bridge, WA
virgB	SAMAR31454	R31454	Wardang Island, SA
virgB	SAMAR36544	R36544	7 km N of Courtabie, SA
virgB	unreg.	PL51	Port Lincoln, SA
virgB	WAMR77930	R77930	41 km SW of Eucla Motel, Qld

Systematics of the snake-eyed skinks, *Cryptoblepharus* Wiegmann (Reptilia: Squamata: Scincidae) – an Australian-based review

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ABSTRACT

Morphologically conservative, *Cryptoblepharus* was once treated as a single polytypic species comprising many geographical subspecies and was considered the world's most broadly distributed lizard. Concentrating on taxa from the Australian region, the study investigates morphological characteristics of the two lineages and operational taxonomic units genetically identified by Horner and Adams (2007). Morphological variation of the genetically identified populations was investigated by multivariate analyses of 21 meristic and 12 mensural variables, and resulted in the identification of 25 Australian taxa. Using comparable analyses, species extralimital to Australia were also investigated, resulting in the recognition of 13 taxa from the southwest Indian Ocean region and 24 from the Indo-Pacific region. Overall, *Cryptoblepharus* was determined to comprise 62 taxa, consisting of 48 monotypic and six polytypic species. Existing types were able to be assigned to 43 taxa and 19 are described as new. Accounts of each taxon are supplied, although those of taxa extralimital to Australia are based on small sample sizes and are less detailed. Dichotomous keys to the identification of taxa from each geographic region are provided. An hypothesis for the biogeography of the genus suggests that it originated in South-east Asia and achieved its present distribution by a combination of rafting and human mediated transport.

Keywords: Reptilia, Scincidae, *Cryptoblepharus*, new species, Australia, Indo-Pacific, South-west Indian Ocean, taxonomy, morphology.

CONTENTS

INTRODUCTION

In a companion paper Horner and Adams (2007) investigated the genetic status of Australian populations of the scincid genus *Cryptoblepharus*, ultimately recognising that species diversity in that region was greatly understated. This paper follows and complements Horner and Adams's (2007) work, investigating the morphological characteristics of genetically identified and other presumptive taxa from Australia and other regions, assessing their taxonomic status and describing or re-describing all known species.

Cryptoblepharus is the most geographically widespread taxon in the family Scincidae, the most species-rich, morphologically diverse and geographically widespread lizard group. Achieving greatest diversity in the Australian/New Guinea and South-east Asian regions (Greer 1970), Scincidae is found in most tropical and temperate regions of the world and comprises about 1200 species in 127 genera (Uetz *et al.* 2000).

Exhibiting a marked degree of morphological conservatism, *Cryptoblepharus* are small (<55 mm snout-vent length), heliotropic, arboreal or saxicoline skinks that range through three broad, geographic regions, the Ethiopian-Malagasy (south-west Indian Ocean), Indo-Pacific and Australian. Historically *Cryptoblepharus* has been treated as monotypic, with the various forms considered to be geographical races of a single species (Mertens 1931), a concept now considered oversimplified (Auffenberg 1980) and many subspecies have been elevated to specific status (e.g. Brygoo 1986; Storr 1976; Zug 1991). Although acknowledged as problematic (Dunn 1927; Storr 1976; Haacke 1977; Crombie and Steadman 1986) there has been no recent attempt to systematically revise *Cryptoblepharus* taxonomy. That 76 years has elapsed since Mertens's monographic work on the genus is perhaps related to a universal perception that the group is taxonomically complicated, as alluded to by Haacke (1977) who, in an article titled 'Snake-eyed Skink', stated: "It floated its way across the world – and any scientist with sense leaves it well alone" and "… are a splitter's dream and a conventional taxonomist's nightmare".

To date, 56 *Cryptoblepharus* taxa have been formally described, 17 of which have since been placed in synonymy leaving 39 recognised taxa, 14 in the south-west Indian Ocean (Ethiopian-Malagasy) region, 19 in the Indo-Pacific region and six in the Australian region. Most are allopatric, insular forms, though many Australian taxa are widespread through the continental landmass (Cogger 2000). *Cryptoblepharus* is noteworthy among Australian skinks in having a distribution that extends beyond southern New Guinea (Hutchinson 1993).

Cryptoblepharus is often associated with littoral zones, such as rocky headlands and beaches and is a common human commensal. Despite this identification of species is often confusing, largely due to possible cryptic taxa (Horner and Adams 2007) and because most original descriptions are based on colour pattern and geographic distribution (29 are allopatric, insular species), with the few traditional scalation characteristics mentioned being attributable to virtually any member of the genus. Literature relevant to *Cryptoblepharus* is limited, and that available is mostly restricted to aspects of taxonomy and biogeography, with knowledge of reproduction, ecology and evolutionary history markedly lacking.

Seven species of *Cryptoblepharus* are currently recognised as Australian taxa (Cogger 2000; Cogger *et al.* 1983a; Stanger *et al.* 1998; Ehmann 1992; Greer 1989; Wilson and Knowles 1988; Wilson and Swan 2003): *C. carnabyi* Storr, 1976; *C. egeriae* (Boulenger, 1889); *C. fuhni* Covacevich and Ingram, 1978; *C. litoralis* (Mertens, 1958); *C. megastictus* Storr, 1976; *C. plagiocephalus* (Cocteau, 1836) and *C. virgatus* (Garman, 1901). All but one are mainland species, with *C. egeriae* restricted to the Australian Territory of Christmas Island in the Indian Ocean. As currently recognised, *C. fuhni*, *C. litoralis* and *C. megastictus* have limited distributions in northern Australia, *C. virgatus* occupies much of eastern and far southern Australia, and *C. carnabyi* and *C. plagiocephalus* have broad continental distributions.

Of *Cryptoblepharus* extralimital to Australia, Mertens (1931) recognised 14 taxa from the south-west Indian Ocean region: *C. boutonii africanus* (Sternfeld, 1918); *C. b. ahli* Mertens, 1928a; *C. b. aldabrae* (Sternfeld, 1918); *C. b. ater* (Boettger, 1913); *C. b. bitaeniatus* (Boettger, 1913); *C. b. boutoni* (Desjardin, 1831); *C. b. caudatus* (Sternfeld, 1918); *C. b. cognatus* (Boettger, 1881); *C. b. degrijsi* Mertens, 1928a; *C. b. gloriosus* (Stejneger, 1893); *C. b. mayottensis* Mertens, 1928a; *C. b. mohelicus* Mertens, 1928a; *C. b. quinquetaeniatus* (Günther, 1874), and *C. b. voeltzkowi* (Sternfeld, 1918). Geographical distribution of these is centred on the Mozambique Channel, with two taxa occurring on the mid-east coast of the African mainland, four on Madagascar and southern islands of the Mozambique Channel, six on northern islands of the Mozambique Channel (including Comoros and Aldabra islands) and one on Mauritius. Since Mertens's (1931) revision, the only taxonomic study on *Cryptoblepharus* from the south-west Indian Ocean region was by Brygoo (1986), who recognised *C. bitaeniatus* as a distinct species, *C. ahli* as a junior synonym of *C. africanus*, *C. quinquetaeniatus* a synonym of *C. degrijsi*, the subspecies *africanus*, *aldabrae*, *ater*, *boutoni*, *caudatus*, *cognatus*, *degrijsi*, *gloriosus*, *voeltzkowi* as provisionally distinct species and *C. mayottensis* and *C. mohelicus* as subspecies of *C. gloriosus*.

In the Indo-Pacific region, Mertens (1931) recognised 19 taxa: *C. boutonii aruensis* Mertens, 1928a; *C. b. baliensis* Barbour, 1911; *C. b. burdeni* Dunn, 1927; *C. b. cursor* Barbour, 1911; *C. b. egeriae* (Boulenger, 1889); *C. b. eximius* Girard, 1857; *C. b. intermedius* (de Jong, 1926); *C. b. keiensis* (Roux, 1910); *C. b. leschenault* (Cocteau, 1832); *C. b. nigropunctatus* (Hallowell, 1860); *C. b. novaeguineae* Mertens, 1928a; *C. b. novocaledonicus* Mertens, 1928a; *C. b. novohebridicus* Mertens, 1928a; *C. b. pallidus* Mertens, 1928a; *C. b. poecilopleurus* (Wiegmann, 1834); *C. b. renschi* Mertens, 1928b; *C. b. rutilus* (Peters, 1879); *C. b. schlegelianus* Mertens, 1928a; *C. b. sumbawanus* Mertens, 1928a. Whilst not specifically challenging Mertens's concept of a single polytypic species, Brongersma (1942) noted apparent sympatry between some subspecies in Indonesia (*C. b. leschenault* and *C. b. schlegelianus* on Samao Island) stating that forms identified as subspecies should not occur in the same locality.

Geographically, Indo-Pacific taxa are found from Christmas Island in the eastern Indian Ocean, through the Lesser Sunda Islands to Timor (Mertens 1931), through the Maluku island chain (including Kai and Aru islands) to and including New Guinea. North of New Guinea *Cryptoblepharus* occurs on the Palau, Caroline, Mariana and Bonin Islands, and eastward on the Bismarck Archipelago, Solomon, Vanuatu, New Caledonia, Fiji, Tonga, Samoa, Phoenix, Cook, Society, Tahiti, Austral, Tuamotu, Marquesa, Hawaiian, Pitcairn and Easter Islands (Adler *et al.* 1995; Mertens 1931). Additionally, there are scattered records of *C. poecilopleurus* from the west coast of South America, including the type locality of 'Perú; gefunden auf den Inseln bei Pisacoma' (Wiegmann 1834).

Taxonomic history. Taxa assignable to *Cryptoblepharus* were first described in 1831 and 1832, however the generic name was not published until 1834 (Bauer and Adler 2001). Coined by A.F.A. Wiegmann, *Cryptoblepharus* did not receive wide recognition as a valid generic name because Wiegmann (1834) designated the name to distinguish *C. boutonii*, *C. leschenault* and his new species *C. poecilopleurus* as a subgeneric group within the then widespread, inclusive genus *Ablepharus* Lichtenstein, 1823. In addition to Wiegmann's (1834) subgeneric designation, Boulenger (1887) using the common character of a transparent disc covering the eye, lumped what are now multiple genera into *Ablepharus*. While Boulenger's action created stability in early scincid taxonomy, his grouping of what were often very different taxa did not erase confusion on the placement of *Cryptoblepharus*. For example, Mertens (1928a) described 12 taxa as *Cryptoblepharus*, but three years later (Mertens 1931) treated the same taxa as *Ablepharus*. Apart from a few generic placement anomalies in 1836 (*Scincus plagiocephalus* Cocteau), 1838 (*Tiliqua buchananii* Gray) and 1839 (when Gray proposed the *nomen nudum* manuscript name *Petia*) most authors have assigned taxa to the genus *Ablepharus*.

Break-up of the '*Ablepharus*' polythetic assemblage began with Smith (1935, 1937) who demonstrated that eyelid fusion was incomplete in some '*Ablepharus*'. In 1952, Mittleman divided Boulenger's concept of *Ablepharus* into three separate genera, *Ablepharus*, *Cryptoblepharus* and *Panaspis*. Mittleman's recognition of *Cryptoblepharus* was not widely accepted (e.g. Mertens 1958; Storr 1961) until Fuhn (1969a), using features of the skull and "conspicuous common characters proving their monophyletic descendence", clearly demonstrated the distinctiveness of *Cryptoblepharus*.

In total, 27 authors have described taxa in the genus, with the two most prolific being Sternfeld, who in 1918 described seven forms, and Mertens, who described 12 forms in 1928 and one in 1958. Mertens (1931) considered the genus monotypic, with the single species (*C. boutonii*) comprising 36 subspecies, 31 of which were insular forms. Since Mertens's work, many subspecies have been elevated to specific status (e.g. Brygoo 1986; Storr 1976), and ten new taxa have been described, all from Australia.

When arrayed in chronological order, several 'periods' of *Cryptoblepharus* taxonomic activity can be distinguished. Between 1831 and 1913, 23 species were described more or less regularly, with an average of about four years between publications. These 'early' descriptions are characterised by brief text, small sample sizes (nine based on a single specimen; only seven on greater than four specimens) and were written by sixteen different authors. In 1918, Sternfeld compared 19 *Cryptoblepharus* taxa, seven of which he described as new. Given in the form of keys to regional taxa, Sternfeld's (1918) descriptions are very brief and mostly based on small sample sizes (see following chronological list). Following a hiatus of eight years, 14 forms were described between 1926 and 1928. The majority of these were the work of Mertens, who in two publications described 12 new taxa. Mertens, the doyen of *Cryptoblepharus* research, published extensively on the genus (Mertens 1928a, 1928b, 1930, 1931, 1933, 1934, 1958, 1964).

Subsequent to Mertens's (1931) monographic work, no new *Cryptoblepharus* taxa were described for 30 years. Then, between 1958 and 1985 ten new Australian taxa were described. Appropriately, Mertens commenced the 'Australian' period with his 1958 description of *A. b. litoralis*, it ended in 1985 with a controversial (see Gans 1985; Grigg and Shine 1985; King and Miller 1985; Tyler 1985; Cogger 1986; Shea 1987; King 1988; Ingram and Covacevich 1988; Underwood and Stimson 1990; Hutchinson and Donnellan 1992) publication by Wells and Wellington (1985) in which four new taxa were described. No *Cryptoblepharus* taxon has been described since 1985.

Listed below, in chronological order, are *Cryptoblepharus* taxa described to date. Included are original name, author, reference, type locality, number of type specimens (in parenthesis), repository and registration number of primary type material.

1831. *Scincus boutonii* Desjardin, in: Ann. Sc. Nat., Vol. 22, p. 298. "Quartier de Flacq, Île Maurice" (= Mauritius). (two specimens). Type presumed lost.

1832. *Ablepharus leschenault* Cocteau, in: Guerin Mag. Zool., tab. 1. "Java". (one specimen). Syntype MNHP 3091

1834. *Ablepharus poecilopleurus* Wiegmann, in: Meyen's Reise um die Erde, p. 452, pl. LVII. fig. 1. "Inseln bei Pisacoma, Perú". (three specimens). Lectotype ZMB 1349.

1836. *Scincus plagiocephalus* Cocteau, in: Etudes Scinc. *Cryptoblepharis* de Péron, p. 7, tab. "Van Diemen's Land". (two specimens). Lectotype MNHP 7150.

1838. *Tiliqua buchananii* Gray, in: Ann. Mag. Nat. Hist., Vol. 2, p. 291. "New Holland". (two specimens). Syntype BMNH 1946.8.19.73.

1839. *Ablepharus peronii* Duméril and Bibron, in: Erp. Gén., Vol. 5, p. 813 (justification for *Cryptoblepharis* de Péron Cocteau). Syntypes MNHP 3088, 7150.

1857. *Cryptoblepharus eximius* Girard, in: Proc. Acad. Nat. Sc. Philadelphia, p. 195. "Feejee islands". (one specimen). Type missing.

1860. *Ablepharus nigropunctatus* Hallowell, in: Proc. Acad. Nat. Sc. Philadelphia, p. 489. "Bonin Islands". (one specimen). Type presumed lost.

1874. *Ablepharus quinquetaeniatus* Günther, in: Proc. Zool. Soc. London, p. 296. "Westküste von Africa". (two specimens). Co-types BMNH 1946.18.51–52.

1879. *Ablepharus rutilus* Peters, in: SB. Ges. Nat. Fr. Berlin, p. 37. "Pelew-Inseln". (one specimen). Holotype ZMB 7926.

1881. *Ablepharus boutonii* var. *cognatus* Boettger, in: Zool. Anz. Vol. 4 p. 359. "Nossi-Bé". (one specimen). Holotype SMF 15548.

1887. *Ablepharus boutonii* var. *metallicus* Boulenger, in: Cat. Liz., Vol. 3, p. 347. "North Australian Expedition". (four specimens). Lectotype BMNH 57.10.24.38.

1889. *Ablepharus egeriae* Boulenger, in: Proc. Zool. Soc. London, p. 535. "Christmas Island". (several specimens). Syntypes BMNH 1946.8.15.86–88.

1890. *Ablepharus boutonii* var. *furcata* Weber, in: Zool. Ergebn. Reise Ost-Indien, Vol. 1, p. 174. "Sikka and Endeh, Flores". (five specimens). Syntype ZMA 10831.

1893. *Ablepharus gloriosus* Stejneger, in: Proc. U.S. Nat. Mus., Vol. 16, p. 723. "Gloriosa Island". (four specimens). Holotype USNM 20463.

1901. *Ablepharus virgatus* Garman, in: Bull. Mus. Comp. Zool., Vol. 39, p. 10. "Cooktown, Australia". (one specimen). Holotype MCZ 6485.

1901. *Ablepharus heterurus* Garman, in: Bull. Mus. Comp. Zool., Vol. 39, p. 11. "Apaiang, Gilbert Islands". (synonym of *C. poecilopleurus* Wiegmann). (several specimens). Type presumed lost.

1908. *Cryptoblepharus poecilopleurus paschalis* Garman, in: Bull. Mus. Comp. Zool., Vol. 52, p. 13. "Easter Island". (nine specimens). Syntypes MCZ 6995–998, 7001–003.

1910. *Ablepharus boutoni* var. *keiensis* Roux, in: Abh. Senckenb. Nat. Ges., Vol. 33, p. 240, tb. 13, fig. 3. "Kei-Inseln". (23 specimens). Type presumed lost.

1911. *Cryptoblepharus boutonii baliensis* Barbour, in: Proc. Biol. Soc. Washington, Vol. 24, p. 18. "Buleleng, Bali Island". (one specimen). Holotype MCZ 7480.

1911. *Cryptoblepharus boutonii cursor* Barbour, in: Proc. Biol. Soc. Washington, Vol. 24, p. 18. "Ampenan, Lombok Island". (one specimen). Holotype MCZ 7479.

1913. *Ablepharus boutoni* var. *bitaeniata* Boettger, in: Voeltzkow, Reise Ostafrika. Rept. Amph., p. 329. "Insel Europa, im Kanal von Mozambique". (numerous specimens). Lectotype SMF 15601.

1913. *Ablepharus boutoni* var. *atra* Boettger, in: Voeltzkow, Reise Ostafrika. Rept. Amph., p. 338. "Küste von Groß-Comoro". (50 specimens). Lectotype SMF 15571.

1918. *Ablepharus boutoni africanus* Sternfeld, in: Abh. Senckenb. Nat. Ges., Vol. 36, p. 423. "Manda, Mandabucht, Malindi, Pemba". (numerous specimens). Lectotype SMF 15550.

1918. *Ablepharus boutoni voeltzkowi* Sternfeld, in: Abh. Senckenb. Nat. Ges., Vol. 36, p. 423. "Majunga, N.- W.- Madagaskar". (two specimens). Lectotype SMF 15584.

1918. *Ablepharus boutoni aldabrae* Sternfeld, in: Abh. Senckenb. Nat. Ges., Vol. 36, p. 423. "Aldabra". (six specimens). Lectotype SMF 15586.

1918. *Ablepharus boutoni caudatus* Sternfeld, in: Abh. Senckenb. Nat. Ges., Vol. 36, p. 423. "Juan de Nova". (eight specimens). Lectotype SMF 15592.

1918. *Ablepharus boutoni pulcher* Sternfeld, in: Abh. Senckenb. Nat. Ges., Vol. 36, p. 423. "Neuholland". (two specimens). Lectotype SMF 15680.

1918. *Ablepharus boutoni australis* Sternfeld, in: Abh. Senckenb. Nat. Ges., Vol. 36, p. 424. "West-Central-Australien". (two specimens). Lectotype SMF 15863.

1918. *Ablepharus boutoni punctatus* Sternfeld, in: Abh. Senckenb. Nat. Ges., Vol. 36, p. 424. "West-Australien". (two specimens). Lectotype SMF 15685.

1926. *Ablepharus boutoni* var. *intermedius* De Jong, in: Treubia, Vol. 7, p. 93. "Rana, Buru Island".(two specimens). Lectotype ZMA 10972.

1927. *Cryptoblepharus boutonii burdeni* Dunn, in: Am. Mus. Nov., Vol. 288, p. 11. "Padar, east coast". (13 specimens). Holotype AMNH 32006.

1928. *Cryptoblepharus boutonii degrijsi* Mertens, in: Zool. Anz., Vol. 78, p. 83. "Insel Anjouan, Comoren". (ten specimens). Holotype SMF 15547.

1928. *Cryptoblepharus boutonii mayottensis* Mertens, in: Zool. Anz., Vol. 78, p. 83. "Insel Mayotte, Comoren". (20 specimens). Holotype ZMB 19451.

1928. *Cryptoblepharus boutonii mohelicus* Mertens, in: Zool. Anz., Vol. 78, p. 84. "Miremani, Insel Moheli, Comoren". (five specimens). Holotype ZMB 33125.

1928. *Cryptoblepharus boutonii ahli* Mertens, in: Zool. Anz., Vol. 78, p. 85. "Insel Moçambique, Ostafrika". (six specimens). Holotype ZMB 33124.

1928. *Cryptoblepharus boutonii sumbawanus* Mertens, in: Zool. Anz., Vol. 78, p. 85. "Sumbawa-Besar, West-Sumbawa". (33 specimens). Holotype SMF 22096.

1928. *Cryptoblepharus boutonii schlegelianus* Mertens, in: Zool. Anz., Vol. 78, p. 86. "Timor". (three specimens). Holotype SMF 15604.

1928. *Cryptoblepharus boutonii aruensis* Mertens, in: Zool. Anz., Vol. 78, p. 87. "Papakoela, Kobroor, Aru-Inseln". (six specimens). Holotype SMF 15517.

1928. *Cryptoblepharus boutonii novae-guineae* Mertens, in: Zool. Anz., Vol. 78, p. 87. "Mamberano, Holländisch-Nord-Neuguinea". (six specimens). Holotype NHMB 8343.

1928. *Cryptoblepharus boutonii pallidus* Mertens, in: Zool. Anz., Vol. 78, p. 88. "Sepik-Gebiet, Kaiser-Wilhelms-Land, Neuguinea". (one specimen). Holotype ZMB 25706.

1928. *Cryptoblepharus boutonii novo-caledonicus* Mertens, in: Zool. Anz., Vol. 78, p. 88. "Hienghiène, Neukaledonien". (15 specimens). Holotype SMF 15520.

1928. *Cryptoblepharus boutonii novo-hebridicus* Mertens, in: Zool. Anz., Vol. 78, p. 89. "Insel Malo, Neue Hebriden". (three specimens). Holotype NHMB 6787.

1928. *Cryptoblepharus boutonii renschi* Mertens, in: Senckenbergiana., Vol. 10, p. 230. "Kambaniroe bei Waingapoe, Nordost-Sumba". (eight specimens). Holotype SMF 22095.

1958. *Ablepharus boutonii litoralis* Mertens, in: Senck. Biol., Vol. 39, p. 54. "Flying Fish Point, 6 mi. östl. Innisfail, Queensland". (11 specimens). Holotype SMF 53219.

1961. *Ablepharus boutonii clarus* Storr, in: West. Aust. Nat., Vol. 7, p. 177. "lower Dalyup River, 20 miles WNW of Esperance, Western Australia". (five specimens). Syntypes WAM 18228–31.

1976. *Cryptoblepharus carnabyi* Storr, in: Rec. West. Aust. Mus., Vol. 4, p. 60. "11 km WSW of Youanmi, Western Australia". (numerous specimens). Holotype WAM 21182.

1976. *Cryptoblepharus megastictus* Storr, in: Rec. West. Aust. Mus., Vol. 4, p. 61. "Mitchell Plateau, Western Australia, in 14°52'S 125°50'E". (ten specimens). Holotype WAM 43245.

1978. *Cryptoblepharus fuhni* Covacevich and Ingram, in: Mem. Qd. Mus., Vol. 18, p. 151. "Melville range, Cape Melville, Cape York, NE.Q.". (eight specimens). Holotype QM 20566.

1981. *Cryptoblepharus plagiocephalus ruber* Börner and Schüttler, in: Misc. Art. Saur., No. VIII, p. 4. "Kalindi-Grotte, Bachsten Creek, NW-Australien". (one specimen). Holotype SMF 32823.

1985. *Cryptoblepharus hawkswoodi* Wells and Wellington, in: Aust. J. Herp. Suppl. Ser., Vol. 1, p. 27. "Yathong Nature Reserve, 100km south of Cobar, New South Wales". (one specimen). Holotype AM 116952.

1985. *Cryptoblepharus horneri* Wells and Wellington, in: Aust. J. Herp. Suppl. Ser., Vol. 1, p. 27. "Cape Wessel Island, Northern Territory". (one specimen). Holotype NTM 7762.

1985. *Cryptoblepharus suburbia* Wells and Wellington, in: Aust. J. Herp. Suppl. Ser., Vol. 1, p. 27. "Sydney, New South Wales". (one specimen). Holotype AM 116951.

1985. *Cryptoblepharus swansoni* Wells and Wellington, in: Aust. J. Herp. Suppl. Ser., Vol. 1, p. 27. "Smith St, Darwin, Northern Territory". (46 specimens). Holotype NTM 2915.

Both Mertens (1931) and Brygoo (1986) expressed doubt about the taxonomic status of *C. quinquetaeniatus*, described by Günther (1874) from two specimens collected on the "west coast of Africa". Mertens (1931) suggested *C. quinquetaeniatus* was related to *C. degrijsi*, but divergent on grounds of having pale dorsal stripes brighter and broader than those of *C. degrijsi*. Mertens noted that the type locality (west coast of Africa) was doubtful, suggesting that *C. quinquetaeniatus* more probably came from an island off east Africa. Brygoo (1986) treated *C. quinquetaeniatus* as a synonym of *C. degrijsi*. As Mertens's recognition of *C. quinquetaeniatus* is entirely based on aspects of colour and pattern of two specimens of doubtful locality, this work follows Brygoo's (1986) synonymising of the two taxa. However, Brygoo's (1986) placement of *C. quinquetaeniatus* into the synonymy of *C. degrijsi* is not accepted. By priority of publication, *C. degrijsi* Mertens, 1928 is considered a junior synonym of the taxon *C. quinquetaeniatus* (Günther, 1874).

It is interesting to compare this revision with that of Mertens (1931), whose methodology and taxa definition differed from that employed in this study. Mertens treated *Cryptoblepharus* as a monotypic genus, composed of a single, morphologically variable species that incorporated 36 separate subspecies. In developing this concept of a polytypic species, Mertens considered orthogenetic development of certain characteristics of geographically neighbouring forms implied a relationship. For example, an inclination to melanism linked his *C. mayottensis, C. mohelicus* and *C. ater* forms, while a directional reduction in pale stripes linked his *C. virgatus* (north-east Australia, with prominent stripes), *C. plagiocephalus* (south and west Australia, with reduced stripes) and *C. metallicus* (central and north-west Australia, with little sign of stripes) forms. These observations led him to suggest the similar morphology of such 'parallel-races' had mislead many previous authors into believing that some forms of *Ablepharus boutonii* had extensive allopatric distributions.

Mertens (1931) defined *A. boutonii* as a morphologically variable "ring-species" in which geographically near forms are most alike. Although recognising that spatial separation indicated prominent forms could be independent species, he preferred to consider them "*Statu nascendi*" or emerging species. Mertens did not dispute that some of his *A. boutonii* subspecies deviated from each other at least as much as other sauria whose systematic position was considered species. Citing what he termed "discontinuous and convergent race formation" Mertens was uncertain about relationships between *Cryptoblepharus* forms, suggesting their vicarious distribution and conservative morphology rendered differentiation, and how it was driven, obscure.

Mertens's concept of the species level in the taxonomic hierarchy was indicated by his suggestion that any thorough, extended study using large sample sizes would always come to the insight that there are actually not any species in nature, only differences resulting from certain factors affecting development trends that, over a limited period of observation, appear as steady gaps that are named as species. Based on use of only a few traditional morphological characters (principally body pattern and colour) to distinguish taxa, Mertens's (1931) intrepretation of *Cryptoblepharus* as a wide-ranging polytypic taxon was justifiable.

Objectives and aims. The aim of this study was to revise the systematics of *Cryptoblepharus,* with the following key objectives being identified: (1) A statistical analysis of morphological variables to identify phenotypic differences within and between genetically identified populations; (2) A comparative analysis of molecular (Horner and Adams 2007) and morphological data to identify species boundaries and investigate intraspecific variability; (3) A biogeographic analysis to determine the origin and radiation patterns of the genus and its members; (4) Provision of detailed descriptions of each taxa, giving illustrations and information on ecology, distribution and behaviour; and (5) Provision of comparative tables listing morphological variables and dichotomous keys to the identification of species.

MATERIAL AND METHODS

Material examined. Data were recorded from specimens collected in the field and from preserved material held in museum collections. All available primary type specimens held in Australian, European and United States museum collections were examined. In total, 1213 *Cryptoblepharus* specimens were examined in detail, and a further 2478 specimens briefly examined for key morphological characters. In general, only adult specimens were examined and, in most cases, these were selected without reference to locality data, this information being noted after examination. Locality data for non-type specimens examined are given in Appendix 4.

Material held in the following Institutions was examined (acronyms in parentheses):

American Museum of Natural History, New York, U.S.A. (AMNH); Australian Museum, Sydney, Australia (AM); Australian National Wildlife Collection, Canberra, Australia (ANWC); Natural History Museum, London, England (BMNH); Museum and Art Gallery of the Northern Territory, Darwin, Australia (NTM); Muséum National d'Histoire Naturelle, Paris, France (MNHP); Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A. (MCZ); Museum of Victoria, Melbourne, Australia (MV); National Museum of Natural History, Washington, U.S.A. (USNM); Museum of Zoology, University of Michigan, Ann Arbor, U.S.A. (UMMZ); Naturhistorisches Museum, Basel, Switzerland (NHMB); Natur-Museum Senckenberg, Frankfurt-am-Main. Germany (SMF); Queensland Museum, Brisbane, Australia (QM); South Australian Museum, Adelaide, Australia (SAM); Western Australian Museum, Perth, Australia (WAM); Zoölogisch Musem, Universiteit van Amsterdam, Amsterdam, The Netherlands (ZMA); Zoologisches Museum, Universität Humboldt, Berlin, Germany (ZMB); University of Papua New Guinea, Port Moresby, Papua New Guinea (UPNG).

Specimens were collected under the auspices of permits issued by: Queensland Parks and Wildlife Service (NO/001995/97/SAA, NO/001995/99.SAA, W4/002672/01/SAA); Department of Environment and Natural Resources, South Australia (U23726-01, S24293-1); Department of Conservation and Land Management, Western Australia (SF001695, SF001789, NE002491), and Parks and Wildlife Commission, Northern Territory (4399, 5436, 6878, 8257, 10381). Handling and preparation of specimens adhered to methodology approved by permit 960901, issued by the Animal Experimentation Ethics Committee of Charles Darwin University.

A subset of 39 specimens, representative of most Australian operational taxonomic units (OTUs) (see Horner and Adams 2007), were selected for osteological examination. These specimens were cleared and double stained with alcian blue and alizarin red for cartilage and bone, using the maceration by enzyme technique (Hanken and Wassersug 1981; Song and Parenti 1995).

Morphological data were recorded from preserved specimens and in general, concentrated on four features of scincid morphology: scalation, body proportions (morphometrics), colour and body pattern. Other features were investigated (e.g. skeletal and hemipenis morphology) but, in most cases, their value in delimiting taxa was limited by small sample sizes or lack of variation.

Scalation characters were scored during examination under a dissecting microscope, with midbody and paravertebral scale counts standardised by pre-marking start and/or finish points with stainless steel micropins. Morphometric characters were measured, under an illuminated magnifying lens, with electronic digital callipers to the nearest 0.01mm. Sex and reproductive condition were assessed through an

'L' shaped incision, made ventrolaterally on the posterior half of body and transversely across the pelvis.

Morphological characters. Morphological character states previously identified by *Cryptoblepharus* taxonomic studies (Mertens 1931; Brygoo 1986; Storr 1976; Horner 1984, 1991) were selected and recorded, however many of those characters proved invariable or showed significant overlap. Therefore, additional characters showing non-random variation were also included in the examination process.

In total, 41 characters were identified as informative and were scored for most specimens examined. Unless noted otherwise, condition of bilaterally symmetrical characters was recorded from the right side. Definitions and character states are as follows.

Morphometric characters

1. Snout-vent length (SVL): distance from tip of snout to posterior margin of preanal plate. Measured along venter, with specimen straightened on long axis (Fig. 1A).
2. Body length (BL): distance from posterior margin of forelimb at axilla to anterior margin of hindlimb at groin. Measured laterally, with specimen straightened on long axis (Fig. 1A).
3. Tail length (TL): distance from posterior margin of preanal plate to tail tip. Measured subcaudally, with tail held straight. Tails were visually assessed for scalation change indicating cases of autotomy and only obviously undamaged, original tails measured.
4. Forelimb length (FL): distance from body wall at axilla to tip of claw on fourth finger. Measured laterally, with limb fully extended at right angle to body (Fig. 1A).
5. Hindlimb length (RL): distance from body wall at groin to tip of claw on fourth toe. Measured laterally, with limb fully extended at right angle to body (Fig. 1A).
6. Forebody length (SFL): distance from posterior margin of forelimb at axilla to tip of snout. Measured with specimen straightened on long axis (Fig. 1A).
7. Head length (HL): distance from tip of snout to anterior margin of ear opening. Measured laterally (Fig. 1B).
8. Head depth (HD): distance from gular scales to parietal scales. Measured laterally, at right angle to longitudinal axis, at deepest part of head in region of jaw articulation (Fig. 1B).
9. Head width (HW): distance of widest part of head. Measured dorsally, at region of jaw articulation (Fig. 1A).
10. Snout length (SE): Distance from tip of snout to anterior margin of orbit. Measured laterally (Fig. 1B).
11. Paravertebral scale width (PVS): Transverse width of mid-dorsal paravertebral scale. Measured at right angle to long axis of body, as straight-line distance between junctions of adjacent overlapping paravertebral and dorsolateral scales (Fig. 1A). Usually measured on right hand side of body. Measured scales were chosen for position at mid-body, uniformity to other paravertebrals and for lack of damage or displacement.

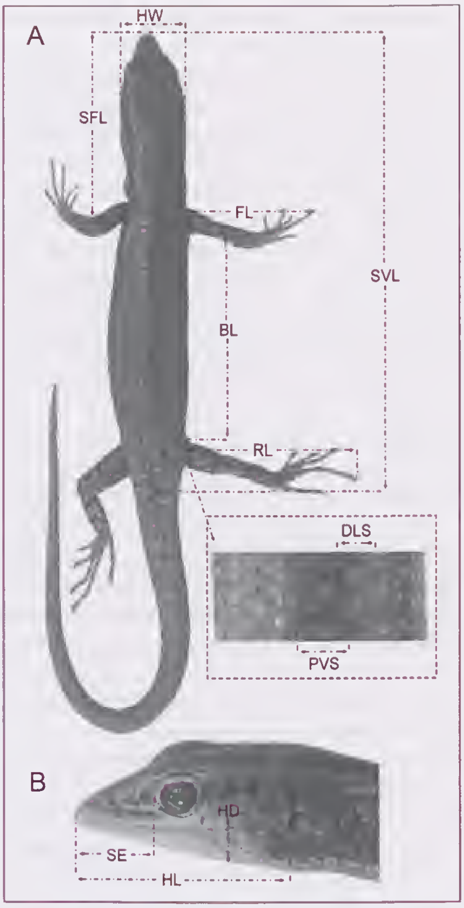

Fig. 1. Illustrative *Cryptoblepharus* (*C. cygnatus* sp. nov., NTM R10970), showing body (**A**) and head (**B**) measuring points for morphometric variables.

12. Dorsolateral scale width (DLS): Transverse width of mid-dorsal dorsolateral scale. Measured at right angle to long axis of body, as straight-line distance between junctions of adjacent overlapping paravertebral and laterodorsal scales (Fig. 1A). Usually measured on right hand side of body and on scale adjacent to measured paravertebral scale. Measured scales were chosen for position at mid-body, uniformity to other dorsolaterals and for lack of damage or displacement.

Scalation characters

13. Midbody scale rows (MR): Number of longitudinal rows of scales at midbody. Recorded at a point midway between axilla and groin.
14. Paravertebral scales (PV): Number of paired scales in vertebral series of neck and body. Recorded longitudinally from scale bordering posterior margin of parietals to scale at midpoint between posterior margins of hindlimbs when held at right angles to body. When undamaged, counts were made of series on right hand side of body.

15. Nuchal scales (NS): Number of enlarged dorsal neck scales immediately posterior to parietals and noticeably differentiated from adjoining paravertebrals (Fig. 2B). Enlarged nuchal scales not always present.
16. Supralabial scales (SL): Number of scales bordering margin of upper lip. Defined as a longitudinal series that begins with scale posterior to lower rostral margin and ends with scale immediately dorsal to the mouth corner (Fig. 2A). Counts made of both lateral series.
17. Infralabial scales (IL): Number of scales bordering margin of lower lip. Defined as a longitudinal series that begins with scale posterior to upper mental margin and ends with scale immediately ventral to the mouth corner (Fig. 2A). Counts made of both lateral series.
18. Supraciliary scales (SC): Number of scales between supraoculars and ciliary scales immediately above eye. Defined as the longitudinal series that begins with scale posterior to outer prefrontal margin and ends with scale ventral to lower margin of fourth supraocular scale (Fig. 2). Counts made of both lateral series.
19. Ciliary scales (CI): Number of enlarged scales on dorsal margin of eye. Defined as the longitudinal series of three or four noticeably large scales between mid-supraciliaries and eye (Fig. 2A). Counts made of both lateral series.
20. Subdigital lamellae of fourth finger (FTL): Number of broad transverse lamellae under fourth digit of forefoot. Series begins with first scale at base of digit noticeably broader than adjoining palmars and ends with terminal scale bordering claw.

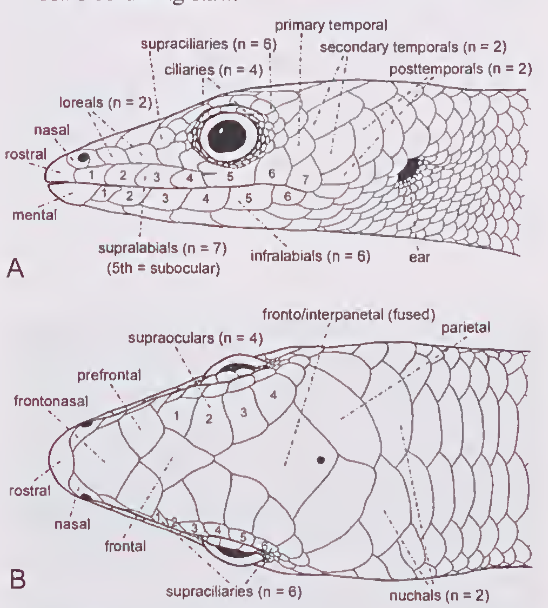

Fig. 2. Diagrammatic head of typical *Cryptoblepharus* (*C. cygnatus* sp. nov., NTM R3014), showing position and nomenclature of lateral (**A**) and dorsal (**B**) head shields.

21. Supradigital lamellae of fourth finger (FTS): Number of broad transverse lamellae above fourth digit of forefoot. Series begins with first scale at base of digit differentiated from scales covering foot and ends with terminal scale bordering claw.
22. Subdigital lamellae of fourth toe (HTL): Number of broad transverse lamellae under fourth digit of hindfoot. Series begins with first scale at base of digit noticeably broader than adjoining plantars and ends with terminal scale bordering claw (Fig. 3).
23. Supradigital lamellae of fourth toe (HTS): Number of broad transverse lamellae above fourth digit of hindfoot. Series begins with first scale at base of digit differentiated from scales covering foot and ends with terminal scale bordering claw.
24. Palmar scales (PAL): Number of juxtaposed scales under sole of forefoot. Count is made of series in a mid-line between basal subdigital lamella of third digit and terminal imbricate scales of limb.
25. Plantar scales (PLN): Number of juxtaposed scales under sole of hindfoot. Count is made of series in a mid-line between basal subdigital lamella of third digit and terminal imbricate scales of limb (Fig. 3).
26. Morphology of plantar scales (CPS): Not commonly used in skink systematics, this character is polymorphic in Australian *Cryptoblepharus*. Assessment is made of the juxtaposed scales on sole of hindfoot, which are scored as variations of two principal character states. First principal character state is 'rounded or ovate' and variations are: most scales plain, dark brown calli absent (Fig. 4A); at least a few scales capped with large prominent dark brown calli (Fig. 4B). Second principal character state is 'pointed to spinose' and variations are: basal scales at heel of foot bluntly pointed (Fig. 4C); basal scales at heel of foot acutely pointed or spinose (Fig. 4D).

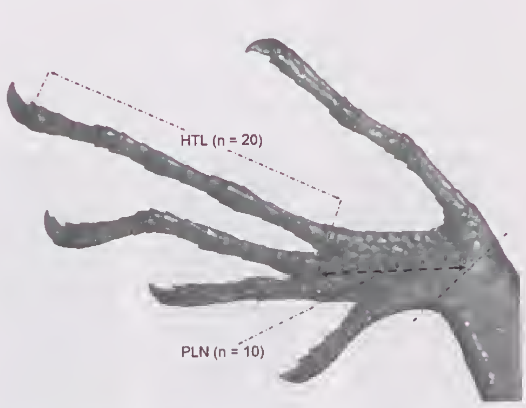

Fig. 3. Illustrative ventral aspect of typical *Cryptoblepharus* hind foot (*C. ustulatus* sp. nov., NTM R22079), showing start and finish points for subdigital lamellae (HTL) and plantar scale (PLN) counts. Number of plantar scales is taken as those in a line (bold arrow) drawn between the basal lamella of third digit and lower imbricate scales of limb.

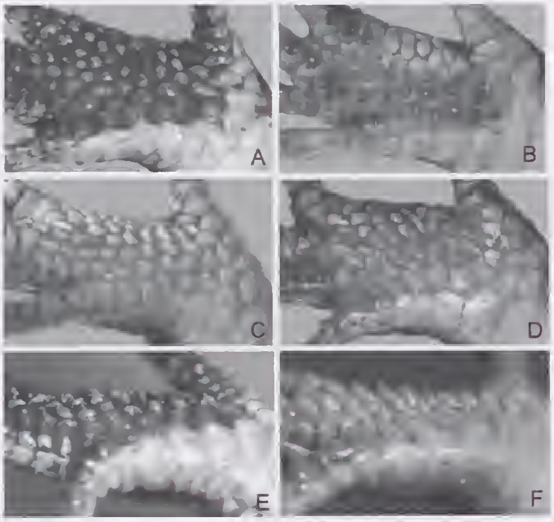

Fig. 4. Examples of *Cryptoblepharus* plantar scale morphology (x20): **A**, plain, ovate, dark pigmentation (*C. pulcher*, NTM R22058); **B**, ovate, pale pigmentation but many scales capped with dark brown calli (*C. metallicus*, NTM R18838); **C**, pale, acute, bluntly pointed (*C. australis*, NTM R23472); **D**, pale, acute, spinose (*C. exochus* sp. nov., NTM R18669); **E**, ovate scales in profile view (*C. pulcher*, NTM R22058); **F**, acute scales in profile view (*C. ochrus* sp. nov. NTM R22024).

27. Morphology of subdigital lamellae (SDL): Based on surface architecture of broad transverse lamellae under fourth toe. Assessment was made of average condition of all fourth toe lamellae. Character states were scored as: smooth (Fig. 5A); callused (Fig. 5B); keeled (Fig. 5C).
28. Relative size of loreal scales (LL): Bilateral series of paired loreal scales are typical in *Cryptoblepharus* (Fig. 2A) Scoring was made between three character states with assessment made of both lateral series: anterior largest; posterior largest; loreals subequal.
29. Postnasal scale (PN): Usually absent in *Cryptoblepharus*, but all *C. gurrmul* sp. nov. and occasional other specimens have a distinct scale located bilaterally between anterior loreal and frontonasal, herein interpreted as a postnasal. Two character states were scored with assessment made of both series as: present (Fig. 6); absent (Fig. 2A).
30. Subocular scale (SO): Elongated supralabial below orbit. Fifth in series is commonly below orbit (Fig. 2A), but occasionally the fourth or sixth may be subocular.
31. Prefrontal scales (PF): Single pair of prefrontals are present on *Cryptoblepharus* and normally in broad median contact. Variation of contact was scored as: broadly separated; narrowly separated (Fig. 2B); in narrow contact; in broad contact.
32. Prefrontal overlap (PFO): Lineages in reptiles have been indicated by the direction of overlap of adjoining paired scales (Greer 1993). This was assessed by the nature of the suture between the paired prefrontal scales. Variation was scored as: right over left; left over right; fused.
33. Posttemporal scales (PTS): *Cryptoblepharus* typically has a single primary temporal followed by upper and lower secondary temporals (1 + 2). Posterior margin of lower secondary temporal may contact either two or three posttemporal scales (Fig. 2A). Number of posttemporals in contact with lower secondary temporal was scored.
34. Interparictal scale (IS): In *Cryptoblepharus* this scale and the frontoparietals are normally fused into a single large, diamond shaped shield. In all *C. egeriae* and occasional other specimens the interparietal is distinct from the fused frontoparietals. Interparietal condition was scored as: fused (Fig. 2B); distinct.
35. Lenticular scale organs (LSO): An irregular series of microscopic circular openings, transversely aligned along the posterior margin of each mid-paravertebral scale (Fig. 7). Present on most body scales, lenticular scale organs have not previously been used as a scincid taxonomic character. Examination was made of epidermal layers from two adjoining mid-paravertebral scales from each specimen. Epidermal layers were removed with fine forceps and mounted on glass slides and examined at x100 magnification. Number of lenticular scale organs per scale was recorded.

Body pattern and colour

36. Dorsal body pattern (BP): Character states were scored

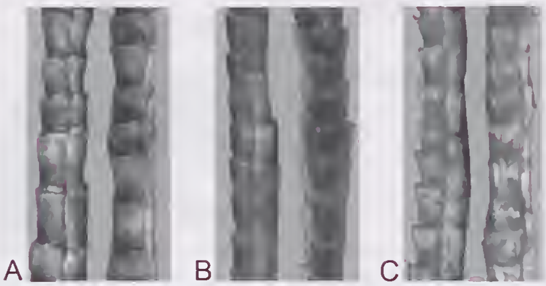

Fig. 5. Examples of *Cryptoblepharus* fourth toe subdigital lamellae, in lateral (left) and ventral (right) views (x62): **A**, smooth lamellae (*C. gurrmul* sp. nov. NTM R10901); **B**, callused lamellae (*C. cygnatus* sp. nov. NTM R22451); **C**, keeled lamellae (*C. mertensi* sp. nov. NTM R22644).

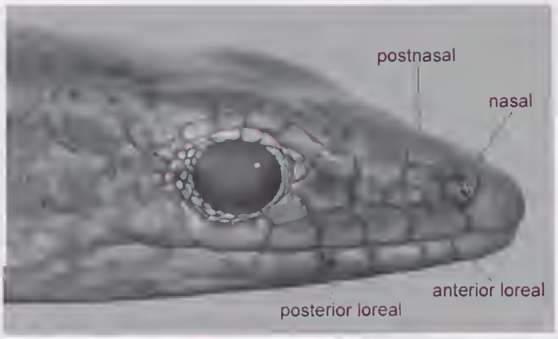

Fig. 6. Position of postnasal scale in *Cryptoblepharus gurrmul* sp. nov. (NTM R10901) (x26).

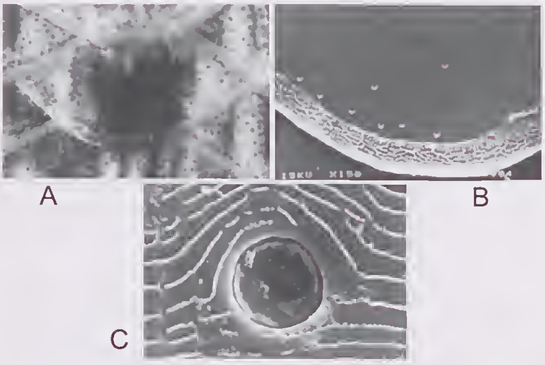

Fig. 7. Lenticular scale organs: **A**, micrograph of mid-paravertebral scale showing position of organs at mid-posterior margin (x47) (*C. cygnatus* sp. nov., NTM R23496); **B**, SEM micrograph showing irregular positioning of organs at posterior margin (x450) (*C. cygnatus* sp. nov., NTM R21709); **C**, SEM micrograph of single lenticular scale organ (x10,500) (*C. litoralis*, NTM R18865).

on typical pattern, with states being: absent; consisting entirely of fine flecks and specks (Fig. 8D); large irregular dark blotches (Fig. 8E); longitudinally aligned, pale laterodorsal stripes/zones present (Fig. 8 A, B and C).

37. Condition of pale laterodorsal stripes (PS): Most *Cryptoblepharus* have pale, longitudinal laterodorsal stripes or zones on the neck and body (Fig. 8 A–C). Condition was usually scored on posterior half of body, with character states being: absent; very narrow, width much less than that of dorsolateral scale, often most prominent on anterior half of body; narrow, width similar to that of dorsolateral scale, usually smooth edged and continuous (Fig. 8 A, B); narrow, width similar to that of dorsolateral scale, but broken into discontinuous series of irregular streaks, blotches and spots; broad, width greater than that of single dorsolateral scale, relatively distinct, edges ragged; very broad stripe or zone often containing flecks and specks, width at least twice that of dorsolateral scale, usually diffuse being delineated by darker vertebral and upper lateral zones (Fig. 8C).
38. Pigmentation of palmar/plantar scales (PP): Many *Cryptoblepharus* have variably patterned palmar/plantar regions; however, the dominant pigment is usually distinct. Character states were scored as: pale (cream to light brown) (Fig. 4C); dark (dark brown to black) (Fig. 4A).

Soft tissue

39. Hemipenis (HPL): *Cryptoblepharus* have two simple lobed, club-shaped hemipenes (Fig. 9) with subtle differences in lobule shape that proved difficult to quantify. Everted hemipenes were not accessible for all taxa, but where available hemipenis length was measured. Fully everted hemipenes were identified by completely expanded lobules and measured as a straight line distance from posterior margin of preanal plate to tip of expanded apical region along longitudinal axis of hemipenis (Fig. 9D).

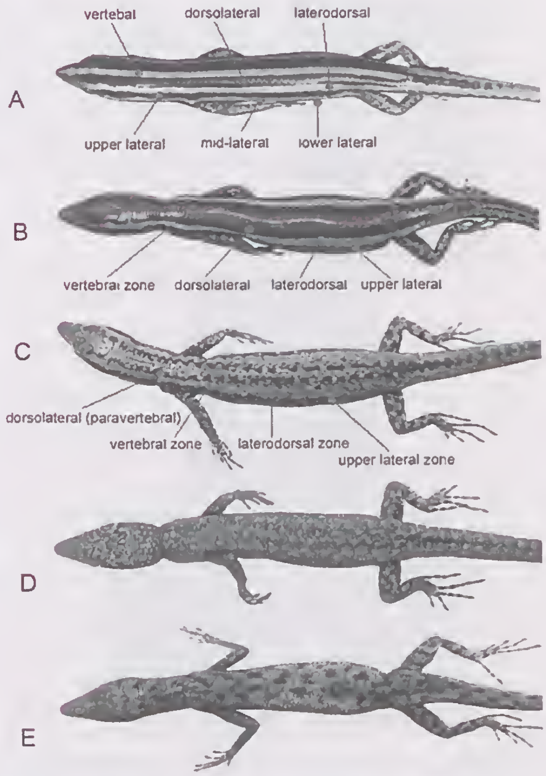

Fig. 8. Examples of *Cryptoblepharus* body patterns showing nomenclature: **A**, simple pattern of longitudinally aligned pale and dark stripes (*C. renschi*, SMF 22209); **B**, simple pattern of longitudinally aligned zones and stripes (*C. virgatus*, NTM R18885); **C**, complex pattern of longitudinally aligned zones, stripes, spots and flecks (*C. metallicus*, NTM R25025); **D**, reduced pattern of flecks and specks (*C. buchananii*, NTM R24773); **E**, random pattern of blotches, spots and flecks (*C. megastictus*, NTM R22788).

Other data recorded

40. Sex: Determined by examination of gonads and scored as either male or female. A few specimens that had been damaged or dissected were indeterminate. Partly everted structures were not relied on to identify males.
41. Reproductive condition: Determined by examination of gonads and scored as either immature, non-reproductive or reproductive. Males were identified as immature by small body size and possession of very small, flattened testes; as non-reproductive by testes and epididymes not being engorged, and as reproductive by having obviously engorged testes and swollen epididymes. Females were identified as immature by small body size and by having very small ovarian follicles, as non-reproductive by having ovarian follicles with no indication of vitellogenesis, and as reproductive by containing vitellogenic follicles or oviducal eggs.

Allometry. Morphometric characters were allometrically adjusted, thereby allowing morphometric values of individuals of all taxa and at all life stages to be directly compared

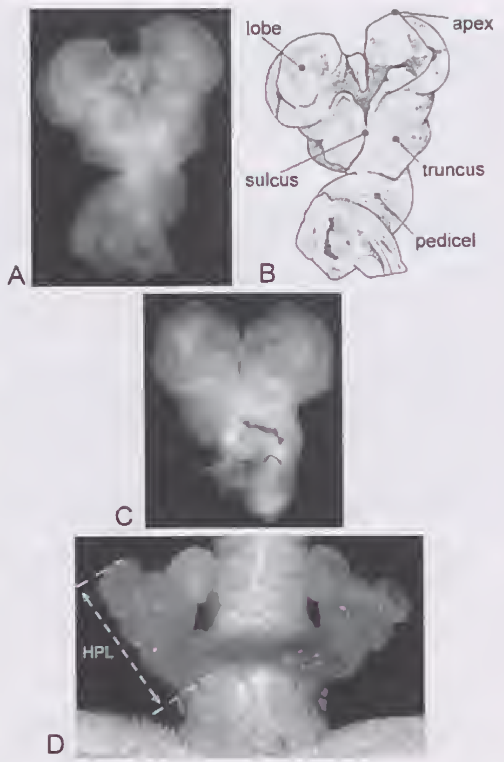

Fig. 9. Sulcal views of typical *Cryptoblepharus* hemipenes: **A**, long hemipenis (x16) (*C. metallicus*, NTM R18655); **B**, diagrammatic interpretation of A, showing nomenclature; **C**, short hemipenis (x13) (*C. litoralis*, NTM R18897); **D**, in situ fully extruded hemipenes (x11), showing measuring points (HPL) (*C. cygnatus* sp. nov., NTM R21709).

following Thorpe (1975). In this study, morphometric character values, of all specimens examined, were adjusted to what they would be if the specimens were of mean body or head size by applying the formula $Y_i = \log Y_i - b(\log X_i - \log X)$, where Y_i is the natural logarithm of the value for the adjusted dependent variable of the ith specimen; Y_i is the value for the unadjusted dependent variable of the ith specimen; b is the pooled regression coefficient of $\log Y$ against $\log X$; X_i is the value for the independent variable of the ith specimen, and X is the value for the grand mean of the independent variable (Thorpe 1975; Shea 1995a). The resulting logarithm value of the dependent variable was transformed to its adjusted value by calculation of the antilog. Allometrically adjusted values were used in statistical analyses only, raw values were universally used in taxon descriptions.

Statistical analyses were carried out on raw meristic characters and allometrically adjusted morphometric values. Ratios or other transformations were excluded. Morphological data were analysed using two approaches. Generally, where sample sizes were large (>30) and variables could be assumed to be normally distributed, discriminant function analysis (DFA) was used. Smaller sample sizes were assessed with one-way analysis of variance (ANOVA). Tests on morphological characters were carried out with the program STATISTICA (Statsoft Inc. 1997). Where results of statistical tests are presented, asterisks shown as superscripts *, **, *** indicate significance at 5%, 1% and 0.5% levels respectively.

To delineate species the Biological Species Concept (BSC) was adopted. This was initially defined by Mayr (1942) as "*Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups*". Later, Mayr (1982) refined the BSC as "*A species is a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature*". Although the BSC stresses a practical aspect of how to recognise species, from its theoretical background it is entirely compatible with 'evolutionary lineages' species concepts (reproductive isolation is a prerequisite for evolutionary lineages to maintain their integrity through time and space) (Helbig *et al.* 2002). Assessed by spatial data as well as morphological and genetic gaps, taxa were recognized as 'reproductively isolated from others' (biological species) if they proved to have unique combinations of three or more (rather than relying only on one character) significant morphological and/or allozyme characters. Taxa were objectively assigned to the subspecies level using the following criteria recommended by Thorpe (1987): (1) geographic races should be distinct and care should be taken to avoid sectioning clinal patterns of variation; (2) variation in characters diagnosing subspecies should predict variation in other, independent, sets of characters; (3) only the main categories or lineages within a species should be identified.

Statistical analyses. Three hundred and ninety-two voucher specimens that contributed tissues to the allozyme electrophoresis study of Horner and Adams (2007) were examined and scored for morphological character states. From the resulting data set, significant morphological differences between genetic OTUs were determined by discriminant function analyses and/or pairwise comparisons using ANOVA.

Further individuals, not analysed genetically, were morphologically examined and assessed for degree of conformity to the morphological parameters determined for each OTU and assigned to the OTU where they 'fitted best'. In cases where assignment of additional individuals was to ambiguous taxa, these were also assessed on the basis of having been collected at the same time and place as a genetically identified voucher specimen. Overall, 528 extra individuals were assigned to OTUs and the final morphological data set included details from 920 individuals.

To test morphological integrity of the OTU complements, each was subjected to a series of statistical analyses. Firstly, sexual dimorphism was investigated and characters identified as sexually dimorphic were either omitted from further analyses or, where sample sizes were sufficient, sexes were analysed separately. To test that individuals within an OTU were morphologically closer to each other than to individuals of any other OTU, multivariate ordinations were generated using Discriminant Function Analysis (DFA).

Sequential Discriminant Function Analyses was used to determine whether individuals were classified as predicted, to investigate differences between or among groups and to assess the relative importance of each predictor variable in classifying groups. As a rule of thumb for this study, sample size of the smallest group aimed to exceed the number of predictor variables. In the few instances where less individuals were investigated, these were incorporated with a larger group and the analysis allowed to predict their position in the ordination.

The process consisted of an initial DFA conducted on all individuals from a particular geographic region to identify OTUs clearly diagnosable from all others. These OTUs were removed from subsequent DFAs and the cycle of OTU diagnosing followed by DFA on a reduced subset of individuals was repeated until all diagnosable OTUs were identified. In cases where sample sizes were small or discriminating characters ambiguous by DFA, pairwise comparisons of OTUs using ANOVA were used to identify significant differences. This approach determined if two or more OTUs were significantly different and if so, which morphological variables discriminated between them.

Results of each DFA are illustrated by a 2D scatter plot. Objective differentiation of OTUs involved recognition of clusters which the DFA determined to comprise 100% correctly assigned individuals. In each scatter plot clusters representing specific OTUs, and/or individuals amalgamated for further analysis, are delineated by hand drawn ellipses or polygons, cluster centroids (means of canonical variables) are indicated by a cross.

Analysis of morphological data resulted in the recognition of OTUs defined as groups of individuals morphologically more-similar to each other than to individuals of any other group.

OTUs congruently distinguished by combinations of unique allozymic (as determined by Horner and Adams 2007) and morphological differences, were assigned species status. Those OTUs with incongruent data sets were assessed by the significance of their morphological divergence and if determined sufficiently distinct, assessed for specific or subspecific status or, if not diagnosable, merged with the OTU(s) from which they were morphologically indistinguishable.

Geographic analysis. Geographic variation was investigated in Australian taxa by assignment of individuals to subgroups based on distribution within continental bioregions. The Interim Bioregionalisation of Australia (Environment Australia 2000), in which bioregions are determined from climate, geomorphology, landform, lithology and characteristic flora and fauna, was selected as most appropriate to subdivide geographic distributions. Seventy-six mainland bioregions (Tasmania is outside *Cryptoblepharus* distribution) were utilised, the location and codes of which are shown in Fig. 10. Commonly, sample sizes within an OTU from a single bioregion were insufficient for analysis. In these cases a larger subgroup was formed by combining samples from adjoining and/or nearby bioregions with those from a well populated bioregion.

RESULTS OF MORPHOLOGICAL ANALYSES

Analysis of Australian populations. Preliminary morphological assessment recognised 14 presumptive operational taxonomic units (OTUs): most *C. carnabyi* (carnA); *C. carnabyi* with very narrow laterodorsal stripes (carnB); *C. carnabyi* with prominent broad laterodorsal stripes (carnC); *C. carnabyi* from central Australia with obtusely pointed plantar scales (carnD); *C. fuhni* (fuhn); *C. litoralis* (litor); *C. litoralis*-like form from Oxley and New Year Islands, NT (oxley); *C. horneri* (horn); most *C. megastictus* (megaA); *C. megastictus*-like form from the Pilbara region of WA (megaB); most *C. plagiocephalus* (plagA); the *nomen nudum C. 'swansoni'* (plagB); *C. virgatus virgatus* (virgA); *C. virgatus clarus* (virgB).

With the exception of OTU oxley, for which tissue samples were unavailable, these presumptive OTUs were genetically investigated by Horner and Adams (2007) using allozyme electrophoresis. That study resulted in recognition of two genetic lineages and 27 operational taxonomic units (OTUs) among mainland Australian *Cryptoblepharus* populations. Although Horner and Adams (2007) identified diagnostic allozyme differences between most OTUs, they found the five combinations of plagA2 and megaA4, carnD and plagA5, carnA5 and virgA3, horn and litor, virgA1 and virgB each displayed similar allozyme profiles and each pair was unable to be separated by the allozyme analysis.

Morphological identification of Australian lineages. As determined by Horner and Adams (2007) Australian genetic OTUs were unevenly allocated between two lineages. Utilising morphological data recorded from the 374 voucher specimens who contributed tissues to the allozyme analysis, divergence was identified between the two Australian genetic lineages in seven morphological features (Table 1). Members of lineage 1 are longer (mean SVL 38.5 versus 35.8 mm), have shorter bodies (mean 18.7 versus 19.2 mm), longer limbs (mean FL = 12.9 versus 12.4; RL = 16.0 versus 15.6 mm) and head (mean 8.0 versus 7.6 mm), more supraciliary scales (mean 6.0 versus 5.1) and less palmar scales (mean 8.3 versus 9.1). Considerable overlap exists in the majority of these characters and most are of little practical use in distinguishing an individual's lineage. However, number of supraciliary scales has the highest significance level, least overlap (lineage 1 = 91.2% have six supraciliary scales bilaterally, 4.6% have 6+5 or 6+7, 2.3% have 7+7 or 7+8, 1.8% have 5+5; lineage 2 = 88.1%

Fig. 10. Map showing Interim Biogeographic Regionalisation for mainland Australia (Environment Australia 2000). Codes for bioregions are: AA, Australian Alps; ARC, Arnhem Coast; ARP, Arnhem Plateau; AW, Avon Wheatbelt; BBN, Brigalow Belt North; BBS, Brigalow Belt South; BHC, Broken Hill Complex; BRT, Burt Plain; CA, Central Arnhem; CAR, Carnarvon; CHC, Channel Country; CK, Central Kimberley; CMC, Central Mackay Coast; COO, Coolgardie; CP, Cobar Peneplain; CR, Central Ranges ; CYP, Cape York Peninsula; DAB, Daly Basin; DAC, Darwin Coastal; DEU, Desert Uplands; DL, Dampierland; DMR, Davenport Murchison Ranges; DRP, Darling Riverine Plains; EIU, Einasleigh Uplands; ESP, Esperance Plains; EYB, Eyre and Yorke Blocks; FIN, Finke; FLB, Flinders Lofty Block; FLI, Flinders; GAS, Gascoyne; GAW, Gawler; GD, Gibson Desert; GFU, Gulf Fall and Uplands; GS, Geraldton Sandplains; GSD, Great Sandy Desert; GUC, Gulf Coastal; GVD, Great Victoria Desert; GUP, Gulf Plains; HAM, Hampton; JF, Jarrah Forest; KAN, Kanmantoo; LSD, Little Sandy Desert; MAC, MacDonnell Ranges; MAL, Mallee; MDD, Murray-Darling Depression; MGD, Mitchell Grass Downs; MII, Mount Isa Inlier; ML, Mulga Lands; MUR, Murchison; NAN, Nandewar; NCP, Naracoorte Coastal Plain; NET, New England Tableland; NK, Northern Kimberley; NNC, NSW North Coast; NSS, NSW South western Slopes; NUL, Nullarbor; OVP, Ord-Victoria Plains; PCK, Pine Creek; PIL, Pilbara; RIV, Riverina; SB, Sydney Basin; SCP, South east Coastal Plain; SEC, South East Corner; SEH, South Eastern Highlands; SEQ, South Eastern Queensland; SSD, Simpson-Strzelecki Dunefields; STP, Stony Plains; STU, Sturt Plateau; SWA, Swan Coastal Plain; TAN, Tanami; TIW, Tiwi Cobourg; VB, Victoria Bonaparte; VM, Victorian Midlands; VVP, Victorian Volcanic Plain; WAR, Warren; WT, Wet Tropics; YAL, Yalgoo.

have five supraciliary scales bilaterally, 7.0% have 5+6 and 4.9% have 6+6 or 6+7), is not subject to sexual dimorphism (Table 1) and thus, is a convenient and relatively reliable guide to morphological identification of genetic lineage in Australian *Cryptoblepharus* specimens.

Hemipenis proportions were not included in morphological analyses due to some OTUs lacking male samples preserved with extruded hemipenes. However, as indicated in Fig. 11 hemipenis length and width alludes to placement within lineages. Lineage 1 OTUs (megaA2, megaA3, plagA5 and plagB) tend towards long hemipenes, while lineage 2 OTUs (carnA1, carnA5, carnB, carnC, litor, virgA1 and virgA2) have relatively short hemipenes. In support, lineage 1 OTUs (megaA2, megaA3, plagA1, plagA5 and plagB) have narrow hemipenes compared to those of lineage 2 OTUs (carnA1, carnA5, carnB, carnC, litor, virgA1 and virgA2). The value of hemipenis proportions as indicators of lineage is questioned, however, by the presence of a 'short' hemipened member in lineage 1 (OTU plagA1) and a 'narrow' hemipened member in lineage 2 (OTU carnA5).

Sexual dimorphism. Investigation of sexual dimorphism in Australian *Cryptoblepharus* was undertaken by comparing variables from genetic OTUs with sample sizes greater than 20 mature adult males and females. As listed in Table 2, this analysis determined that sexual dimorphism is expressed in six morphometric characters (snout-vent length, body length, forelimb length, hindlimb length, forebody length and head length) and one meristic variable (number of paravertebral scales). Thus *Cryptoblepharus* are sexually dimorphic, with males being

Table 1. Phenotypic characters, recorded from 375 tissue donor specimens, which discriminate between the two Australian genetic lineages.

character	p	lineage	sex	mean (mm)	N	mode	range	std.dev
snout-vent length	0.001***	1	m	37.5	123	-	27.8–44.4	3.68
			f	39.8	93	-	21.0–47.9	4.62
		2	m	34.6	81	-	24.3–44.0	4.02
			f	36.7	103	-	27.5–51.0	4.52
body length	0.001***	1	m	18.4	123	-	15.7–20.5	0.88
			f	19.1	93	-	17.6–20.9	0.74
		2	m	18.9	81	-	16.6–21.3	0.90
			f	19.6	103	-	17.8–22.1	0.94
forelimb length	0.001***	1	m	13.1	123	-	11.1–15.6	0.77
			f	12.5	93	-	10.8–15.2	0.79
		2	m	12.9	81	-	11.1–17.1	0.90
			f	12.1	103	-	10.8–13.9	0.75
hindlimb length	0.001***	1	m	16.3	114	-	14.2–19.8	0.95
			f	15.5	76	-	14.0–18.7	0.91
		2	m	16.1	85	-	13.8–21.7	1.08
			f	15.0	99	-	12.7–18.1	1.01
head length	0.001***	1	m	8.1	123	-	7.3–8.9	0.23
			f	7.8	93	-	7.1–8.7	0.28
		2	m	7.9	81	-	7.2–9.1	0.32
			f	7.4	103	-	6.7–8.2	0.30
number of supraciliary scales	0.001***	1	m	6.0	123	6	5–7	0.23
			f	6.0	93	6	5–8	0.24
		2	m	5.1	81	5	5–6	0.27
			f	5.1	103	5	5–7	0.25
number of palmar scales	0.001***	1	m	8.2	123	8	6–10	1.02
			f	8.4	93	9	6–11	1.09
		2	m	9.2	81	9	7–13	1.38
			f	9.0	103	10	6–12	1.41

Table 2. Characters expressing sexual dimorphism in *Cryptoblepharus*. Determined from Australian OTUs with sample sizes greater than 20 mature adult males and females (characters are allometrically adjusted).

OTU	character	p	mean (♂ vs ♀)	N (♂ vs ♀)	std.dev. (♂ vs ♀)
carnA5	snout-vent length	0.003***	33.5 vs 35.2 mm	40 vs 47	2.21 vs 2.85
	body length	0.003***	19.1 vs 19.6 mm	40 vs 47	0.80 vs 0.81
	forelimb length	0.001***	12.8 vs 12.0 mm	40 vs 47	0.72 vs 0.54
	hindlimb length	0.001***	15.8 vs 15.0 mm	40 vs 47	0.74 vs 0.64
	forebody length	0.001***	15.9 vs 15.2 mm	40 vs 47	0.74 vs 0.56
	head length	0.001***	7.9 vs 7.4 mm	40 vs 47	0.27 vs 0.22
	paravertebral scales	0.006**	46.9 vs 48.4	40 vs 47	2.26 vs 2.72
plagA5	snout-vent length	0.009**	38.9 vs 40.3 mm	131 vs 94	3.41 vs 4.50
	body length	0.001***	18.5 vs 19.3 mm	127 vs 91	0.90 vs 0.88
	forelimb length	0.001***	13.0 vs 12.3 mm	127 vs 91	0.66 vs 0.58
	hindlimb length	0.001***	16.0 vs 15.1 mm	131 vs 94	0.69 vs 0.71
	forebody length	0.001***	16.2 vs 15.6 mm	127 vs 91	0.59 vs 0.49
	head length	0.001***	8.1 vs 7.8 mm	131 vs 94	0.25 vs 0.29
	paravertebral scales	0.001***	49.4 vs 50.6	131 vs 94	2.58 vs 2.47
plagB	body length	0.007**	18.8 vs 19.4 mm	41 vs 30	1.04 vs 0.86
	forelimb length	0.001***	12.9 vs 12.1 mm	41 vs 30	0.60 vs 0.76
	hindlimb length	0.001***	16.2 vs 15.2 mm	41 vs 30	0.73 vs 0.75
	forebody length	0.001***	16.1 vs 15.3 mm	41 vs 30	0.57 vs 0.66
	head length	0.001***	8.1 vs 7.7 mm	41 vs 30	0.22 vs 0.24
	paravertebral scales	0.044*	48.7 vs 49.8	41 vs 30	2.22 vs 2.36
virgA1	snout-vent length	0.001***	34.5 vs 36.5 mm	36 vs 43	2.40 vs 2.72
	body length	0.006**	19.1 vs 19.7 mm	36 vs 43	0.85 vs 1.06
	forelimb length	0.001***	12.3 vs 11.8 mm	36 vs 43	0.54 vs 0.52
	hindlimb length	0.001***	15.6 vs 14.7 mm	36 vs 43	0.69 vs 0.67
	forebody length	0.001***	15.6 vs 15.1 mm	36 vs 43	0.51 vs 0.69
	head length	0.001***	7.6 vs 7.2 mm	36 vs 43	0.21 vs 0.33

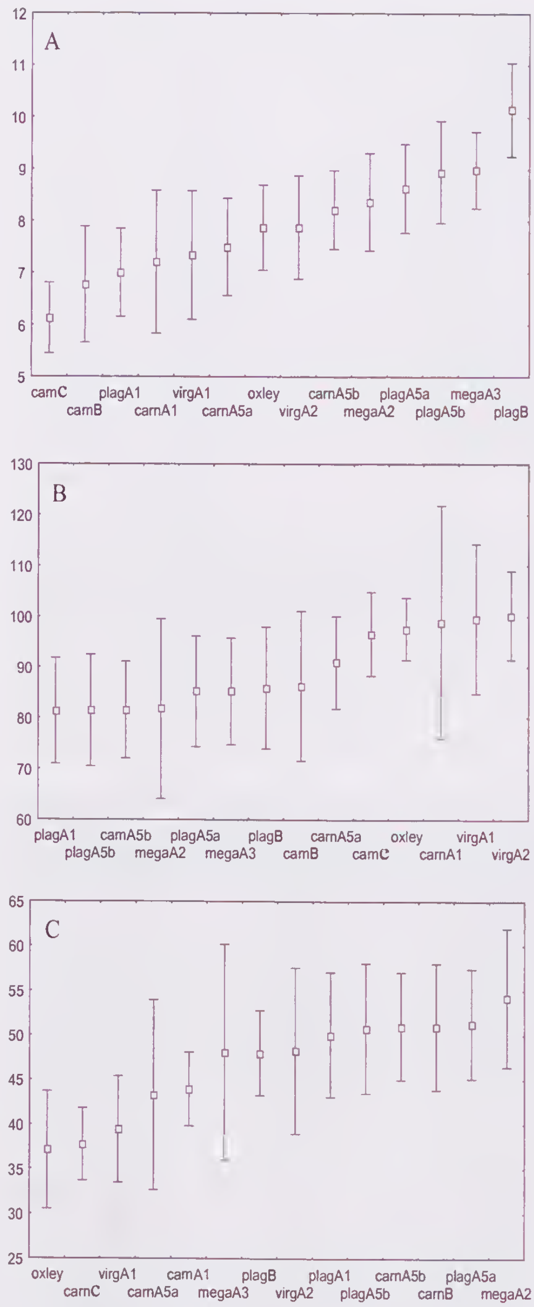

Fig. 11. Hemipene proportions for Australian *Cryptoblepharus* OTUs. **A**, length (% of snout-vent length); **B**, width (% of hemipene length); **C**, pedicel length (% of hemipene length). Shown are means, plus and minus one standard deviation.

smaller with a shorter body but longer limbs, forebody and head and fewer paravertebral scales than females. In all subsequent analyses these sexually dimorphic variables were either omitted or, where sample sizes were sufficient, tested separately.

Morphological identification of Australian OTUs. Identified by analysis of allozyme data and preliminary morphological assessment were 28 Australian OTUs (carnA1, carnA2, carnA3, carnA4, carnA5, carnB, carnC, carnD, fuhn, horn, litor, megaA1, megaA2, megaA3, megaA4, megaA5, megaB, oxley, plagA1, plagA2, plagA3, plagA4, plagA5, plagB, virgA1, virgA2, virgA3 and virgB). Note the genetic OTU virgA1x3, which is of virgA1 x virgA3 hybrid origin, was omitted from morphological analyses.

Nine separate DFAs were ultimately undertaken to identify the final morphological OTUs. DFA 1 investigated all OTUs, represented by 889 individuals, and resulted in the identification of five clusters (Fig. 12), designated Groups 1, 2, 3, 4 and 5. These clusters showed obvious correlation with the morphotypes recognized in the initial determination of presumptive taxa. Group 1 comprised individuals allied with the described species *C. carnabyi* (carnA1, carnA2, carnA3, carnA4, carnA5, carnB, carnC and carnD), Group 2 comprised individuals associated with the described species *C. plagiocephalus* (plagA1, plagA2, plagA3, plagA4, plagA5 and plagB), Group 3 comprised individuals associated with the described species *C. megastictus* (megaA1, megaA2, megaA3, megaA4, megaA5 and megaB), Group 4 comprised individuals associated with the described species *C. fuhni* and *C. litoralis* (fuhn, horn, litor and oxley) and Group 5 those associated with the described species *C. virgatus* (virgA1, virgA2, virgA3 and virgB). In the ordination space cluster groups 1, 2+4, 3 and 5 were distinguished by the first discriminant function and groups 2 and 4 by the second discriminant function. (Appendix 1). For further analysis each group was independently subjected to its own series of stepwise DFAs.

Group 1. DFA 2 investigated 305 individuals allocated to eight Group 1 OTUs (carnA1, carnA2, carnA3, carnA4,

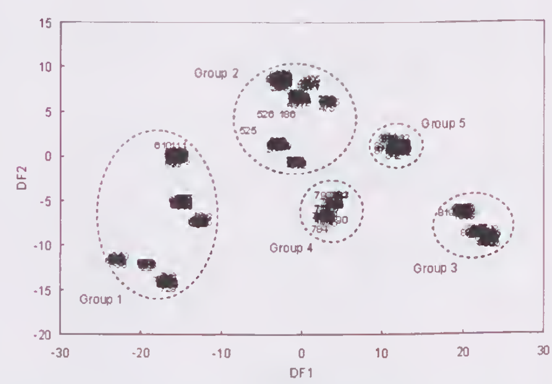

Fig. 12. DFA 1, scatterplot of 889 *Cryptoblepharus* specimens assigned to 26 OTUs (Wilks' *lambda* = 0.001). Legend for clusters: Group 1 = OTUs carnA1, carnA2, carnA3, carnA4; carnA5, carnB, carnC and carnD; Group 2 = plagA1, plagA2, plagA3, plagA4, plagA5 and plagB; Group 3 = megaA1,megaA2, megaA3, megaA4, megaB and megaA5; Group 4 = fuhn, horn, lit and oxley; Group 5 = virgA1, virgA2 and virgA3.

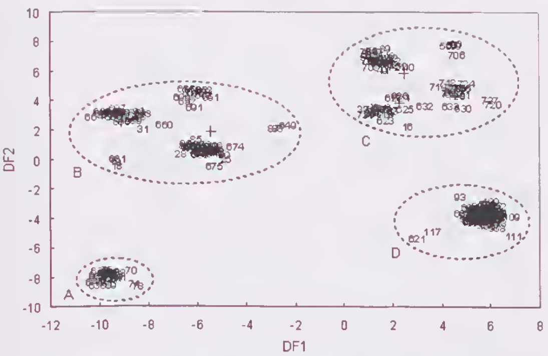

Fig. 13. DFA 2, scatterplot of 305 *Cryptoblepharus* specimens assigned to morphological Group 1 (Wilks' *lambda* = 0.001). Legend for clusters: A = OTU carnB; B = carnA2, carnA3, carnA4 and carnC; C = carnA1 and carnA5; D = carnD.

carnA5, carnB, carnC and carnD) and identified four clusters (Fig. 13). Clusters A and B were distinguished from clusters C and D by the first discriminant function and clusters A from B and C from D by the second discriminant function (Appendix 1). Clusters A and D were entirely composed of individuals allocated to discrete OTUs (cluster A = carnB, cluster D = carnD) and these were considered morphologically defined. Clusters B and C each contained individuals of two or more OTUs (cluster B = carnA2, carnA3, carnA4 and carnC; cluster C = carnA1 and carnA5) and were subjected to further analysis, 'B' by DFA and 'C' by ANOVA.

DFA 3 investigated Cluster B (Fig. 13), which comprised 79 individuals allocated to four OTUs (carnA2, carnA3, carnA4 and carnC) and identified three clusters (Fig. 14). Clusters B1 and B2 were distinguished by the second discriminant function and cluster B3 by the first discriminant function (Appendix 1). Two clusters were entirely composed of individuals allocated to discrete OTUs (cluster B1 = carnC, cluster B2 = carnA3) and these were considered morphologically defined. Cluster B3 comprised individuals of two OTUs (carnA2 and carnA4) and was further investigated by ANOVA, which identified a single significant difference, slight variation in plantar scale condition (bluntly versus acutely pointed, p = 0.009**). Unable to be adequately distinguished by morphological characters, OTUs carnA2 and carnA4 were henceforth considered a single morphological taxon named OTU 'carnA2+carnA4'.

Pairwise comparison of characters between OTUs in cluster C (Fig. 13) revealed five differences between carnA1 and carnA5 (Appendix 2), numbers of midbody and posterior temporal scales, conditions of plantar scales and subdigital lamellae and plantar pigmentation. OTUs carnA1 and carnA5 were considered morphologically defined OTUs.

Of the initial eight Group 1 OTUs analysed, two (carnA2 and carnA4) were indistinguishable and considered a single morphological taxon, thus the analysis resulted in recognition of seven Group 1 OTUs (carnA1, carnA2+carnA4, carnA3, carnA5, carnB, carnC, and carnD).

Group 2. DFA 4 investigated 271 individuals allocated to six Group 2 OTUs (plagA1, plagA2, plagA3, plagA4, plagA5 and plagB) and identified two clusters (Fig. 15), which were distinguished by the first discriminant function (Appendix 1). Cluster E was entirely composed of individuals allocated to OTU plagB and this was recognised as morphologically defined. Cluster F comprised individuals representing five OTUs and was subjected to further analysis by DFA, which failed to differentiate clusters of individuals referrable to a discrete OTU. Identification of OTUs in cluster F was further investigated by ANOVA.

Cluster F (Fig. 15) comprised 200 individuals representing OTUs plagA1, plagA2, plagA3, plagA4 and plagA5. Due to the morphological ambiguity of genetic OTUs plagA2 and plagA3 few individuals made up their complements (total numbers = plagA2 7 ♂'s, 3 ♀'s; plagA3 2 ♂'s, 3 ♀'s). As listed in Appendix 2, ANOVA determined that OTUs plagA2 and plagA3 differed only in head width, a sexually dimorphic character that remained significant when sexes were analysed separately. However, lacking additional morphological differentiation plagA2 and plagA3 could not be adequately distinguished from each other and were

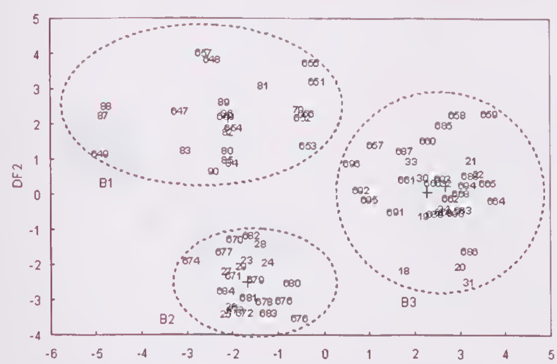

Fig. 14. DFA 3, scatterplot of 79 Group 1 *Cryptoblepharus* specimens (ex cluster B, Fig. 13) (Wilks' *lambda* = 0.021). Legend for clusters: B1 = OTU carnC; B2 = carnA3; B3 = carnA2 and carnA4.

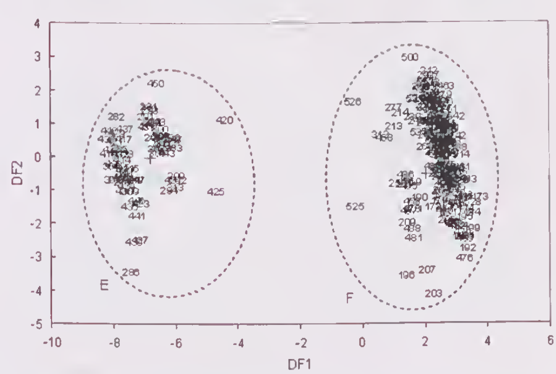

Fig. 15. DFA 4, scatterplot of 273 *Cryptoblepharus* specimens assigned to morphological Group 2 (Wilks' *lambda* = 0.021). Legend for clusters: E = OTU plagB; F = plagA1, plagA2, plagA3, plagA4 and plagA5.

recognised as a single morphological taxon named OTU 'plagA2+plagA3'.

OTUs 'plagA2+plagA3' and plagA1 differed in body and forelimb length and number of paravertebral scales, however when these sexually dimorphic characters were analysed as separate sexes only forelimb length remained significant (Appendix 2). Again, lacking morphological differentiation 'plagA2+plagA3' and plagA1 could not be adequately distinguished from each other and were recognised as a single morphological taxon named OTU 'plagA1+plagA2+plagA3'.

OTU 'plagA1+plagA2+plagA3' differed from OTUs plagA4 and plagA5 in numbers of fourth finger and toe subdigital and supradigital lamellae, and body pattern (Appendix 2). It further differed from OTU plagA4 in head width, number of palmar scales and condition of pale laterodorsal stripes and from OTU plagA5 in tail length, numbers of paravertebral, midbody, nuchal, finger and toe supradigital and posterior temporal scales. OTU 'plagA1+plagA2+plagA3' was recognised as morphologically defined.

OTUs plagA4 and plagA5 differed in snout-vent and tail lengths, head width, numbers of paravertebral, midbody, palmar and posterior temporal scales, conditions of plantar scales and pale laterodorsal stripes (Appendix 2) and were recognised as morphologically defined OTUs.

Of the initial six Group 2 OTUs analysed, three (plagA1, plagA2 and plagA3) were indistinguishable and considered a single morphological OTU, thus, the analysis resulted in recognition of four Group 2 OTUs ('plagA1+plagA2+plagA3', plagA4, plagA5 and plagB).

Group 3. DFA 5 investigated 103 individuals allocated to six Group 3 OTUs (megaA1, megaA2, megaA3, megaA4, megaA5 and megaB) and identified three clusters (Fig. 16). Clusters G and H were distinguished from cluster I by the first discriminant function and cluster G from H by the second discriminant function (Appendix 1). Clusters H and I were entirely composed of individuals allocated to discrete OTUs (cluster H = megaA3, cluster I = megaB) and were considered morphologically defined. Cluster G comprised individuals of four OTUs (megaA1, megaA2, megaA4 and megaA5) and was subjected to further analysis by DFA.

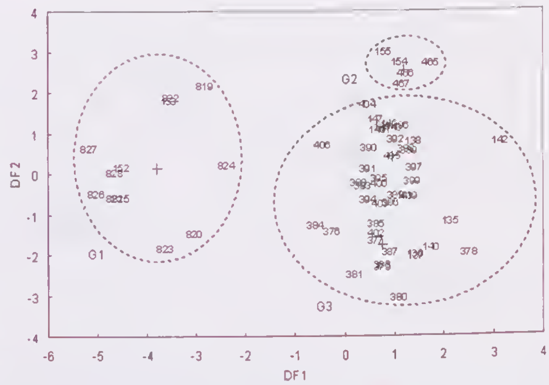

Fig. 17. DFA 6, scatterplot of 60 morphological Group 3 *Cryptoblepharus* specimens (ex cluster G, Fig. 16) (Wilks' *lambda* = 0.068). Legend for clusters: G1 = OTU megaA4; G2 = megaA5; G3 = megaA1 and megaA2.

DFA 6 investigated 60 cluster G individuals and identified three clusters (Fig. 17), two of which were entirely composed of individuals allocated to discrete OTUs (cluster G1 = megaA5, cluster G2 = megaA4) and these were considered morphologically defined. Cluster G1 was distinguished by the first discriminant function and clusters G2 and G3 by the second discriminant function (Appendix 1). Differentiation between OTUs meagA1 and megaA2 (cluster G3) was further investigated by ANOVA which revealed differences in head depth, body pattern and numbers of plantar and posterior temporal scales (Appendix 2) and these were recognised as morphologically defined OTUs.

Of the initial six Group 3 OTUs all were morphologically distinguishable and the analysis resulted in recognition of six OTUs (megaA1, megaA2, megaA3, mega A4, mega A5 and megaB).

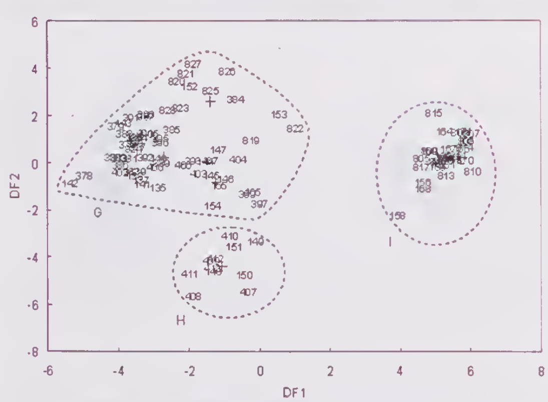

Fig. 16. DFA 5, scatterplot of 103 *Cryptoblepharus* specimens assigned to morphological Group 3 (Wilks' *lambda* = 0.002). Legend for clusters: G = OTUs megaA1, megaA2, megaA4 and megaA5; H = megaA3; I = megaB.

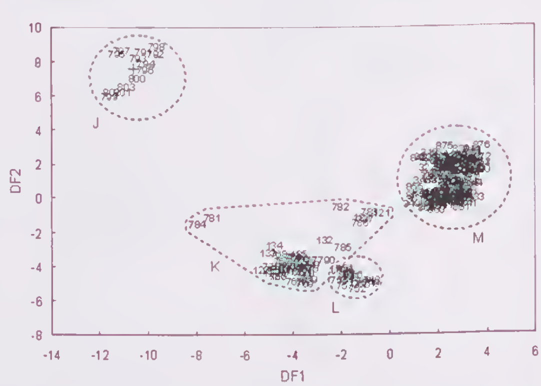

Fig. 18. DFA 7, scatterplot of 212 *Cryptoblepharus* specimens assigned to morphological Groups 4 and 5 (Wilks' *lambda* = 0.001). Legend for clusters: J = OTU oxley; K = horn and litor; L = fuhn; M = virgA3, virgA1 and virgA2.

Groups 4 and 5. Morphological groups 4 and 5 each comprised four OTUs and were combined for investigation by DFA.

DFA 7 investigated 212 individuals allocated to Group 4 (fuhn, horn, litor and oxley) and Group 5 OTUs (virgA1, virgA2, virgA3 and virgB) and identified four clusters (Fig. 18). Cluster J was distinguished from clusters K, L and M by the second discriminant function, clusters K and L from M by the first discriminant function and clusters K and L were close in the ordination space (Appendix 1). Cluster J was entirely composed of individuals allocated to OTU oxley and was recognised as a morphologically defined.

Cluster K comprised individuals allocated to OTUs horn and litor however, as illustrated in Figure 18, exhibited a noticeable lack of cohesiveness and was also in close proximity to cluster L in the ordination space. These clusters were subjected to additional DFA as was cluster M.

DFA 8 investigated 60 individuals allocated to OTUs fuhn, litor and horn and identified three clusters (Fig. 19). Cluster L1 was distinguished by the first discriminant function and cluster K1 from K2 by the second discriminant function (Appendix 1). Cluster L1 was entirely composed of individuals allocated to OTU fuhn and was recognised as morphologically defined. Clusters K1 (OTU horn) and K2 (OTU litor) partially overlapped in the ordination space (Fig. 19) and differentiation was further investigated by pairwise comparison. ANOVA revealed that OTU litor was distinguished from OTU horn by numbers of palmar, plantar and fourth finger supradigital scales, width of paravertebral scales and comparative size of loreal scales (Appendix 2) and these were recognised as morphologically defined OTUs.

DFA 9 investigated 133 individuals allocated to OTUs virgA1, virgA2, virgA3 and virgB and identified four clusters (Fig. 20). Clusters M1 and M2 were distinguished from clusters M3 and M4 by the first discriminant function, while the second discriminant function distinguished M3 from M4 and partially distinguished M1 and M2 (Appendix 1).

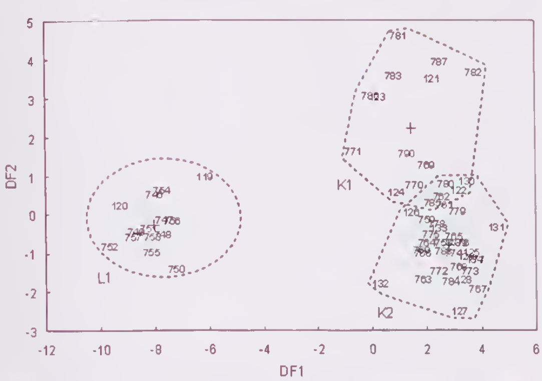

Fig. 19. DFA 8, scatterplot of 60 morphological Group 4 *Cryptoblepharus* specimens (ex clusters K and L, Fig. 18) (Wilks' *lambda* = 0.018). Legend for clusters: K1 = OTU horn; K2 = litor; L1 = fuhn.

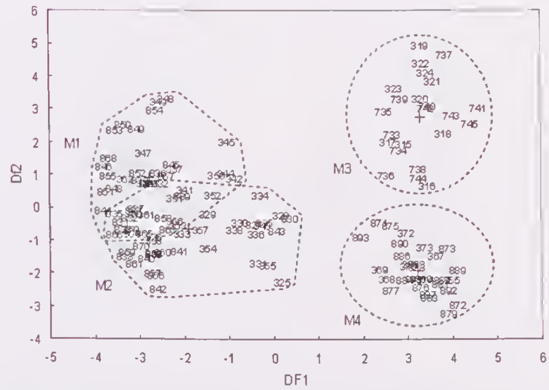

Fig. 20. DFA 9, scatterplot of 133 morphological Group 5 *Cryptoblepharus* specimens (ex cluster M, Fig. 18) (Wilks' *lambda* = 0.016). Legend for clusters: M1 = OTU virgB; M2 = virgA1; M3 = virgA3; M4 = virgA2.

Clusters M3 and M4 were entirely composed of individuals allocated to discrete OTUs (cluster M3 = virgA3, cluster M4 = virgA2) and were recognised as morphologically defined. Clusters M1 (OTU virgA1) and M2 (OTU virgB) partially overlapped in the ordination space (Fig. 20) and differentiation was further investigated by ANOVA which identified that OTU virgA1 was distinguished from OTU virgB by numbers of fourth finger and toe subdigital lamellae, plantar scales, midbody scale rows and condition of pale laterodorsal stripes and that male specimens differed in snout-vent length and females in number of paravertebral scales (Appendix 2). OTUs virgA1 and virgB were recognised as morphologically defined.

Of the initial eight OTUs in groups 4 and 5, all were morphologically distinguishable and the analysis resulted in recognition of eight OTUs (fuhn, horn, litor, oxley, virgA1, virgA2, virgA3 and virgB).

Summary. Of the initial 28 OTUs analysed five were unable to be clearly differentiated and, in two combinations, were amalgamated as composite OTUs ('carnA2+carnA4' and 'plagA1+plagA2+plagA3'). Therefore, analysis of the morphological data set resulted in recognition of 25 Australian morphological OTUs. Composition of these OTUs in relation to morphogroups (Fig. 12) is: Group 1 = carnA1, 'carnA2+carnA4', carnA3, carnA5 carnB, carnC and carnD; Group 2 = 'plagA1+plagA2+plagA3', plagA4, plagA5 and plagB; Group 3 = megaA1, megaA2, megaA3, megaA4, megaA5 and megaB; Group 4 = fuhn, horn, litor and oxley; Group 5 = virgA1, virgA2, virgA3 and virgB.

Morphological identification of south-west Indian Ocean taxa. Four separate DFAs were ultimately undertaken to determine the status of 104 individuals allocated to 13 south-west Indian Ocean taxa (*C. africanus; C. ahli; C. aldabrae; C. ater; C. bitaeniatus; C. boutoni; C. caudatus; C. cognatus; C. gloriosus; C. mayottensis; C. mohelicus; C. quinquetaeniatus* and *C. voeltzkowi*).

DFA 10 investigated all 13 taxa and identified four clusters (Fig. 21), with cluster N distinguished by the second

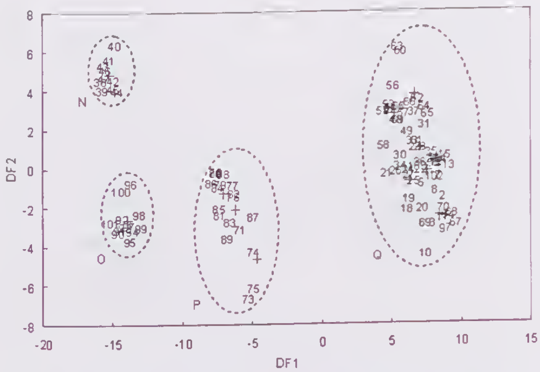

Fig. 21. DFA 10, scatterplot of 104 *Cryptoblepharus* specimens from the south-west Indian Ocean region (Wilks' *lambda* = 0.001). Legend for clusters: N = *C. bitaeniatus*; O = *C. quinquetaeniatus*; P = *C. gloriosus*, *C. mayottensis* and *C. mohelicus*; Q = *C. africanus*, *C. ahli*, *C. aldabrae*, *C. ater*, *C. boutonii*, *C. caudatus*, *C. cognatus* and *C. voeltzkowi*.

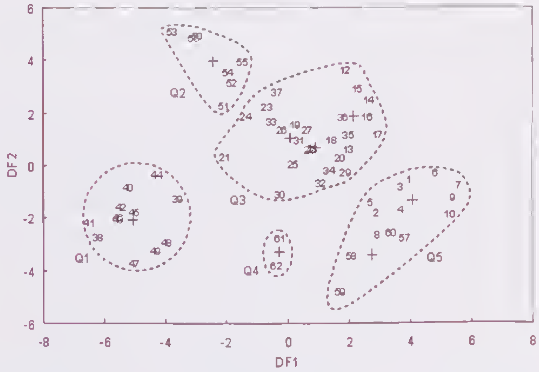

Fig. 23. DFA 12, scatterplot of 62 *Cryptoblepharus* specimens (ex cluster Q, Fig. 21) (Wilks' *lambda* = 0.001). Legend for clusters: Q1 = *C. boutonii*; Q2 = *C. caudatus*; Q3 = *C. ahli*, *C. aldabrae* and *C. ater*; Q4 = *C. voeltzkowi*; Q5 = *C. africanus* and *C. cognatus*.

discriminant function and clusters O, P and Q by the first discriminant function (Appendix 1). Clusters N and O were entirely composed of individuals allocated to discrete taxa (N = *C. bitaeniatus*; O = *C. quinquetaeniatus*) and were recognised as morphologically defined. Clusters P and Q comprised individuals of three or more taxa (P = *C. gloriosus, C. mayottensis, C. mohelicus*: Q = *C. africanus; C. ahli; C. aldabrae; C. ater; C. boutonii; C. caudatus; C. cognatus* and *C. voeltzkowi*)) and were subjected to further DFA.

DFA 11 investigated 19 cluster P individuals and identified three clusters (Fig. 22). Clusters P1 and P3 were distinguished by the first discriminant function and cluster P2 by the second discriminant function (Appendix 1). Each cluster was entirely composed of individuals allocated to discrete taxa (P1 = *C. gloriosus*, P2 = *C. mohelicus*, P3 = *C. mayottensis*) and these were recognised morphologically defined (Appendix 2).

DFA 12 investigated 62 cluster Q individuals and identified five clusters (Fig. 23). Cluster Q1 was distinguished from Q4 by the first discriminant function, Q2 from Q1 and Q4 by the second discriminant function and Q3 and Q5 by both discriminant functions (Appendix 1). Three clusters were entirely composed of individuals allocated to discrete taxa (Q1 = *C. boutonii*, Q2 = *C. caudatus*, Q4 = *C. voeltzkowi*) and were recognised as morphologically defined. Clusters Q3 and Q5 comprised individuals of two (Q5) and three (Q3) taxa and were subjected to further analysis, Q3 by DFA and Q5 by ANOVA.

DFA 13 investigated 27 individuals allocated to cluster Q3 and identified three clusters (Fig. 24). Cluster Q6 was distinguished by the first discriminant function and clusters Q7 and Q8 by the second discriminant function (Appendix 1). Each cluster was entirely composed of individuals allocated to discrete taxa (Q6 = *C. aldabrae*, Q7 = *C. ater*, Q8 = *C. ahli*) and were recognised as morphologically defined taxa. Pairwise comparisons between *C. africanus* and *C. cognatus* (cluster Q5) identified six differences (tail length, head depth, paravertebral scale width, finger and toe subdigital lamellae, toe supradigital scales) (Appendix 2) and these were recognised as morphologically defined taxa.

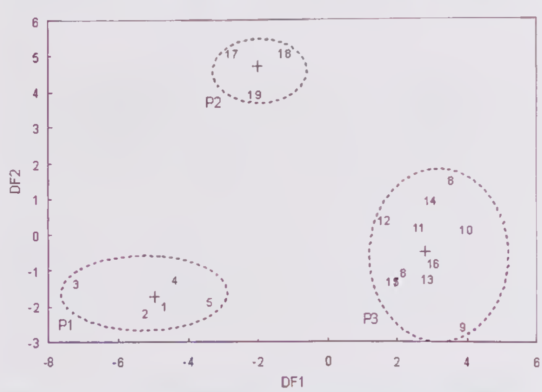

Fig. 22. DFA 11, scatterplot of 19 *Cryptoblepharus* specimens (ex cluster P, Fig. 21) (Wilks' lambda = 0.010). Legend for clusters: P1 = C. *gloriosus*; P2 = C. *mohelicus*; P3 = C. *mayottensis*.

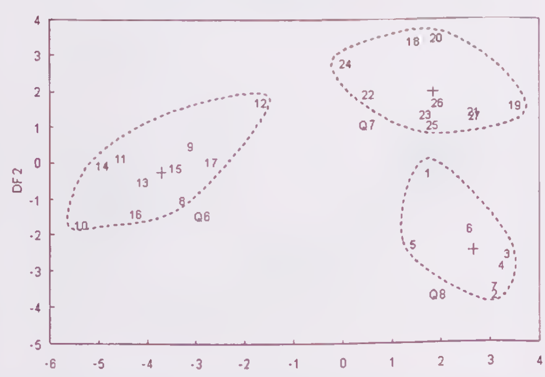

Fig. 24. DFA 13, scatterplot of 27 *Cryptoblepharus* specimens (ex cluster Q3, Fig. 23) (Wilks' lambda = 0.022). Legend for clusters: Q6 = C. *aldabrae*; Q7 = C. *ater*; Q8 = C. *ahli*.

In summary, all 13 *Cryptoblepharus* taxa from the south-west Indian Ocean region were recognised, each being distinguished by two or more significant morphological differences.

Morphological identification of Indo-Pacific taxa. Nineteen described taxa are identified from this region: *C. aruensis*; *C. baliensis*; *C. burdeni*; *C. cursor*; *C. egeriae*; *C. eximius*; *C. intermedius*; *C. keiensis*; *C. leschenault*; *C. nigropunctatus*; *C. novaeguineae*; *C. novocaledonicus*; *C. novohebridicus*; *C. pallidus*; *C. poecilopleurus*; *C. renschi*; *C. rutilus*; *C. schlegelianus*, and *C. sumbawanus*. Although treated here as provisionally distinct, some of these names are not formally recognised. Mertens (1964) synonymised *C. intermedius* with *C. keiensis*, and *C. aruensis* with *C. novaeguineae*. Further, examination of type material of *Ablepharus boutoni furcata* Weber, 1890, synonymised with *C. leschenault* (Mertens, 1931), and *C. poecilopleurus paschalis* Garman, 1908, synonymised with *C. poecilopleurus* (Mertens, 1931), indicated that Mertens's treatment of *A. b. furcata* as a synonym of *C. leschenault* was correct but *C. p. paschalis* was perceived to diverge slightly from *C. poecilopleurus* and was included in the analysis. Added to the above complement were two Australian taxa that have been recorded as occurring on or near Papua New Guinea (OTU virgA2: Torres Strait, cited in Wilson and Knowles (1988) and Wilson and Swan (2003) as *C. virgatus;* and OTU litor: Torres Strait and New Guinea, cited in Covacevich and Ingram (1978) and Cogger (2000) as *C. litoralis*) and an additional four presumptive forms recognised by preliminary morphological examination (OTU Nor from Normanby Island, Milne Bay region, New Guinea; OTU Sam from Samalona Island, South Sulawesi; and OTUs Mis and TransF from Misima Island and the Trans-Fly region, New Guinea). New Guinea forms that represented Australian OTUs virgA2 and litor were re-designated OTUs virgA2PNG and litorPNG.

Three taxa (*C. intermedius*, *C. nigropunctatus* and *C. pallidus*) had sample sizes of two and a further three taxa (*C. cursor*, *C. schlegelianus* and *C. rutilus*) were represented only by single individuals. The latter three were included in the initial Indo-Pacific DFA, but differentiation was later assessed on perceived morphological differences.

Four separate DFAs were ultimately undertaken to determine the status of the 186 individuals allocated to 26 Indo-Pacific taxa (*C. aruensis*; *C. baliensis*; *C. burdeni*; *C. cursor*; *C. egeriae*; *C. eximius*; *C. intermedius*; *C. keiensis*; *C. leschenault*; *C. nigropunctatus*; *C. novaeguineae*; *C. novocaledonicus*; *C. novohebridicus*; *C. pallidus*; *C. p. paschalis*, *C. p. poecilopleurus*; *C. renschi*; *C. rutilus*; *C. schlegelianus*, *C. sumbawanus* and OTUs litorPNG, Mis, Nor, Sam, TransF and virgA2PNG)

DFA 14 investigated all 26 taxa and identified ten clusters (Fig. 25). three clusters were entirely composed of individuals allocated to discrete taxa (V = *C. schlegelianus*; X = *C. nigropunctatus*; AA = *C. burdeni*) and seven clusters

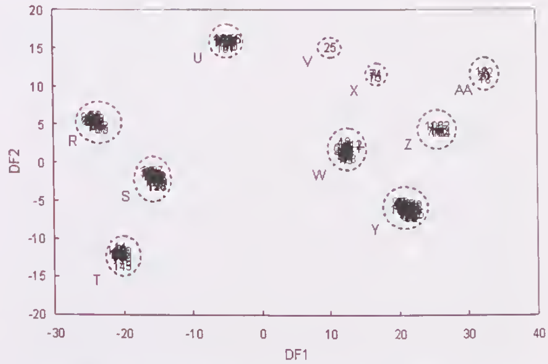

Fig. 25. DFA 14, scatterplot of 186 *Cryptoblepharus* specimens from the Indo-Pacific region (Wilks' *lambda* = 0.001). Legend for clusters: R = OTUs Nor and litorPNG; S = *C. baliensis* and *C. sumbawanus;* T = *C. egeriae, C. paschalis* and *C. poecilopleurus;* U = OTU Mis; V = *C. schlegelianus;* W = *C. aruensis, C. cursor, C. eximius, C. intermedius, C. novaeguineae, C. pallidus;* X = *C. nigropunctatus;* Y = *C. keiensis, C. leschenault, C. novohebridicus, C. renschi*, OTUs Sam and virgA2PNG; Z = *C. novocaledonicus* and *C. rutilus;* AA = *C. burdeni.*

comprised individuals of two or more taxa (R = OTUs Nor and litorPNG; S = *C. baliensis* and *C. sumbawanus*; T = *C. egeriae, C. paschalis* and *C. poecilopleurus*; U = OTUs Mis and TransF; W = *C. aruensis, C. cursor, C. eximius, C. intermedius, C. novaeguineae* and *C. pallidus*; Y = *C. keiensis, C. leschenault, C. novohebridicus, C. renschi*, OTUs Sam and virgA2PNG; Z = *C. novocaledonicus* and *C. rutilus*).

Clusters V, X and AA were distinguished from other clusters by the second discriminant function and from each other by the first discriminant function (Fig. 25), hence *Cryptoblepharus burdeni*, *C. nigropunctatus* and *C. schlegelianus* were recognised as morphologically defined. The remaining clusters (R, S, T, U, W, Y and Z) were distinguished in the ordination space by combinations of both discriminant functions and were further investigated by DFA (clusters T, W and Y) or pairwise comparisons (clusters R, S, U and Z).

DFA 15 investigated 34 individuals allocated to cluster T and identified three clusters (Fig. 26) each being composed of individuals allocated to discrete taxa (T1 = *C. egeriae*, T2 = *C. paschalis*, T3 = *C. poecilopleurus*). Cluster T1 was distinguished by the first discriminant function and *C. egeriae* was recognised as a morphologically defined. Clusters T2 and T3 overlapped in the ordination space, being only partly distinguished by the second discriminant function (Appendix 1) and differentiation was further investigated by pairwise comparisons which identified two significant differences, numbers of paravertebral and plantar scales (Appendix 2). *Cryptoblepharus egeriae, C. paschalis* and *C. poecilopleurus* were recognised as morphologically defined.

DFA 16 investigated 26 individuals allocated to cluster W and identified four clusters (Fig. 27). Clusters W1, W2 and W3 were entirely composed of individuals allocated

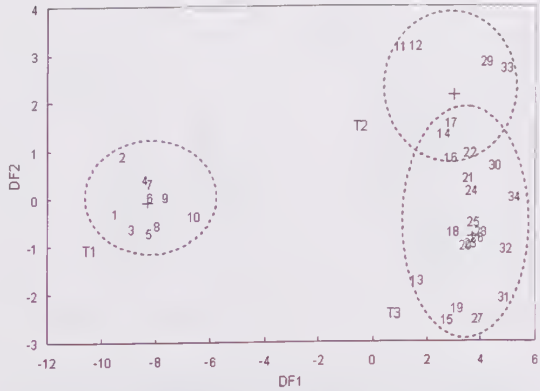

Fig. 26. DFA 15, scatterplot of 34 *Cryptoblepharus* specimens (ex cluster T, Fig. 25) (Wilks' *lambda* = 0.012). Legend for clusters: T1 = *C. egeriae*; T2 = *C. paschalis;* T3 = *C. poecilopleurus.*

to discrete taxa (W1 = *C. cursor*, W2 = *C. eximius*, W3 = *C. intermedius*) and were recognised as morphologically defined. Cluster W4 comprised representatives of three taxa (*C. aruensis, C. novaeguineae* and *C. pallidus*). Clusters W1 and W2 were distinguished from W3 and W4 by the first discriminant function, while the second discriminant function distinguished W1 from W2 and W3 from W4.). Differentiation between taxa in cluster W4 was further investigated by ANOVA. Although represented by small sample sizes, no significant differences were identified between the available specimens of *C. novaeguineae* and *C. pallidus* (including holotypes). Mertens (1928) differentiated these taxa by divergence in the condition of pale laterodorsal stripes. However, as colour and pattern are poor defining characters (pale specimens with obscure patterns occur in some well-patterned north Australian taxa, pers. obs.) these taxa are determined as synonymous. Comparison of *C. novaeguinea+C. pallidus* to *C. aruensis* revealed only minor differentiation in limb length and number of fourth finger subdigital lamellae (Appendix 2). As morphological differentiation between these taxa was very low they were all considered synonymous, in concordance with Mertens's (1964) placement of *C. aruensis* in the synonymy of *C. novaeguineae.*

DFA 17 investigated 40 individuals allocated to cluster Y and identified four clusters (Fig. 28). Clusters Y1, Y3 and Y4 were entirely composed of individuals allocated to discrete taxa (Y1 = *C. keiensis*, Y3 = *C. novohebridicus*, Y4 = OTU Sam) and were recognised as morphologically defined. Cluster Y2 comprised representatives of three taxa (*C. leschenault, C. renschi* and OTU virgA2PNG). Clusters Y1 and Y2 were distinguished from Y3 and Y4 by the first discriminant function, while the second discriminant function distinguished Y1 from Y2 and Y3 from Y4.). Differentiation between taxa in cluster Y2 (Fig. 28) was further investigated by pairwise comparisons. OTU virgA2PNG, *C. leschenault* and *C. renschi* are all boldly striped taxa, but were differentiated by body pattern details. *Cryptoblepharus leschenault* and *C. renschi* are simply patterned with five or six pale stripes on blackish ground colour, with *C. renschi* being patterned with five pale (vertebral, laterodorsals and mid-laterals) and six dark stripes (dorsolaterals, upper laterals and lower laterals), while *C. leschenault* is patterned with six, narrow pale stripes (paravertebrals, laterodorsals and mid-laterals) and seven, broader dark stripes (vertebral, dorsolaterals, upper laterals and lower laterals) with the pale paravertebral stripes mergeing into a broader pale vertebral stripe above the forelimb. *Cryptoblepharus renschi* further differed from *C. leschenault* in midbody scale rows, fourth toe supradigital scales and paravertebral scale width (Appendix 2). OTU virgA2PNG's dorsal pattern consists of a broad vertebral zone of brown ground colour bordered by dark dorsolateral and pale laterodorsal stripes. OTU virgA2PNG is further distinguished from both *C. leschenault* and *C. renschi* by having shorter limbs, shorter forebody and a shorter, narrower head (Appendix 2). Additionally, OTU virgA2PNG differs from *C. leschenault* by fewer midbody scale rows and from *C. renschi* by more fourth finger supradigital scales (Appendix 2). *Cryptoblepharus*

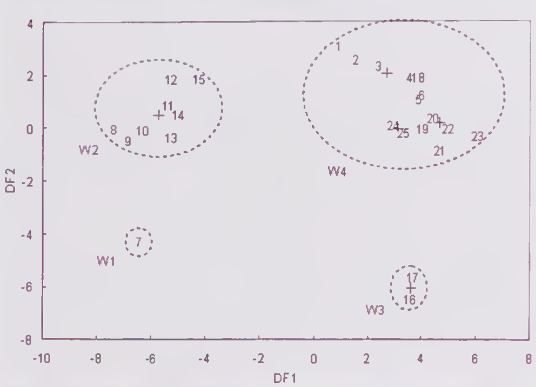

Fig. 27. DFA 16, scatterplot of 26 *Cryptoblepharus* specimens (ex cluster W, Fig. 25) (Wilks' *lambda* = 0.001). Legend for clusters: W1 = *C. cursor;* W2 = *C. eximius;* W3 = *C. intermedius;* W4 = *C. aruensis, C. novaeguineae* and *C. pallidus.*

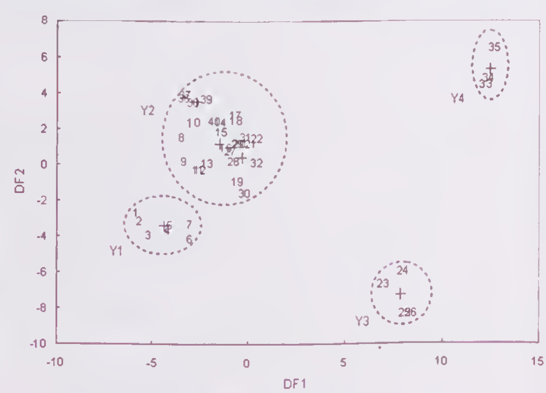

Fig. 28. DFA 17, scatterplot of 40 *Cryptoblepharus* specimens (ex cluster Y, Fig. 25) (Wilks' *lambda* = 0.001). Legend for clusters: Y1 = *C. keiensis;* Y2 = *C. leschenault, C. renschi* and OTU virgA2PNG; Y3 = *C. novohebridicus;* Y4 = OTU Sam.

leschenault, C. renschi and OTU virgA2PNG were recognised as morphologically defined.

Differentiation between taxa in clusters R, S and U (Fig. 25) was investigated by pairwise comparisons. OTUs litorPNG and Nor (cluster R) were differentiated by five significant characters (Appendix 2) (head proportions, numbers of paravertebral scales, fourth toe subdigital lamellae and plantar scales) and were recognised as morphologically defined.

Cryptoblepharus baliensis and *C. sumbawanus* (cluster S) were differentiated by three significant characters (Appendix 2) (forelimb and hindlimb lengths, number of nuchal scales). Closely allied, *C. baliensis* and *C. sumbawanus* have similar body patterns and adjoining distributions (Bali and Lombok versus Sumbawa), but on grounds of slight morphological differentiation were recognised as morphologically defined taxa.

OTUs Mis and TransF (Cluster U) were differentiated by 12 significant differences, 75% of which were non-sexually dimorphic (Appendix 2), and were recognized as morphologically defined taxa.

Cryptoblepharus rutilus was allied with *C. novocaledonicus* by DFA (Fig. 25, cluster Z). From examination of the holotype (the only available specimen), *C. rutilus* was the only Indo-Pacific taxon with 20 midbody scale rows and was further differentiated from *C. novocaledonicus* by number of paravertebral scales (47 versus 48–59). *Cryptoblepharus novocaledonicus* and *C. rutilus* were recognised as morphologically defined taxa. Similarly, the holotype of *C. schlegelianus* (the only available specimen) was clearly distinguished from Indo-Pacific congeners by DFA (Fig. 25, cluster V) and was recognised as a morphologically defined taxon.

In summary, 24 of the 26 *Cryptoblepharus* taxa from the Indo-Pacific region were recognised (*C. aruensis* and *C. pallidus* were considered synonymous with *C. novaeguineae*), each being distinguished by two or more significant morphological differences.

TAXONOMIC STATUS OF *CRYPTOBLEPHARUS* TAXA

Australian OTUs. A total of 29 Australian OTUs were identified by independent analyses of allozyme and morphological data sets. Thirteen (carnA1, carnA3, carnB, carnC, fuhn, megaA1, megaA2, megaA3, megaA5, megaB, plagA4. plagB and virgA2) were congruently identified by both data sets, each being distinguished by unique combinations of significant allozyme and morphological characters. Under the biological species criterion, these 13 taxa were assigned to the 'species' level of the taxonomic hierarchy.

Sixteen OTUs were not congruently identified by both data sets, one of which, OTU virgA1x3, was of hybrid origin and was omitted from morphological analyses. The remaining 15 OTUs (carnA2, carnA4, carnA5, carnD, horn, litor, oxley, megaA4, plagA1, plagA2, plagA3, plagA5, virgA1, virgA3 and virgB) were taxonomically assessed as follows:

OTUs carnA2 and carnA4. Morphological analysis identified only one significant difference between these two taxa, a minor variation in degree of acuity of plantar scales ($p = 0.040^{*}$). Differentiated by four fixed allelic differences (9% FDs, Horner and Adams 2007), these two taxa are independent lineages and likely biological species. However, they are virtually indistinguishable morphologically or by ecological preferences and have adjoining distributions in the Northern Kimberley (NK) bioregion of WA. Due to morphological conservatism, OTUs carnA2 and carnA4 cannot be recognised as discrete species for practical purposes and are herein treated as a composite taxon (OTU 'carnA2+carnA4') that is acknowledged as comprising two morphologically indeterminate species.

OTUs carnA5 and virgA3. These taxa have previously been recognised as separate species (Cogger *et al.* 1983a; Wilson and Knowles 1988; Ehmann 1992; Cogger 2000; Wilson and Swan 2003) (as *C. carnabyi* and *C. virgatus*). They have similar allozyme profiles (Horner and Adams 2007), but differ morphologically by distinctive plantar scale conditions (acute versus ovate) and four other significant morphological variables (Appendix 2; Fig. 12, groups 1 versus 5). Both OTUs have been recorded from Hillgrove Station in Queensland and, on grounds of significant morphological differentiation in sympatry indicating reproductive isolation, they are considered discrete biological species.

OTUs horn and litor. These OTUs display similarities in allozyme profiles and ecological preferences, but have five significant morphological differences (number of palmar, plantar and fourth finger supradigital scales, loreal scale dimensions and paravertebral scale width) (Appendix 2). They have disjunct distributions (Arnhem Land coast versus north-east Queensland coast) but as the allozyme data cannot rule out gene flow, litor and horn are not independent lineages. Additionally, the disjunct population of OTU litorPNG from Port Moresby, New Guinea was determined to differ from Australian litor and horn by two morphological variables (mean paravertebral scales: 50.8 versus 54.5 and 56.6, and plantar scales: 15.5 versus 10.9 and 11.8). Showing obvious morphological and ecological relationships, OTUs litor, litorPNG and horn exhibit morphological differentiation, have allopatric distributions and herein are considered incipient biological species and recognized as subspecific components of a polytypic taxon.

OTU oxley. Identification of this OTU was based on morphological analysis of 13 representative specimens. Clearly distinguished by DFA (Fig. 18, cluster J), OTU oxley is a distinctive taxon differing from congeners by possessing unique postnasal scales and plantar scale morphology. On grounds of a unique combination of significant morphological characters, OTU oxley was considered a distinct biological species.

OTUs plagA2 and megaA4. That *Cryptoblepharus* species boundaries are problematical is highlighted by the obvious morphological and ecological differentiation between allozymic sister-OTUs plagA2 and megaA4 (Fig. 12, groups 2 versus 3). Supported by sympatric distributions on the Mitchell Plateau WA, the morphological divergence is sufficient to have warranted long recognition as separate species (Storr 1976; Storr *et al.* 1981; Cogger *et al.* 1983a; Wilson and Knowles 1988; Horner 1991; Ehmann 1992; Cogger 2000; Wilson and Swan 2003) (as *C. plagiocephalus* and *C. megastictus*). Although having similar allozyme profiles (Horner and Adams 2007), each OTU has unique combinations of significant morphological and ecological (saxicoline versus arboreal) differences and on grounds of significant morphological differentiation in sympatry indicating reproductive isolation, each was considered a discrete biological species. OTU plagA2 is further considered below.

OTUs plagA1, plagA2 and plagA3. These OTUs (along with congruently identified plagA4) were considered a recently speciated complex in which some members had not yet differentiated morphologically. Allozyme data indicates they (and OTU megaA4, see above) are closely related (Horner and Adams 2007) although each are differentiated by two fixed allelic differences. Analysis of morphological characters identified a single significant difference between plagA2 and plagA3, a minor variation in head width (Appendix 2). Sharing ecological preferences and with adjoining distributions, plagA2 and plagA3 cannot be recognised as discrete species for practical purposes and were treated as a composite taxon (OTU 'plagA2+plagA3'), that is acknowledged as representing a complex of two morphologically indeterminate species.

Fifteen specimens representing the taxon-complex 'plagA2+plagA3' were compared to 21 specimens of OTU plagA1 and only a single significant difference was detected, variation in forelimb length (Appendix 2). These taxa each include the Northern Kimberley (NK) bioregion as all or part of their distributions and have similar ecological preferences. OTUs plagA1 and 'plagA2+plagA3' cannot be recognised as discrete species for practical purposes and were treated as a composite taxon (OTU 'plagA1+plagA2+plagA3'), that is acknowledged as representing a complex of three morphologically indeterminate species.

OTUs plagA5 and carnD. Previously recognized as separate species (Storr 1976; Storr *et al.* 1981; Cogger *et al.* 1983a; Horner 1991; Cogger 2000; Wilson and Swan 2003) (as *C. plagiocephalus* and *C. carnabyi*), these OTUs have similar allozyme profiles (Horner and Adams 2007) but differ morphologically by distinctive plantar scale conditions and a further five significant morphological variables (Appendix 2; Fig. 12, groups 1 versus 2). OTUs plagA5 and carnD are probably sympatric in distribution (both occur in Brigalow Belt North, Brigalow Belt South, Davenport Murchison Ranges, Einasleigh Uplands, Mitchell Grass Downs and Mount Isa Inlier bioregions). Hence, on grounds of significant morphological differentiation in sympatry indicating reproductive isolation, they are considered discrete biological species.

OTUs virgA1 and virgB. These OTUs have similar allozyme profiles (Horner and Adams 2007) and ecological preferences, but differ in several significant morphological characters (numbers of midbody scale rows, finger and toe subdigital lamellae, plantar scales, condition of pale dorsolateral stripes, male virgB are larger than those of virgA1 and female virgB have more paravertebral scales than those of virgA1) (Appendix 2). They have disjunct distributions (southern coastal regions of Western and South Australia versus east coast of Queensland and New South Wales) but, as the allozyme data cannot rule out gene flow, they are not independent lineages. However, on grounds of identifiable morphological differentiation and allopatric distributions these taxa are considered incipient biological species and recognized as subspecific components of a polytypic taxon.

Taxonomic assessment of Australian OTUs determined the region holds 23 taxa, comprising 21 monotypic species (OTUs carnA1, 'carnA2+carnA4', carnA3, carnA5, virgA3, carnB, carnC, fuhn, megaA1, megaA2, megaA3, megaA5, megaB, oxley, 'plagA1+plagA2+plagA3', megaA4, plagA4, plagA5, carnD, plagB and virgA2), and two polytypic species (OTUs 'horn+litor+litorPNG' and 'virgA1+virgB').

This result is an almost fourfold increase over the number of Australian *Cryptoblepharus* species formerly recognised. Recent listings of Australian herpetofauna recognise six species: *C. carnabyi, C. fuhni, C. litoralis, C. megastictus, C. plagiocephalus* and *C. virgatus* (Greer 1989; Horner 1992; Cogger 2000; Wilson and Swan 2003); with a few authors also including *C. egeriae* (from Christmas Island, an Australian Territory in the Indian Ocean) as part of the Australian fauna (Cogger *et al.* 1983b; Ehmann 1992; Stanger *et al.* 1998). These listings are based principally on taxonomic work by Storr (1976), but include Mertens's (1958) description of *C. litoralis* and Covacevich and Ingram's (1978) description of *C. fuhni*. As demonstrated in this study, relatively subtle morphological differences considerably influence species boundaries in *Cryptoblepharus*. A striking example of which is the presence or absence of a single supraciliary scale (five versus six in the series) being a relatively reliable indicator of genetic lineage. The revised taxonomy owes its increased species diversity to a combination of two factors: (1) recognition of populations not previously sampled (OTUs oxley and megaA3), and (2) investigation of populations that have been synonymised with or referred to Storr's (and others) species simply on the basis of agreement with nominal diagnostic characters.

South-west Indian Ocean taxa. Analysis of morphological data recognised 13 *Cryptoblepharus* taxa from the south-west Indian Ocean region, all being distinguished by three or more statistically significant morphological characters. Three taxa (*C. gloriosus, C. mayottensis* and *C. mohelicus*) were treated by Brygoo (1986) as subspecies of a polytypic taxon, a finding supported by DFA (Fig. 21, cluster P). Although showing an obvious morphological relationship, *C. gloriosus*, *C. mayottensis* and *C. mohelicus* each exhibit morphological differentiation (Fig. 22), have allopatric distributions and, following Brygoo (1986), are considered incipient biological species and recognized as subspecific components of a polytypic taxon. The remaining ten taxa were considered sufficiently distinct to be at the species level of the taxonomic hierarchy.

This analysis does not entirely coincide with Brygoo's (1986) results. Support was given for his recognition of *C. bitaeniatus* as a distinct species and for his provisional recognition of *C. africanus, C. aldabrae, C. ater, C. boutoni, C. caudatus, C. cognatus, C. quinquetaeniatus (as C. degrijsi), C. gloriosus and C. voeltzkowi* as distinct species and *C. mayottensis* and *C. mohelicus* as subspecies of *C. gloriosus*. On the basis of significant morphological divergence (identified by DFA; Fig. 23, clusters Q3 versus Q5), Brygoo's (1986) placement of *C. ahli* as a junior synonym of *C. africanus* was not supported.

Indo-Pacific taxa. Analysis of morphological data identified 23 of the 25 *Cryptoblepharus* taxa from the Indo-Pacific region (*C. aruensis* and *C. pallidus* were determined synonymous with *C. novaeguineae*).

Thirteen described taxa (*C. burdeni, C. egeriae, C. eximius, C. intermedius, C. keiensis, C. leschenault, C. novaeguineae, C. nigropunctatus, C. novocaledonicus, C. novohebridicus, C. renschi, C. rutilus and C. schlegelianus*) were clearly differentiated by morphological data and considered sufficiently distinct to be at the species level of the taxonomic hierarchy. The remaining described taxa (*C. baliensis, C. cursor, C. paschalis, C. poecilopleurus* and *C. sumbawanus*) and six undescribed OTUs (litorPNG, Mis, Nor, Sam, TransF and virgA2PNG) were taxonomically assessed as follows:

***Cryptoblepharus baliensis* and *C. sumbawanus*.** Allied by DFA (Fig. 25, cluster S), but differ by three significant characters (fore and hindlimb lengths and number of nuchal scales) (Appendix 2) and disjunct distributions (Bali and Lombok versus Sumbawa). Exhibiting morphological differentiation and having allopatric distributions, they are considered incipient biological species and recognized as subspecific components of a polytypic taxon.

***Cryptoblepharus paschalis* and *C. poecilopleurus*.** Allied by DFA where they overlapped in the ordination space (Fig. 26, clusters T2 and T3), *C. paschalis* and *C. poecilopleurus* differ by two significant characters (numbers of paravertebral and plantar scales) (Appendix 2) and disjunct distributions (Easter Island versus other Pacific islands). Exhibiting morphological differentiation and having allopatric distributions, they are considered incipient biological species and recognized as subspecific components of a polytypic taxon.

OTU litorPNG. This taxon has been assessed above as a subspecific component of the Australian polytypic taxon 'litor+litorPNG+horn'.

OTUs Mis and TransF. These OTUs were represented by 11 (OTU Mis) and five (OTU TransF) specimens, with the two populations separated by approximately 1,300 kilometres. Although allied by DFA (Fig. 25, cluster U), investigation of the two populations revealed 12 significant differences, the majority of which (75%) were non-sexually dimorphic. On grounds of significant morphological differgence indicating reproductive isolation, each population was considered a discrete biological species.

OTU Nor. Similar in appearance and ecological preference to the polytypic taxon OTU 'litor+litorPNG+horn', but morphologically divergent. OTU Nor differs from OTU litorPNG by five significant morphological differences (head depth and width, numbers of paravertebral scales, fourth toe subdigital lamellae and plantar scales (Appendix 2) and from litor and horn by numbers of fourth finger subdigital lamellae, fourth toe subdigital lamellae, fourth toe supradigital scales, palmar and plantar scales (Appendix 2). It further differs from OTU litor in head width and from horn in head depth and number of paravertebral scales (Appendix 2). On grounds of significant morphological divergence being an indicator of reproductive isolation, OTU Nor was considered a distinct biological species.

OTU Sam and *C. cursor*. Although represented by a small sample (n = 3) OTU Sam was clearly associated with and distinguished from *C. keiensis, C. leschenault, C. renschi, C. novohebridicus* and OTU virgA2PNG by DFA (Fig. 25, cluster Y; Fig. 28, cluster Y4). OTU Sam is similar in appearance to the holotype of *C. cursor*, but was differentiated by DFA (Fig. 25, clusters Y versus W). These two taxa differ in number of mid-body scale rows (26 versus 24), however, till further examples of each become available they are considered incipient biological species and recognized as subspecific components of a polytypic taxon.

OTU virgA2PNG. As indicated by its designation, virgA2PNG was initially considered allied with the presumptive Australian taxon OTU virgA. However, ANOVA proved virgA2PNG differed markedly from other OTUs allied with presumptive *C. virgatus* (virgA1, virgA2, virgA3 and virgB). Although sample size was small (n = 5), representatives of OTU virgA2PNG differed from Australian OTUs virgA1, virgA2 and virgA3 by snout-vent length, numbers of paravertebral, finger subdigital lamellae and plantar scales (Appendix 2). OTU virgA2PNG further differed from OTUs virgA1, virgA3 and virg B by head length and numbers of toe subdigital lamellae and palmar scales and from OTU virgA2 by forebody length and midbody scale rows (Appendix 2). Additional divergence to OTU virgA3 was shown in hindlimb length and to OTU virgA1 in number of supraciliary scales. On grounds of significant morphological differgence indicating reproductive isolation, OTU virgA2PNG was considered a discrete biological species.

Taxonomic assessment of Indo-Paciifc taxa determined the region holds 21 species, comprising: 17 monotypic (*C. burdeni, C. egeriae, C. eximius, C. intermedius, C. kei-*

ensis, C. leschenault, C. nigropunctatus, C. novaeguineae, C. novocaledonicus, C. novohebridicus, C. renschi, C. rutilus, C. schlegelianus and OTUs Mis, TransF, virgA2PNG and Nor); three polytypic species (*C. b. baliensis* + *C. b. sumbawanus, C. c. cursor* + OTU Sam, *C. p. poecilopleurus* + *C. p. paschalis*) and a subspecific representative of an Australian OTU (litorPNG). *Cryptoblepharus aruensis* and *C. pallidus* were determined synonymous with *C. novaeguineae*.

Mertens (1931) recognised 19 subspecies of *A. burtonii* from the region: *A. b. aruensis, A. b. baliensis, A. b. burdeni, A. b. cursor, A. b. egeriae, A. b. eximius, A. b. intermedius, A. b. keiensis, A. b. leschenault, A. b. nigropunctatus, A. b. novaeguineae, A. b. novocaledonicus, A. b. novohebridicus, A. b. palliduss, A. b. poecilopleurus, A. b. renschi, A. b. rutilus, A. b. schlegelianus, A. b. sumbawanus*. Later, Mertens (1964) retained his concept of *A. burtonii* as a polytypic taxon but synonymised *A. b. intermedius* with *A. b. keiensis* and *A. b. aruensis* with *A. b. novaeguineae*.

Mertens's taxonomy is not supported by results of this study. His synonymising of *C. aruensis* with *C. novaeguineae* was supported, although *C. pallidus* was also determined to be a synonym of *C. novaeguineae*. Mertens's placements of *C. intermedius* in the synonymy of *C. keiensis* and *C. paschalis* in the synonymy of *C. poecilopleurus* (Mertens 1931) were not supported and *C. baliensis* and *C. sumbawanus* were recognised as subspecies of a polytypic taxon.

Summary of taxonomic assessment of *Cryptoblepharus* taxa. Overall, the taxonomic assessment recognised the generic content of *Cryptoblepharus* as 54 species (48 monotypic, six polytypic), a marked increase over the 39 taxa previously recognised (Mertens 1931, Greer 1989). From a geographical perspective there are 23 species in the Australian region (21 monotypic and two polytypic), 11 species in the south-west Indian Ocean region (10 monotypic and one polytypic) and 21 species in the Indo-Pacific region (17 monotypic species, three polytypic species and a subspecifc representative of an Australian taxon).

Nomenclature of *Cryptoblepharus* taxa. Consideration of *Cryptoblepharus* nomenclature involved placements of existing names, recognition of names previously synonymised, placement of names into synonymy and construction of new binomial/trinomial combinations. Application of previously published binomials/trinomials to a particular taxon was determined by comparison of morphological attributes of type specimens.

Australian OTUs. Twenty-five taxa were recognised from the Australian region, comprising 21 monotypic species and two polytypic species each with two regional subspecies (one with an additional extralimital subspecies). Valid, published scientific names were determined to apply to 12 of these and 13 were deemed new to science. Scientific names applicable to Australian OTUs were:

OTU carnA1 = *C. plagiocephalus* (Cocteau, 1836); OTU carnD = *C. australis* (Sternfeld, 1918) (herein raised from synonymy of *C. plagiocephalus*, see Mertens (1964)); OTU fuhn = *C. fuhni* Covacevich and Ingram, 1978; OTU litor = *C. litoralis litoralis* (Mertens, 1958); OTU horn = *C. litoralis horneri* Wells and Wellington, 1985 (herein raised from synonymy of *C. litoralis*, see Horner (1999)); OTU megaA4 = *C. megastictus* Storr, 1976; OTU 'plagA1+plagA3+plagA2' = *C. ruber* Börner and Schüttler, 1981 (herein raised from synonymy of *C. plagiocephalus*, see Cogger *et al.* (1983a)); OTU plagA4 = *C. buchananii* (Gray, 1838) (herein raised from synonymy of *C. plagiocephalus*, see Storr, (1976)); OTU plagA5 = *C. metallicus* (Boulenger, 1887) (herein raised from synonymy of *C. plagiocephalus*, see Storr (1976)); OTU virgA1 = *C. pulcher pulcher* (Sternfeld, 1918) (herein raised from synonymy of *C. virgatus*, see Mertens (1931)); OTU virgB = *C. pulcher clarus* (Storr, 1961); OTU virgA2 = *C. virgatus* (Garman, 1901)

Name combinations coined for taxa deemed new to science were (etymology is provided in species descriptions): OTU carnA3 = *C. ochrus* sp. nov.; OTU 'carnA2+carnA4' = *C. tytthos* sp. nov.; OTU carnA5 = *C. pannosus* sp. nov.; OTU carnB = *C. exochus* sp. nov.; OTU carnC = *C. mertensi* sp. nov.; OTU megaA1 = *C. daedalos* sp. nov.; OTU megaA2 = *C. juno* sp. nov.; OTU megaA3 = *C. wulbu* sp. nov.; OTU megaA5 = *C. zoticus* sp. nov.; OTU megaB = *C. ustulatus* sp. nov.; OTU oxley = *C. gurrmul* sp. nov.; OTU plagB = *C. cygnatus* sp. nov.; OTU virgA3 = *C. adamsi* sp. nov.

The proposed nomenclature for Australian *Cryptoblepharus* species and subspecies is summarised in Table 3, which also gives OTU designations, genetic lineage and offers vernacular names for each taxon.

South-west Indian Ocean taxa. Nomenclatural changes to specific epithets of south-west Indian Ocean taxa consist of treating *C. boutoni degrijsi* as a synonym of *C. quinquetaeniatus* and resurrecting *C. ahli* from the synonymy of *C. africanus* (see Brygoo 1986).

Binomials/trinomials applicable to the 13 taxa from the south-west Indian Ocean region were: *C. africanus* (Sternfeld, 1918); *C. ahli* Mertens, 1928a; *C. aldabrae* (Sternfeld, 1918); *C. ater* (Boettger, 1913); *C. bitaeniatus* (Boettger, 1913); *C. boutoni* (Desjardin, 1831); *C. caudatus* (Sternfeld, 1918); *C. cognatus* (Boettger, 1881); *C. gloriosus gloriosus* (Stejneger, 1893); *C. gloriosus mayottensis* Mertens, 1928a; *C. gloriosus mohelicus* Mertens, 1928a; *C. quinquetaeniatus* (Günther, 1874); *C. voeltzkowi* (Sternfeld, 1918).

Indo-Pacific taxa. Twenty-four taxa were recognised from the Indo-Pacific region, comprising 17 monotypic species, three polytypic species (each with two subspecies) and a subspecifc representative of an Australian taxon. Valid, published scientific names were determined to apply to 18 taxa, and six were deemed new to science (Table 4).

Scientific names applicable to described monotypic species were: *C. burdeni* Dunn, 1927; *C. egeriae* (Boulenger, 1889); *C. eximius* Girard, 1857; *C. intermedius* (de Jong, 1926); *C. keiensis* (Roux, 1910); *C. leschenault* (Cocteau, 1832); *C. nigropunctatus* (Hallowell, 1860); *C. novaeguineae* Mertens, 1928a; *C. novocaledonicus* Mertens, 1928a; *C. novohebridicus* Mertens, 1928a; *C. renschi* Mertens,

Table 3. Australian *Cryptoblepharus* taxa, giving OTU designations, genetic lineage and proposed scientific and common names.

OTU	Lineage	Proposed scientific nomenclature	Proposed common name
virgA3	2	*C. adamsi* sp. nov.	Adams' snake-eyed skink
carnD	1	*C. australis* (Sternfeld, 1918)	Inland snake-eyed skink
plagA4	1	*C. buchananii* (Gray, 1838)	Buchanan's snake-eyed skink
plagB	1	*C. cygnatus* sp. nov.	Swanson's snake-eyed skink
megaA1	1	*C. daedalos* sp. nov.	Dappled snake-eyed skink
carnB	2	*C. exochus* sp. nov.	Noble snake-eyed skink
fuhni	2	*C. fuhni* Covacevich and Ingram, 1978	Fuhn's snake-eyed skink
oxley	2	*C. gurrmul* sp. nov.	Arafura snake-eyed skink
megaA2	1	*C. juno* sp. nov.	Juno's snake-eyed skink
horn	2	*C. litoralis horneri* Wells and Wellington, 1985	Horner's snake-eyed skink
litor	2	*C. litoralis litoralis* (Mertens, 1958)	Coastal snake-eyed skink
megaA4	1	*C. megastictus* Storr, 1976	Blotched snake-eyed skink
carnC	2	*C. mertensi* sp. nov.	Mertens' snake-eyed skink
plagA5	1	*C. metallicus* (Boulenger, 1887)	Metallic snake-eyed skink
carnA3	2	*C. ochrus* sp. nov.	Pale snake-eyed skink
carnA5	2	*C. pannosus* sp. nov.	Ragged snake-eyed skink
carnA1	2	*C. plagiocephalus* (Cocteau, 1836)	Péron's snake-eyed skink
virgB	2	*C. pulcher clarus* (Storr, 1961)	Bright snake-eyed skink
virgA1	2	*C. pulcher pulcher* (Sternfeld, 1918)	Elegant snake-eyed skink
plagA1+plagA2+plagA3	1	*C. ruber* Börner and Schüttler, 1981	Tawny snake-eyed skink
carnA2+carnA4	2	*C. tytthos* sp. nov.	Pygmy snake-eyed skink
megaB	2	*C. ustulatus* sp. nov.	Russet snake-eyed skink
virgA2	2	*C. virgatus* (Garman, 1901)	Striped snake-eyed skink
megaA3	1	*C. wulbu* sp. nov.	Spangled snake-eyed skink
megaA5	2	*C. zoticus* sp. nov.	Agile snake-eyed skink

Table 4. List of *Cryptoblepharus* taxa extralimital to Australia, giving proposed and original scientific nomenclature.

Proposed scientific nomenclature	Original combination (or designated OTU)
South-west Indian Ocean region	
C. africanus (Sternfeld, 1918)	*Ablepharus boutoni africanus* Sternfeld, 1918
C. ahli Mertens, 1928	*Cryptoblepharus boutonii ahli* Mertens, 1928
C. aldabrae (Sternfeld, 1918)	*Ablepharus boutoni aldabrae* Sternfeld, 1918
C. ater (Boettger, 1913)	*Ablepharus boutoni atra* Boettger, 1913
C. bitaeniatus (Boettger, 1913)	*Ablepharus boutoni bitaeniata* Boettger, 1913
C. boutonii (Desjardin, 1831)	*Scincus boutonii* Desjardin, 1831
C. caudatus (Sternfeld, 1918)	*Ablepharus boutoni caudatus* Sternfeld, 1918
C. cognatus (Boettger, 1881)	*Ablepharus boutoni cognatus* Boettger, 1881
C. gloriosus gloriosus (Stejneger, 1893)	*Ablepharus gloriosus* Stejneger, 1893
C. gloriosus mayottensis Mertens, 1928	*Cryptoblepharus boutonii mayottensis* Mertens, 1928
C. gloriosus mohelicus Mertens, 1928	*Cryptoblepharus boutonii mohelicus* Mertens, 1928
C. quinquetaeniatus (Günther, 1874)	*Ablepharus quinquetaeniatus* Günther, 1874
C. voeltzkowi (Sternfeld, 1918)	*Ablepharus boutoni voeltzkowi* Sternfeld, 1918
Indo-Pacific region	
C. baliensis baliensis Barbour, 1911	*Cryptoblepharus boutonii baliensis* Barbour, 1911
C. baliensis sumbawanus Mertens, 1928	*Cryptoblepharus boutonii sumbawanus* Mertens, 1928
C. burdeni Dunn, 1927	*Cryptoblepharus boutonii burdeni* Dunn, 1927
C. cursor cursor Barbour, 1911	*Cryptoblepharus boutonii cursor* Barbour, 1911
C. cursor larsonae sp. nov.	OTU Sam
C. egeriae (Boulenger, 1889)	*Ablepharus egeriae* Boulenger, 1889
C. eximius Girard, 1857	*Cryptoblepharus eximius* Girard, 1857
C. furvus sp. nov.	OTU Nor
C. intermedius (de Jong, 1926)	*Ablepharus boutoni intermedius* de Jong, 1926
C. keiensis (Roux, 1910)	*Ablepharus boutoni keiensis* Roux, 1910
C. leschenault (Cocteau, 1832)	*Ablepharis leschenault* Cocteau, 1832
C. litoralis vicinus ssp. nov.	OTU litorPNG
C. nigropunctatus (Hallowell, 1860)	*Ablepharus nigropunctatus* Hallowell, 1860
C. novaeguineae Mertens, 1928	*Cryptoblepharus boutonii novaeguineae* Mertens. 1928
C. novocaledonicus Mertens, 1928	*Cryptoblepharus boutonii novocaledonicus* Mertens, 1928
C. novohebridicus Mertens, 1928	*Cryptoblepharus boutonii novohebridicus* Mertens, 1928
C. poecilopleurus paschalis Garman, 1908	*Cryptoblepharus poecilopleurus paschalis* Garman, 1908
C. poecilopleurus poecilopleurus (Wiegmann, 1834)	*Ablepharus poecilopleurus* Wiegmann, 1834
C. renschi Mertens, 1928	*Cryptoblepharus boutonii renschi* Mertens, 1928
C. richardsi sp. nov.	OTU Mis1
C. rutilus (Peters, 1879)	*Ablepharus rutilus* Peters, 1879
C. schlegelianus Mertens, 1928	*Cryptoblepharus boutonii schlegelianus* Mertens, 1928
C. xenikos sp. nov.	OTU Mis2
C. yulensis sp. nov.	OTU virgA2PNG

1928b; *C. rutilus* (Peters, 1879); *C. schlegelianus* Mertens, 1928a.

Name combinations coined for taxa deemed new to science were (etymology is provided in species descriptions): OTU litorPNG = *C. litoralis vicinus* ssp. nov.; OTU Mis = *C. richardsi* sp. nov.; OTU Nor = *C. furvus* sp. nov.; OTU Sam = *C. cursor larsonae* ssp. nov. OTU TransF = *C. xenikos* sp. nov.; and OTU virgA2PNG = *C. yulensis* sp. nov.

By 'Principle of Priority' (International Commission on Zoological Nomenclature 1999) the polytypic species were named: *C. baliensis* Barbour, 1911 (comprising *C. baliensis baliensis* Barbour, 1911 and *C. baliensis sumbawanus* Mertens, 1928a); *C. cursor* Barbour, 1911 (comprising *C. cursor* Barbour, 1911 and *C. cursor larsonae* ssp. nov.); *C. poecilopleurus* (Wiegmann, 1834) (comprising *C. poecilopleurus paschalis* Garman, 1908 and *C. poecilopleurus poecilopleurus* (Wiegmann, 1834)

Proposed taxonomy and nomenclature for *Cryptoblepharus* taxa extralimital to Australia are summarised in Table 4, which also gives original combinations of scientific names.

SYSTEMATICS

Cryptoblepharus Wiegmann, 1834

Cryptoblepharus Wiegmann, 1834: 12 (type species: *Ablepharus poecilopleurus* Wiegmann, 1834, by subsequent designation, see Stejneger, 1899).

Cryptoblepharis Cocteau, 1836: 8, emendation *pro*.

Petia Gray, 1839: 335, *nomen nudum*, manuscript name introduced in synonymy of *Cryptoblepharus* Wiegmann, 1834. Never validly introduced.

Diagnosis. Member of the *Eugongylus* subgroup of the *Eugongylus* group of lygosomine skinks (Greer 1979). Eye covered by immovable, transparent disc, bordered by small, granular scales and usually three enlarged upper ciliary scales. Frontoparietal and interparietal shields normally fused, forming a large, roughly diamond shaped shield. Frontal short, about as long as wide. Limbs well developed, pentadactyl with long, subcylindrical digits.

Description. In general, small (maximum snout-vent lengths between 35 and 51 mm), pentadactyl, arboreal or saxicoline skinks.

Cryptoblepharus lack movable eyelids, the eye being covered by a transparent disc bordered on sides and below by small, oblong granules and above usually by three enlarged upper ciliary scales. External ear opening small, vertically suboval, without lobules. Rostral wider than high. Nasal entire, nostril central with post- or subnasal groove variably present, nasals usually separated by frontonasal. Supranasals usually absent. Frontonasal slightly wider than long, usually in contact with rostral. Prefrontals large, usually in broad median contact. Loreals two, usually subequal. Seven supralabials (except for *C. egeriae* which has eight), fifth usually subocular. Preoculars two, anterior largest. Postoculars three. Frontal short, about as long as wide. Supraciliaries usually five or six. Supraoculars four. Frontoparietals and interparietal fused, forming a large, roughly diamond shaped shield (except *C. egeriae*, in which frontoparietals are fused but interparietal is distinct). Single pair of enlarged parietal shields. Usually single pair of transversely enlarged nuchal scales, but may have as many as four pairs. Primary temporals usually one, secondary temporals two and posterior temporals two or three. Infralabials six or seven. Mental wider than high. Postmental subequal to mental, in contact with first two infralabials on each side.

Dorsal scales usually smooth, often glossy in texture, subequal in size or with paravertebral series enlarged. Longitudinal rows of scales at midbody between 20 and 30. Paravertebral series of scales between 37 and 61. Enlarged preanal scales subequal.

Limbs well developed, pentadactyl with long, subcylindrical digits, fourth digit longest in each series. Forelimbs shorter than hindlimbs. Adpressed limbs overlap. Fourth finger and toe covered by single row of scales above and by transverse lamellae below. Subdigital lamellae smooth, callused or keeled. Plantar and palmar scales rounded or acute, smooth or callused and few or many in number (7 to 17). Original tails moderately long, between 120% and 162% of snout-vent length.

Dorsal ground colours vary from russet-red, through brown and grey to an almost melanotic black. Body patterns can involve random blotches, simple stripes, combinations of broad zones and stripes, complex combinations of zones, stripes, spots, specks and flecks or be reduced to generalised speckling. 'Soft' colours often present in life mostly lost through leaching in preservation, for example the russet-reds of some Australian saxicoline forms and the blue tail of *C. egeriae*.

Intraspecific variation in meristic and mensural variables of individual taxa is summarised in Appendix 3.

Distribution. *Cryptoblepharus* has the broadest geographic distribution of any scincid genus (Fig. 29). Found in Australia (Fig. 30), and in the south-west Indian Ocean region on the Mascarene Islands, Seychelles, Archipelago des Comores, Madagascar, islands of the Mozambique Channel and the east African coast. In the Indo-Pacific region on Christmas Island, the Sunda and Maluku islands of Indonesia, New Guinea, Micronesia, Melanesia, Polynesia, Ogasawara-Gunto (Japan), Hawaiian Islands, Pitcairn Island, Easter Island and west coast of South America.

Content. *Cryptoblepharus* is proposed to contain 62 taxa (48 monotypic and six polytypic species). Grouped geographically these are – AUSTRALIAN REGION: *C. adamsi* sp. nov.; *C. australis* (Sternfeld, 1918); *C. buchananii* (Gray, 1838); *C. cygnatus* sp. nov.; *C. daedalos* sp. nov.; *C. exochus* sp. nov.; *C. fuhni* Covacevich and Ingram, 1978; *C. gurrmul* sp. nov.; *C. juno* sp. nov.; *C. litoralis horneri* Wells and Wellington, 1985; *C. litoralis litoralis* (Mertens, 1958); *C. megastictus* Storr, 1976; *C. mertensi* sp. nov.; *C. metallicus* (Boulenger, 1887); *C. ochrus* sp. nov.;

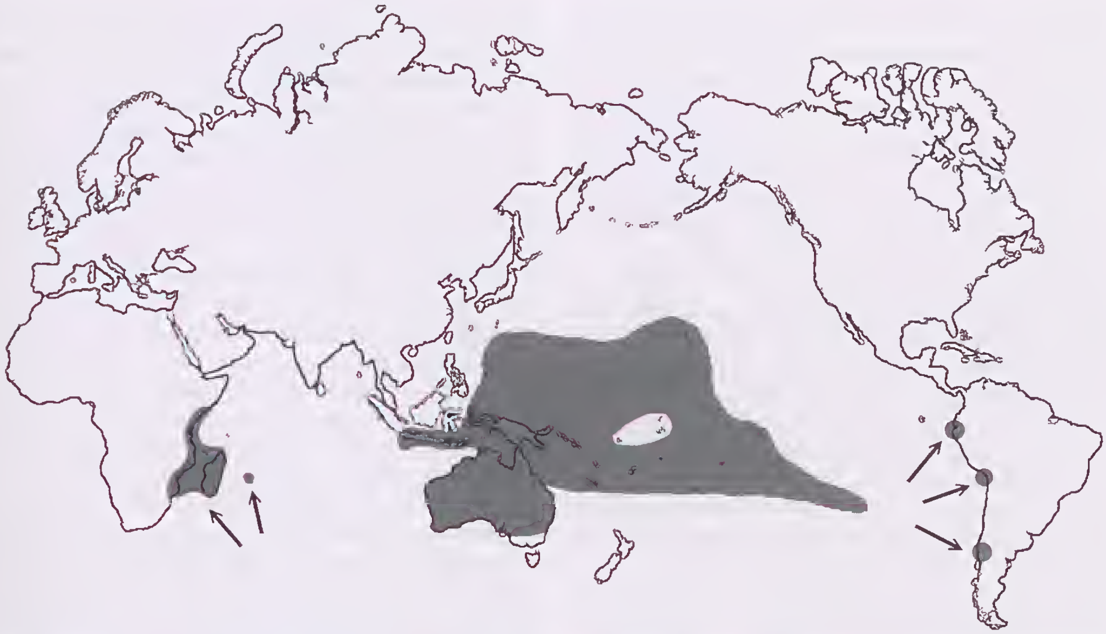

Fig. 29. Known distribution of *Cryptoblepharus* (shaded areas). Note disjunct south-west Indian Ocean populations and seattered records on the west coast of South America.

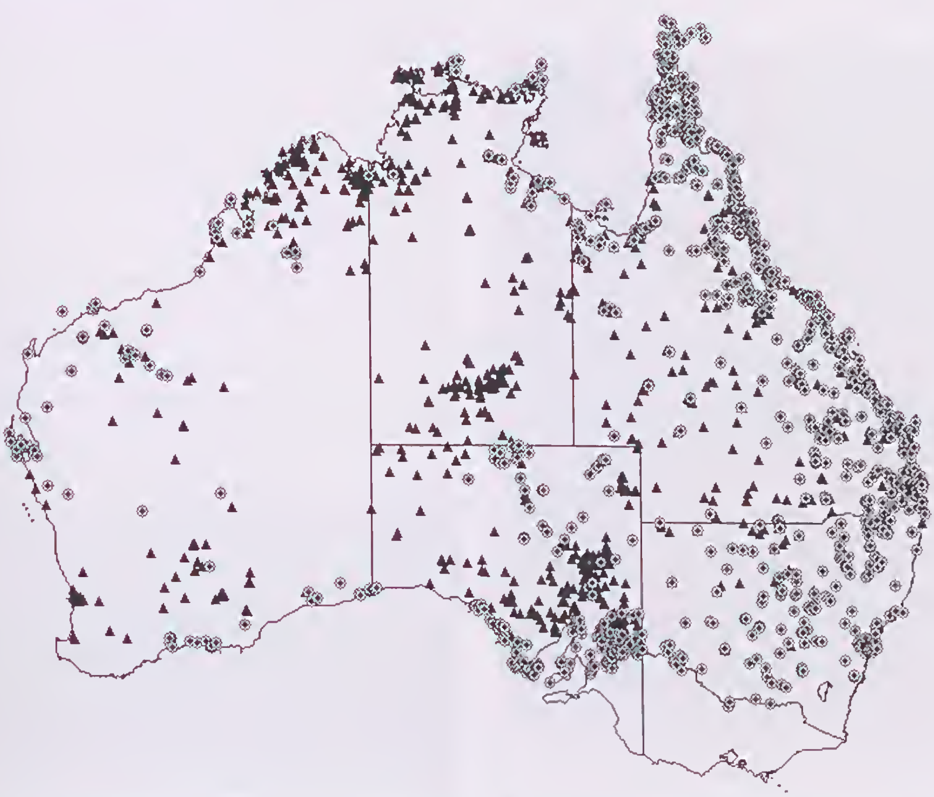

Fig. 30. Known distribution of *Cryptoblepharus* in Australia. Legend: triangles = genetie lineage 1; eircled diamonds = genetic lineage 2 (sec Horner and Adams 2007).

C. pannosus sp. nov.; *C. plagiocephalus* (Cocteau, 1836); *C. pulcher clarus* (Storr, 1961); *C. pulcher pulcher* (Sternfeld, 1918); *C. ruber* Börner and Schüttler, 1981; *C. tytthos* sp. nov.; *C. ustulatus* sp. nov.; *C. virgatus* (Garman, 1901); *C. wulbu* sp. nov., and *C. zoticus* sp. nov. SOUTH-WEST INDIAN OCEAN REGION: *C. africanus* (Sternfeld, 1918); *C. ahli* Mertens, 1928a; *C. aldabrae* (Sternfeld, 1918); *C. ater* (Boettger, 1913); *C. bitaeniatus* (Boettger, 1913); *C. boutoni* (Desjardin, 1831); *C. caudatus* (Sternfeld, 1918); *C. cognatus* (Boettger, 1881); *C. gloriosus gloriosus* (Stejneger, 1893); *C. gloriosus mayottensis* Mertens, 1928a; *C. gloriosus mohelicus* Mertens, 1928a; *C. quinquetaeniatus* (Günther, 1874), and *C. voeltzkowi* (Sternfeld, 1918). INDO-PACIFIC REGION: *C. baliensis baliensis* Barbour, 1911; *C. baliensis sumbawanus* Mertens, 1928a; *C. burdeni* Dunn, 1927; *C. cursor cursor* Barbour, 1911; *C. cursor larsonae* ssp. nov.; *C. egeriae* (Boulenger, 1889); *C. eximius* Girard, 1857; *C. furvus* sp. nov.; *C. intermedius* (de Jong, 1926); *C. keiensis* (Roux, 1910); *C. leschenault* (Cocteau, 1832); *C. litoralis vicinus* ssp. nov.; *C. nigropunctatus* (Hallowell, 1860); *C. novaeguineae* Mertens, 1928a; *C. novocaledonicus* Mertens, 1928a; *C. novohebridicus* Mertens, 1928a; *C. poecilopleurus paschalis* Garman, 1908; *C. poecilopleurus poecilopleurus* (Wiegmann, 1835); *C. renschi* Mertens, 1928b; *C. richardsi* sp. nov.; *C. rutilus* (Peters, 1879); *C. schlegelianus* Mertens, 1928a; *C. xenikos* sp. nov.; and *C. yulensis* sp. nov.

Natural history. *Cryptoblepharus* are heliotropic, scansorial, diurnal, oviparous skinks. Many species are restricted to supralittoral, rocky habitats and often are island endemics. A variety of tropical and temperate environments are occupied, ranging from oceanic islands, the forests of eastern Indonesia to arid central Australia.

Although the broad distribution of *Cryptoblepharus* suggests an ecological generalist, Greer (1989) suggested it is actually adapted to a narrow set of ecological parameters or microhabitats. In most instances, *Cryptoblepharus* are found on vertical surfaces receiving full sun and lacking or severely restricted in fresh water (Greer 1989). They are normally arboreal or saxicoline, though terrestrial when inhabiting shorelines lacking in vertical structures. Terrestrial forays, some metres from vertical structures, are common (pers. obs.) and specimens are often captured in ground-based pitfall traps.

Cryptoblepharus are agile and swift-moving, often leaping gaps greater than their own length between branches and rocks. If disturbed on trees, they invariably circle the trunk keeping it placed between themselves and potential predators. Movement is not restricted to flat or vertical surfaces, but is equally agile on the undersides of branches or ceilings of rock overhangs. Species that forage in the intertidal zone swim readily (Horner 1984) and may cling to submerged rocks (Dunn 1927).

Often locally abundant, large numbers (~ 10–30 specimens) may be observed at any one time on large, rough-barked trees or rock outcrops. Clerke (1989) recorded a population density for *Cryptoblepharus* (as *C. virgatus*, but may have been *C. adamsi* sp. nov. or *C. pulcher*) at Townsville, Queensland, as 2500 specimens per hectare. Arboreal species normally shelter under bark, in hollow limbs or cracks in dead timber, while saxicoline forms retreat to narrow crevices or exfoliations. Very occasionally, shelter will be sought under ground debris, leaf litter or in earth cracks. *Cryptoblepharus* are commonly commensal with man and with other lizards. Valentic and Turner (2001) noted on a large dead River Red Gum (*Eucalyptus camaldulensis*) near Moree, NSW, an undisclosed number of *Cryptoblepharus* (as *C. carnabyi*, but either *C. australis* or *C. pannosus* sp. nov.) as well as two *Gehyra dubia* and a *Diplodactylus williamsi* under flaking bark. In an urban situation, Hoser (2004) recorded an aggregation of 19 *C. pulcher* (as *C. virgatus*) and a single adult Garden Skink *Lampropholis guichenoti* basking on a small (60 x 30 x 20 cm), isolated, sandstone rock in a light industrial region of suburban Sydney.

Cryptoblepharus prey on arthropods (Fig. 31), but will probably take any animal of appropriate size they can catch. Gut contents examined contained insects, insect larvae and arachnids. Predation on swarming winged ants (Greer and Jeffreys 2001) and disturbed termites (pers. obs.) has been observed. Littoral foraging species also consume small crustaceans (Fricke 1970; Horner 1984; Canaris 1973) and polychaetes (Horner 1984). Fricke (1970) recorded predation on juvenile fish (*Periophthalmus koehlreuteri*), and the gut of a *C. daedalos* sp. nov. (NTM R.13269) contained an autonomised tail of another *C. daedalos* sp. nov. Some species use piracy as a feeding strategy, stealing morsels from burdened ants carrying food along a busy ant trail (Greer 1989, and see remarks on *C. juno* sp. nov.). *Cryptoblepharus pulcher* (as *C. virgatus*) has been observed taking paralysed arthropods from mud nests of solitary wasps (Phillips 2005).

Cryptoblepharus are important prey for a variety of vertebrate and invertebrate predators, although this has been poorly documented. Fearn and Trembath (2004) record *Cryptoblepharus* (as *C. virgatus*, but may have been *C. adamsi* sp. nov. or *C. pulcher*) at Townsville, Queensland as a common prey item of the legless lizard *Lialis burtonis* (Pygopodidae). *Cryptoblepharus cygnatus* sp. nov. has been observed as prey of a centipede (Scolopendridae), although this was in an artificial situation with both animals confined in a pitfall trap (T. Johansen pers. comm.) (Fig. 32).

Longevity is probably about one year (Clerke 1989, as *C. virgatus* but may have been *C. adamsi* sp. nov. or

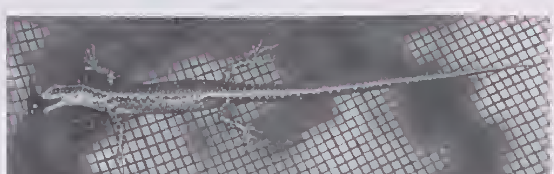

Fig. 31. *Cryptoblepharus cygnatus* sp. nov. on window insect screen with captured fly (Muscidae) (Mary River, NT).

C. pulcher) and reproduction is bisexual and oviparous, with two eggs being the typical clutch size (Greer 1989; Smith 1976; Schwaner 1980; pers. obs.). Greer (1989) directs attention to "one of the minor mysteries associated with *Cryptoblepharus*": what it does with its eggs. Although a common human commensal, abundant and widespread in distribution, very few egg clutches have been recorded. Evidence indicates that the genus practises communal egg-laying. On the Hawaiian island of Maui, McGregor (1904) found large quantities of *C. p. poecilopleurus* eggs deposited in damp earth in a railway pit cattle guard, in some instances these were stuck together in bunches of four or five with one 'set' consisting of over 70 eggs in all stages of incubation. On Cosmoledo Atoll (Aldabra Group, Seychelles) Honegger (1966) discovered over 70 *C. aldabrae* eggs under a clump of broken coral. In Fiji, Zug (1991) found probable *C. eximius* clutches interspersed with eggs of the gecko *Lepidodactylus lugubris*, beneath rock slabs.

In Sydney, the recurring use of an urban oviposition site was noted by Stammer (1988) who recorded *C. pulcher*'s (as *C. virgatus*) use of a brick wall, and its inner cavity, as a "nursery" and egg-laying area for four successive years. The maximum number of hatchlings sighted by Stammer (1988) in any one year was five, indicating that communal nesting was taking place.

An arboreal oviposition site was recorded by Neill (1946) at Waigani Swamp, near Port Moresby, New Guinea. He found eggs of an unidentified *Cryptoblepharus* inside ant-plants (Rubiaceae), globular, intricately chambered, epiphytes which grow upon the branches of trees and are infested by ants. When broken open, a cavity in one of these "yielded 11 small, white eggs" which, when broken open contained fully developed young *Cryptoblepharus*. Another ant-plant was discovered to contain four eggs (Neill 1946). Additional records of ant-plants as communal oviposition sites are found in the Queensland Museum collection. Two *C. virgatus* clutches (J46576, four egg cases and five hatchlings; J46577, 20 eggs and four hatchlings in different stages of development) were collected inside ant-plants on Horn Island, Torres Strait, Queensland, by K. Houston and C. Freebairn in December 1986. The use of ant-plants in New Guinea as shelter sites by unidentified lizards was originally noted by Lam (1924).

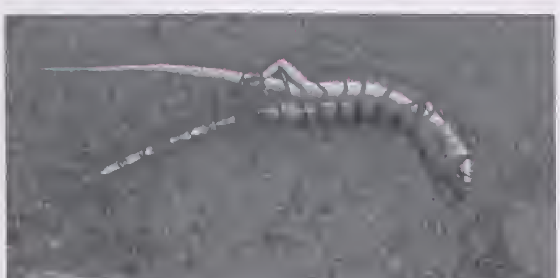

Fig. 32. *Cryptoblepharus cygnatus* sp. nov. being eaten by centipede (Scolopendridae) in pitfall trap (Annaburroo Station, NT). Photo by T. Johansen.

Cryptoblepharus are sexually dimorphic, with males being smaller and having a shorter body but longer limbs, forebody and head than females (Table 2). Correlated with their longer body, females may also have more numerous paravertebral scales than males. No sexually dimorphic colours or body patterns were detected. Hatchlings and juveniles are miniatures of adults in colour and pattern.

Two forms of intraspecific interaction have been observed (pers. obs.), both involving *C. cygnatus* sp. nov. Male/male dominance, or territorial behaviour, involved close circling, punctuated by vicious biting (Fig. 33A) and shaking of rival's hindquarters. Mating behaviour involved the male following the female using jerky movements and sinuous tail waving, then gripping the female immediately behind her forelimb with his jaws, positioning his hindquarters under hers and maintaining his grip until copulation was completed (Fig. 33B). Tail waving or vibrating has been observed in *C. daedalos* sp. nov. Intraspecific aggression has also been observed at Cardwell, Queensland (Valentic 1997, as *C. virgatus*, but may have been *C. adamsi* sp. nov. or *C. pulcher*), involving three adults on a vertical wooden power pole. In this instance, the aggressor pursued another to the ground where, aligned parallel to one another, rhythmic tail waving preceded violent biting to the jaw and body. The interaction ended with the aggressor pursuing its opponent up the pole, where it then proceeded to harass the third individual by repeatedly biting its hindquarters whilst it tried to escape.

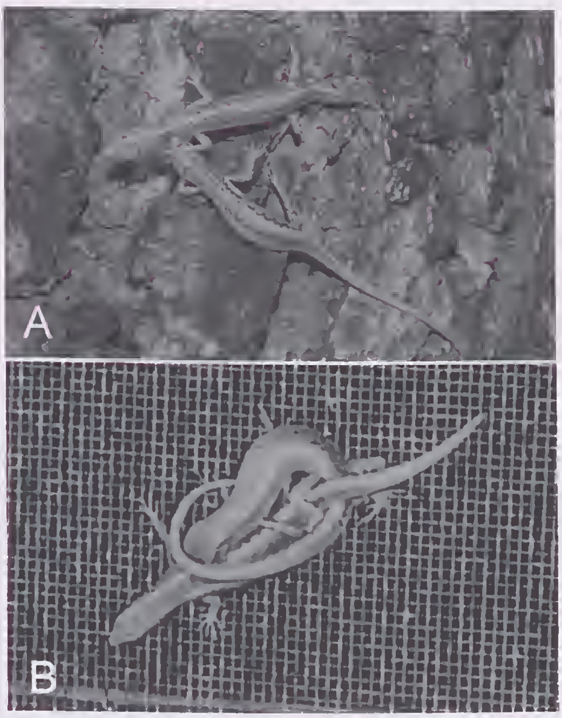

Fig. 33. *Cryptoblepharus cygnatus* sp. nov. intraspecific interactions: (**A**) male-male territorial combat (Annaburroo Station, NT). Photo by T. Johansen; (**B**) copulating pair on window insect screen (Virginia, Darwin, NT). Photo by S. Gregg.

Clerke (1989) considered *Cryptoblepharus* (as *C. virgatus*, but may have been *C. adamsi* sp. nov. or *C. pulcher*) at Townsville, Queensland, to be non-territorial.

Parasites. At least two species of coccidian Protozoa are known to infect *Cryptoblepharus*. *Isospora cryptoblephari* (Finkelman and Paperna 1994) and *Eimeria jamescooki* (Paperna 2003) have both been described from *Cryptoblepharus* (as *C. virgatus*, but may have been *C. adamsi* sp. nov. or *C. pulcher*).

Suggested common name. Several vernacular names have been applied to the genus. 'Snake-eyed skink' has been used in Australia (Cogger 1967; Horner 1991; Wilson and Knowles 1988; Bush *et al.* 1995), as has 'Fence skink/lizard' (Swanson 1987; Bush *et al.* 1995; Wilson and Swan 2003), 'Wall skink/lizard' (Worrell 1963; Hutchinson and Edwards 2000; Wilson and Swan 2003), 'Sun skink' (Bush *et al.* 1995) and Shinning-skink (Ehmann 1992, Stanger *et al.* 1998). Internationally, the most commonly used name is 'Snake-eyed skink' (Loveridge 1946; Hunsaker and Breese 1967; Haacke 1977; McKeown 1978; McCoid *et al.* 1995).

In deference to the international distribution of *Cryptoblepharus*, and notwithstanding its equal application to other scincid genera with the ablepharine-eye condition, the name 'Snake-eyed skink' is suggested as most appropriate for the genus.

AUSTRALIAN REGION TAXA

Twenty-five taxa are recognised from the Australian continent and fringing islands (Fig. 30). Comprising 21 monotypic and two polytypic species, the generic content for the Australian region is: *C. adamsi* sp. nov.; *C. australis*; *C. buchananii*; *C. cygnatus* sp. nov.; *C. daedalos* sp. nov.; *C. exochus* sp. nov.; *C. fuhni*; *C. gurrmul* sp. nov.; *C. juno* sp. nov.; *C. litoralis horneri*; *C. litoralis litoralis*; *C. megastictus; C. mertensi* sp. nov.; *C. metallicus*; *C. ochrus* sp. nov.; *C. pannosus* sp. nov.; *C. plagiocephalus*; *C. pulcher clarus*; *C. pulcher pulcher*; *C. ruber*; *C. tytthos* sp. nov.; *C. ustulatus* sp. nov.; *C. virgatus*; *C. wulbu* sp. nov. and *C. zoticus* sp. nov.

Although not an Australian region taxon, the description of *C. litoralis vicinus* ssp. nov. is included here for convenience and comparison with conspecifics.

Key to Australian *Cryptoblepharus* taxa

1 a. Usually six supraciliary scales 2
b. Usually five supraciliary scales 10

2 a. Body pattern of random dark blotches, spots or flecks (Fig. 8E); ground colour reddish in life; head relatively shallow (mean <37% of head length); limbs relatively long (mean: forelimb >35% hindlimb >44% of SVL); saxicoline 3
b. Body pattern longitudinally aligned, consisting of zones and/or stripes, with or without obscure spots and specks (Fig. 8A-C); ground colour grayish or brownish; head relatively deep (mean >40% of head length); limbs relatively short (mean: forelimb <34% hindlimb <43% of SVL); arboreal 6

3 a. Paravertebral scales usually more than 44; fourth toe subdigital lamellae usually 20 or less; head relatively long (mean >21% of SVL) 4
b. Paravertebral scales usually less than 44 (modally 39); fourth toe subdigital lamellae usually 22; head relatively short (mean <20% of SVL) .... *C. wulbu* sp. nov.

4 a. Body pattern typically dark flecks and/or speckling; paravertebral scales usually more than 47; palmar scales usually 9 or more; plantar scales usually 11 or more 5
b. Body pattern typically large, dark irregular blotches; paravertebral scales usually less than 46 (modally 45); palmar scales usually 8; plantar scales usually 10 .... *C. megastictus*

5 a. Palmar scales usually 10; plantar scales usually 15; head relatively deep (mean 36% of head length); posttemporal scales generally two .... *C. daedalos* sp. nov.
b. Palmar scales usually 9; plantar scales usually 12; head relatively shallow (mean 34% of head length); posttemporal scales generally three ....*C. juno* sp. nov.

6 a. Plantar scales rounded (cobblestone-like) (Fig. 4A), often callused (Fig. 4B) or speckled 7
b. Plantar scales acute (pointed) (Fig. 4C), always plain .... *C. australis*

7 a. Fourth toe subdigital lamellae mostly smooth (Fig. 5A) (often 2 or 3 basal lamellae are surfaced with dark shiny calli); most plantar scales surfaced with dark shiny calli (Fig. 4B) (remaining plantars plain) 8
b. Most fourth toe subdigital lamellae surfaced with dark shiny calli (Fig. 5B); plantar scales typically peppered with minute brown spots, not callused or plain ....*C. cygnatus* sp. nov.

8 a. Size relatively large (mean SVL >40.0 mm), tail relatively short (mean <135% of SVL); paravertebral scales usually more than 50; posttemporal scales generally three 9
b. Size medium (mean SVL = 38.6 mm); tail relatively long (mean 144% of SVL); paravertebral scales usually less than 50 (modally 48); posttemporal scales generally two ....*C. metallicus*

9 a. Paravertebral scales usually 52; fourth finger subdigital lamellae usually 14; pale laterodorsal zones often indistinct (Fig. 8D) .... *C. buchananii*

b. Paravertebral scales usually 54; fourth finger subdigital lamellae usually 16; pale laterodorsal zones usually distinct (Fig. 8C) .... *C. ruber*

10 a. Plantar scales acute (pointed) (Fig. 4D) 11

b. Plantar scales rounded (cobblestone-like) (Fig. 4A) 16

11 a. Size medium (mean SVL >33.0 mm); forelimbs relatively long (mean >33% of SVL); pale laterodorsal stripes distinct, typically prominent to hindlimbs 12

b. Size small (mean SVL <31.5 mm); forelimbs relatively short (mean <32.5% of SVL); narrow, pale laterodorsal stripes usually obscure on posterior third of body ... . *C. tytthos* sp. nov.

12 a. Fourth toe subdigital lamellae keeled; paravertebral scales usually 50 or less; plantar scales usually 12 or less; ground colour gray-brown 13

b. Fourth toe subdigital lamellae smooth; paravertebral scales usually 51; plantar scales usually 12; ground colour olive-brown .... *C. exochus* sp. nov.

13 a. Fourth toe subdigital lamellae generally strongly keeled; head relatively small (mean: depth <40.5% of length; width <62.5% of length); pale laterodorsal stripes usually ragged-edged 14

b. Fourth toe subdigital lamellae weakly keeled; head relatively large (mean: depth 43.4% of length; width 63.2% of length); pale laterodorsal stripes usually smooth-edged .... *C. mertensi* sp. nov.

14 a. Size medium (mean SVL <35 mm); forelimbs relatively short (mean <34% of SVL); fourth toe supradigital scales usually 15; fourth toe subdigital lamellae strongly keeled; pale laterodorsal stripes relatively broad (>1.5 laterodorsal scales wide) .. 15

b. Size relatively large (mean SVL = 39.0 mm); forelimbs relatively long (mean 34% of SVL); fourth toe supradigital scales usually 16; fourth toe subdigital lamellae relatively weakly keeled; pale laterodorsal stripes relatively narrow (about one laterodorsal scale wide) .... *C. ochrus* sp. nov.

15 a. Paravertebral scales usually 48; palmar scales usually 10; fourth toe subdigital lamellae usually 19; posttemporal scales generally 3; head relatively short (mean <21% of SVL); body relatively long (mean >50% of SVL); fourth toe subdigital lamellae strongly keeled ....*C. pannosus* sp. nov.

b. Paravertebral scales usually 50; palmar scales usually 9; fourth toe subdigital lamellae usually 20; posttemporal scales generally 2; head relatively long (mean >21% of SVL); body relatively short (mean <50% of SVL); fourth toe subdigital lamellae moderately keeled ....*C. plagiocephalus*

16 a. Limbs relatively short (mean: forelimb <36% hindlimb <46% of SVL); fourth finger subdigital lamellae usually 16 or less; fourth toe supradigital scales usually 16 or less; pale laterodorsal stripes (if present) continuous 17

b. Limbs relatively long (mean: forelimb 40.7% hindlimb 52.8% of SVL); fourth finger subdigital lamellae usually 18; fourth toe supradigital scales usually 18; pale laterodorsal stripes discontinuous (series of silvery streaks) .... *C. fuhni*

17 a. Postnasal scale absent; midbody scale rows 26 or less; plantar scales relatively numerous (modally 9 or more) 18

b. Postnasal scale present (Fig. 6); midbody scale rows 28; plantar scales relatively few (modally 7) ....*C. gurrmul* sp. nov.

18 a. Midbody scale rows usually 26; paravertebral scales relatively numerous (modally 55 or more); fourth toe subdigital lamellae usually 20; size large (mean SVL >38 mm) 19

b. Midbody scale rows usually 24 or less; paravertebral scales relatively few (modally 50 or less); fourth toe subdigital lamellae usually 19 or less; size medium (mean SVL <36 mm) 20

19 a. Palmar scales usually 11; paravertebral scales usually 57; anterior loreal generally largest; fourth toe subdigital lamellae narrowly callose ....*C. litoralis litoralis*

b. Palmar scales usually 9; paravertebral scales usually 54; loreals usually subequal; fourth toe subdigital lamellae broadly callose ....*C. litoralis horneri*

20 a. Ground colour reddish (in life); limbs relatively long (mean: forelimb >34.5% hindlimb >42% of SVL); head shallow (mean <35% of head length); saxicoline 21

b. Ground colour brown, gray or black; limbs relatively short (mean: forelimb <33.5% hindlimb <41.5% of SVL); head deep (mean >37% of head length); arboreal 22

21 a. Body pattern longitudinally aligned, with broad vertebral zone of ground colour; midbody scale rows usually 22; hindlimb relatively long (mean 44.3% of SVL); head relatively deep (mean 34.7% of head length) .... *C. ustulatus* sp. nov.

b. Body pattern not longitudinally aligned, dorsum patterned with irregular scattered dark blotches, spots or flecks; midbody scale rows usually 24; hindlimb relatively short (mean 42.2% of SVL); head relatively shallow (mean 32.5% of head length) .... *C. zoticus* sp. nov.

22 a. Midbody scale rows usually 24; paravertebral scales usually 50; plantar scales usually 9; forelimb relatively short (mean 32.2% of SVL); head relatively wide (mean >61% of head length) 23
b. Midbody scale rows usually 22; paravertebral scales usually 47; plantar scales usually 10; forelimb relatively long (mean 33.1% of SVL); head relatively narrow (mean 57.6% of head length) .... *C. virgatus*

23 a. Plantar scales dark (brown/black) (Fig. 4A); pale laterodorsal stripes narrow (about 0.5–0.75 of laterodorsal scale width) with smooth edges; fourth finger subdigital lamellae usually 15; fourth toe subdigital lamellae usually 19 24
b. Plantar scales pale (cream/gray); pale laterodorsal stripes relatively broad (about width of laterodorsal scale) with ragged edges; fourth finger subdigital lamellae usually 16; fourth toe subdigital lamellae usually 18 .... *C. adamsi* sp. nov.

24 a. Plantar scales usually 9; midbody scale rows usually 23; fourth toe subdigital lamellae usually 18 .... *C. pulcher pulcher*
b. Plantar scales usually 10; midbody scale rows usually 24; fourth toe subdigital lamellae usually 19 .... *C. pulcher clarus*

Cryptoblepharus adamsi sp. nov.

Adams's snake-eyed skink

(Plate 1.1; Figs 34–37; Table 5)

Type material examined. *Cryptoblepharus adamsi* Horner. HOLOTYPE: Adult male, NTM R18921 (Tissue sample No. ABTC CC8), Mount Gordon rest area, Bruce Highway, Bowen, Queensland, 20°02'55"S 148°13'43"E. coll. P. and R. Horner, 5 January 1998. PARATYPES (23 specimens): QUEENSLAND: SAM R2955, Wondecla, 17°25'S 145°24'E, R. Southcott, 22 August 1943; SAM R2956, Irvinebank, 17°26'S 145°12'E, R. Southcott, 27 September 1944; NTM R18858, 40 km east of Mount Surprise, 18°12'12"S 144°34'11"E, P. and R. Horner, 19 December 1997, ABTC BX1; NTM R18859, 10 km west of Ravenshoe, 17°38'35"S 145°27'28"E, P. and R. Horner, 19 December 1997, ABTC BX2; NTM R18863-864, council Park, Mareeba, 16°59'20"S 145°25'08"E, P. and R. Horner, 21 December 1997, ABTC BX3-BX4; NTM R18909-912, Ayr (town area), 19°34'32"S 147°23'58"E, P. and R. Horner, 4 January 1998, ABTC CB5-CB8; NTM R18916-918, R18920, Lynch's Beach, 16 km east of Ayr, 19°27'23"S 147°28'52"E, P. and R. Horner, 5 January 1998, ABTC CC3-CC5, CC7; NTM R18922-923, R18925, Mount Gordon rest area, Bowen, 20°02'54"S 148°13'43"E, 71; P. and R. Horner, 5 January 1998, ABTC CC9, CD1, CD3; NTM R18937-938, 5.4 km west of Dingo Beach, 20°08'15"S 148°30'05"E, P. and R. Horner, 6 January 1998, ABTC CE6-CE7; NTM R18941, Ayr (town area), 19°34'32"S 147°23'58"E, P. and R. Horner, 4 January 1998; NTM R18942-944, Mount Gordon rest area, Bowen, 20°02'54"S 148°13'43"E, 71; P. and R. Horner, 5 January 1998.

Diagnosis. A small (<40 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from Australian congeners by combination of usually having: five supraciliary scales; 24 mid-body scale rows; 50 paravertebral scales; callused, pale, ovate plantar scales; and moderately broad, ragged-edged, pale dorsolateral stripes.

Description (24 specimens). Postnasals absent; prefrontals in broad contact (100%); supraciliaries 5–7 (mean 5.2), modally 5; enlarged upper ciliaries 3–4 (mean 3.1), modally 3; loreals usually subequal (54%), occasionally posterior (25%) or anterior (21%) loreal largest; supralabials 7–8 (mean 7.3), modally 7; fifth supralabial usually subocular (77%), occasionally sixth (23%); infralabials 6; nuchals 2–4 (mean 2.1), modally 2; bilateral posttemporals 2+2 (37%), 2+3 (33%), or 3+3 (30%).

Midbody scale rows 22–26 (mean 23.8), modally 24; paravertebrals 43–52 (mean 47.8), modally 50; subdigital lamellae smooth, 13–16 below fourth finger (mean 15.1) modally 16, 16–21 below fourth toe (mean 18.5) modally 18; 11–14 supradigital lamellae above fourth finger (mean 12.8) modally 13, 14–17 above fourth toe (mean 16.0) modally 16; palmar and plantar scales rounded, usually capped with dark brown calli and skin not visible between scales (Fig. 34); plantars 8–11 (mean 9.3), modally 9; palmars 6–9 (mean 7.4), modally 8.

Snout-vent length to 37.3 mm (mean 34.2 mm). *Percentages of snout-vent length*: body length 46.6–53.6% (mean 50.7%); tail length 113.0–132.2% (mean 120.4%); forelimb length 28.4–35.4% (mean 32.2%); hindlimb length 38.4–44.0% (mean 40.9%); forebody length 38.9–45.4% (mean 41.7%); head length 19.0–22.1% (mean 20.3%). *Percentages of head length*: head depth 35.7–47.8% (mean 40.2%); head width 58.5–65.8% (mean 61.7%); snout length 42.2–49.8% (mean 45.2%). Paravertebral scale width 3.7–4.9% (mean 4.2%) of snout-vent length; dorsolateral scale width 73.6–105.6% (mean 89.9%) of paravertebral scale width.

Lenticular scale organs 3–8 (mean 5.4), modally 6. Premaxillary teeth 5; maxillary teeth 19–20 (mean 19.5), modally 19; mandibular teeth 24–25 (mean 24.8), modally 25. Hemipenis: length 7.2–9.0% (mean 8.2%) of snout-vent length; width 72.4–94.9% (mean 81.6%) of hemipenis length; trunk 45.5–58.7% (mean 51.0%) of hemipenis length.

Details of holotype. NTM R18921, adult male (Fig. 35): Postnasals absent; prefrontals in broad contact; supraciliaries 5 (right), 6 (left); enlarged upper ciliaries 3; posterior loreal largest; supralabials 8; sixth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 24; paravertebrals 47; subdigital lamellae smooth, 14 below fourth finger; 18 below fourth toe; supradigital lamellae 13 above fourth finger; 17 above fourth toe; palmars and plantars rounded, skin not visible between scales; plantars 10; palmars 8. Snout-vent length 33.2 mm; body length 16.7 mm; tail not original;

Fig. 34. Ventral surface of hind foot of *Cryptoblepharus adamsi* sp. nov. showing pale ovate plantar scales (NTM R18924. Bowen. Qld). Scale: x20.

Fig. 35. Holotype of *Cryptoblepharus adamsi* sp. nov. (NTM R18921, Mount Gordon rest area, Bruce Highway, Bowen, Queensland, Australia, 20°02'55"S 148°13'43"E). Scale bar = 10 mm.

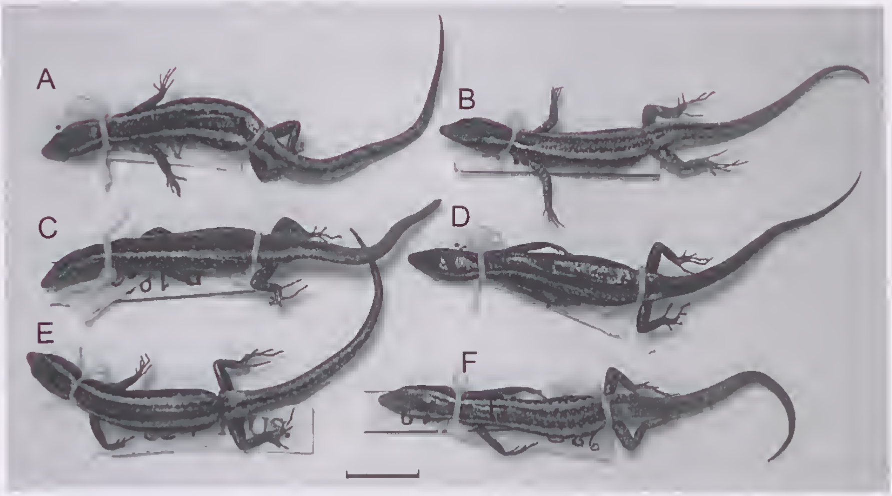

Fig. 36. *Cryptoblepharus adamsi* sp. nov. NTM preserved material from Queensland: **A**, = R18917, Lynch's Beach; **B**, = R18921, Bowen (holotype); **C**, = R18911, Ayr; **D**, = R18863, Mareeba; **E**, = R18920, Lynch's Beach; **F**, = R18910, Ayr. Scale bar = 10 mm.

forelimb length 11.6 mm; hindlimb length 14.3 mm; forebody length 14.2 mm; head length 6.8 mm; head depth 2.8 mm; head width 4.2 mm; snout length 3.0 mm.

Colouration and pattern. Dark brown to blackish, with longitudinally aligned, complex body pattern dominated by narrow, brown vertebral zone, black paravertebral and prominent, pale laterodorsal stripes (Plate 1.1, Fig. 36). Intensity of body patterning is variable, ranging from obscure to prominent (Fig. 36). Most specimens conform to the following description.

Dorsal ground colour brown or brown-black, with narrow vertebral zone of ground colour extending from above eye to hindlimb. Vertebral zone as wide as or slightly wider than mid-paravertebral scale, usually mottled with blackish flecks. Distinct, black paravertebral stripes extend from above eye onto tailbase, where they merge creating blackish, ragged-edged, tapering median stripe on anterior half of tail. Inner margin of dark paravertebral stripes ragged, interdigitating with paler vertebral zone. Prominent, moderately broad, pale grey to silvery laterodorsal stripes extend from above eye onto tail. Pale laterodorsal stripes usually ragged-edged and without patterning, about width of mid-laterodorsal scale. Head concolorous with vertebral zone or coppery brown, usually with dark mottling on scales. Laterally patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Pale lower temporal region flecked with dark spots and streaks. Labials cream to brown with fine dark margins to scales.

Laterally, a black upper zone, similar in width to dark paravertebral stripes, extending from loreals onto tail, forming ragged outer border to pale dorsolateral stripes. Flecked with pale specks and spots, upper lateral zone about two lateral scales wide, coalescing gradually into grey-brown lower lateral zone. Lower lateral zone peppered with small pale and/or dark spots and streaks and coalescing with pale venter. Tail concolorous with body, patterned with continuations of blackish paravertebral and pale dorsolateral stripes. Limbs and toes concolorous with body, patterned with pale and dark speckling. Venter immaculate off-white. Palmar and plantar surfaces light grey to pale brown, patterned with dark brown calli on outer rows of plantar scales.

Sex ratio and reproductive biology. Sex ratio favoured females (16:8), but was not significantly different from parity ($X^2 = 2.67$). Males mature at about 30 mm snout-vent length and females at 32 mm. Breeding is indeterminate, with 90% of samples collected in December and January.

Of these, most were reproductively active. Reproductives were also recorded in August (one female) and September (one male).

Comparison with Australian congeners. Fixed allelic differences place *C. adamsi* sp. nov. in lineage 2 of Australian *Cryptoblepharus* and also distinguish it from most congeners within that lineage (as OTU virgA3, Horner and Adams 2007). With no fixed allelic differences, *C. adamsi* sp. nov. is genetically similar to *C. pannosus* sp. nov. (as OTU carnA5, Horner and Adams 2007).

Morphologically distinguished from lineage 1 members *C. australis*, *C. buchananii*, *C. cygnatus* sp. nov., *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus*, *C. metallicus*, *C. ruber* and *C. wulbu* sp. nov. by usually having five, rather than six, supraciliary scales and a simple striped body pattern on a blackish ground colour. Distinguished from lineage 2 congeners *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. by having rounded, instead of acute, plantar scales and simple striped body pattern on a blackish ground colour. Distinguished from *C. litoralis* and *C. gurrmul* sp. nov. by fewer mid-body scale rows (modally 24 versus 26–28) and paravertebral scales (modally 50 versus 55–57); from *C. fuhni*, *C. ustulatus* sp. nov. and *C. zoticus* sp. nov. by more paravertebral scales (modally 50 versus 45–46) and deeper head (mean 40.2 versus 32.5–36.1 % of head length).

Cryptoblepharus adamsi sp. nov. is most similar to *C. pulcher* and *C. virgatus* in having combinations of simple striped body pattern, flat ovate plantar scales and being arboreal. However, it differs from *C. pulcher* in having pale, callused plantar scales (rather than dark, plain plantars), moderately broad, ragged edged, pale laterodorsal stripes instead of narrow smooth edged stripes and more fourth finger supradigital scales (modally 13 instead of 12). It also differs from *C. virgatus* in usually having 24 midbody scale rows instead of 22, more numerous paravertebral scales (modally 50 instead of 47), moderately broad, ragged edged, pale laterodorsal stripes instead of narrow smooth edged stripes and narrower paravertebral scales (mean % of SVL 4.2 instead of 4.5).

Notwithstanding allozymic similarity (Horner and Adams 2007), comparison of 24 *C. adamsi* sp. nov. to 64 *C. metallicus* identified the following morphological differences: smooth versus keeled subdigital lamellae; ovate versus acute plantar scales; shorter forelimbs (mean 11.9 versus 12.5 mm) and fewer fourth toe subdigital lamellae (modally 18 versus 19), palmar (modally 8 versus 9), plantar scales (modally 9 versus 11) and posterior temporal scales (modally 2 versus 3).

Distribution. Mid-north coastal regions of Queensland, from Mount Molloy, south to Mount Larcom and inland to west of Mount Surprise (Fig. 37).

Sympatry. *Cryptoblepharus adamsi* sp. nov. occurs in sympatry with *C. metallicus* from lineage 1 and *C. l. litoralis*, *C. pannosus* sp. nov., *C. pulcher* and *C. virgatus* from lineage 2 (Table 5).

Geographic variation. Geographic variation was investigated by separating specimens into three groups: *BBN*, nine (1 ♂, 8 ♀) samples from bioregion BBN; *CMC*, nine (5 ♂, 4 ♀) samples from bioregion CMC; and *WT*, six (2 ♂, 4 ♀) samples from bioregions EIU and WT. Small sample sizes of *BBN* and *WT* males prevented analysis of separate sexes. ANOVA of allometrically adjusted values revealed little geographic variation in *C. adamsi*. Group *BBN* was larger than *CMC* and *WT* in snout-vent length (mean 35.7 versus 33.4 and 33.0 mm), but had a shorter head than group *CMC* (mean 7.4 versus 7.6 mm). Groups *CMC* and *WT* differed in number of fourth toe subdigital lamellae (mean 17.9 versus 19.5). Allowing for sexual dimorphism, it is likely that the large size and short head of group *BBN* was influenced by the predominance of females in that group.

Habits and habitats. Poorly known. *C. adamsi* is arboreal, recorded from *Eucalyptus* trunks in tall woodland,

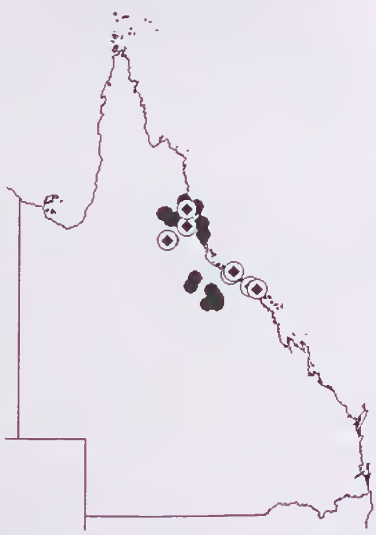

Fig. 37. Map of Queensland showing distribution of *Cryptoblepharus adamsi* sp. nov. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

Table 5. List of congeners sympatric with *Cryptoblepharus adamsi* sp. nov., giving areas of sympatry.

Congeners sympatric with *Cryptoblepharus adamsi* sp. nov.	Area of sympatry
C. l. litoralis	Qld: Flying Fish Point, Dunk Island
C. metallicus	Qld: Mount Molloy, Chillagoe, Ayr, Warrawee Stn
C. pannosus sp. nov.	Qld: Hillgrove Stn
C. p. pulcher	Qld: Mount Larcom
C. virgatus	Qld: Cairns, Mareeba

on grass tree trunks (*Xanthorrhoea* sp.), on fig trees behind beach and on tree trunks and pine logs in town parks.

Etymology. Named for Mark Adams (Evolutionary Biology Unit, South Australian Museum) in recognition of his contributions to scincid taxonomy.

Cryptoblepharus australis (Sternfeld, 1918)
Inland snake-eyed skink

(Plate 1.2; Figs 38–41; Table 6)

Ablepharus boutoni australis Sternfeld, 1918: 424 (West-Central-Australien).

Ablepharus boutonii (Desjardin, 1831). – Waite, 1929: 166.

Ablepharus boutonii metallicus Sternfeld, 1918. – Mertens, 1931: 120; Loveridge 1934: 375-376; Worrell 1963: 35; Mertens 1964: 106.

Cryptoblepharus plagiocephalus (Cocteau, 1836). – Storr 1976: 56, fig. 1; Storr *et al.* 1981: 24; Gow 1981a; Cogger *et al.* 1983a: 142; Wilson and Knowles 1988: 120; Covacevich and Couper 1991: 357; Ehmann 1992: 182; Reid *et al.* 1993: 61: van Oosterzee 1995: 109; Stanger *et al.* 1998: 23; Storr *et al.* 1999: 24; Cogger 2000: 406; Hutchinson and Edwards 2000: 113; Wilson and Swan 2003: 148.

Cryptoblepharus australis (Sternfeld, 1918). – Wells and Wellington, 1985: 27.

Cryptoblepharus hawkeswoodi Wells and Wellington, 1985: 27.

Cryptoblepharus carnabyi Storr, 1976. – Horner 1991: 16, fig. 21; Henle 1996: 15, 17.

Type material examined. *Ablepharus boutoni australis* Sternfeld, 1918. LECTOTYPE: SMF 15683, Hermannsburg, central Australia, M. v. Leonhardi, 1907.

Non-type material examined. See Appendix 4.

Diagnosis. A large (45–50 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from Australian congeners by combination of usually having: six supraciliary scales; 24 mid-body scale rows; mean values of hindlimb length 41.1% of snout-vent length, head depth 42.3% of head length; smooth subdigital lamellae; immaculate, acute plantar scales; greyish, longitudinally aligned body pattern and arboreal habits.

Description (105 specimens). Postnasals absent; prefrontals usually in broad contact (92.9%), occasionally in narrow contact (4.0%) or narrowly separated (3.1%); supraciliaries 5–8 (mean 6.01), modally 6; enlarged upper ciliaries 2–4 (mean 3.0), modally 3; loreals subequal (54.4%) or posterior largest (36.9%), occasionally anterior is largest (8.7%); supralabials 6–8 (mean 7.0), modally 7; fifth supralabial usually subocular (96.6%), occasionally sixth (3.4%); infralabials 6–7 (mean 6.0), modally 6; nuchals usually 2 (92.3%), occasionally 3 (4.8%), 4 (1.9%) or 5 (1.0%); bilateral posttemporals usually 3+3 (73.8%), occasionally 2+3 (13.1%), 2+2 (10.7%) or 3+4 (2.4%).

Midbody scale rows 22–28 (mean 24.9), modally 24, often 26; paravertebrals 43–57 (mean 50.1), usually between 47–53 (82.7% modally 52); subdigital lamellae smooth, 14–18 below fourth finger (mean 19.2) modally 16, 16–23 below fourth toe (mean 19.2), modally 19; 12–15 supradigital lamellae above fourth finger (mean 13.1) modally 13, 13–18 above fourth toe (mean 15.5), modally 15; palmar and plantar scales acute (Fig. 38), but less so than those of lineage 2 members with acute plantars, being intermediate those and the rounded plantars of other lineage 1 members, no skin visible between scales; plantars 9–14 (mean 11.6), modally 12; palmars 7–11 (mean 9.2), modally 9.

Snout-vent length to 46.2 mm (mean 40.4 mm). *Percentages of snout-vent length*: body length 42.3–57.6% (mean 51.2%); tail length 116.2–155.8% (mean 136.1%); forelimb length 28.0–37.1% (mean 33.5%); hindlimb length 34.7–46.7% (mean 41.1%); forebody length 37.9–48.8% (mean 41.6%); head length 18.7–26.1% (mean 20.8%). *Percentages of head length*: head depth 32.0–55.2% (mean 42.3%); head width 55.6–73.3% (mean 62.2%); snout length 40.3–48.9 (mean 44.9%). Paravertebral scale width 3.0–4.9% (mean 4.0%) of snout-vent length; dorsolateral scale width 69.9–104.1% (mean 88.3%) of paravertebral scale width.

Lenticular scale organs 4–14 (mean 8.3), modally 7 or 9. Premaxillary teeth 5–6 (mean 5.2), modally 5; maxillary teeth 20–23 (mean 21.6), modally 22; mandibular teeth 24–27 (mean 25.4), modally 25. Hemipenis: length 7.1–10.3% (mean 8.9%) of snout-vent length; width 57.6–92.5% (mean 81.5%) of hemipenis length; trunk 37.8–60.3% (mean 50.6%) of hemipenis length.

Details of lectotype. SMF 15683 (Fig. 39): Postnasals absent; prefrontals in broad contact; supraciliaries 6; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2; posttemporals 2 (left side only). Midbody scale rows 24; paravertebrals 51; subdigital lamellae smooth, 15 below fourth finger; 19 below fourth toe; supradigital lamellae 13 above fourth finger; 16 above fourth toe; palmars and plantars acute, with no skin visible between scales; plantars 10; palmars 9. Snout-vent length 41.6mm; body length 21.5mm; tail length 57mm; forelimb length 12.8mm; hindlimb length 15.7mm; forebody length 16.8mm; head length 8.3mm; head depth 3.7mm; head width 5.8mm; snout length 3.7mm.

Colouration and pattern. Greyish ground colour, with complex body pattern dominated by dark, broad vertebral zone and broad pale laterodorsal zones (Plate 1.2). Intensity of body pigmentation and patterning variable, ranging from pale and indistinct, to dark and prominent (Fig. 40).

Dorsal ground colour grey to grey-brown, with dark vertebral zone extending from above eye to hindlimbs. Vertebral zone about as wide as paired paravertebral scales, dark grey to dark brown, dotted with paler specks and short longitudinal black streaks and spots. Latter spots most prominent on outer edges of paravertebral scales and usually forming two broken, narrow black stripes from neck to tailbase, where they merge creating blackish median, tapering stripe on anterior third of tail. Pale grey to pale brown laterodorsal zones extending from above eye onto tail, broadest on posterior

Fig. 38. Ventral surface of hind foot of *Cryptoblepharus australis* showing pale, acute plantar scales (NTM R23472, Camooweal, Qld). Scale: x20.

Fig. 39. Lectotype of *Ablepharus boutoni australis* Sternfeld, 1918. SMF 15683, Hermannsburg, Northern Territory, Australia.

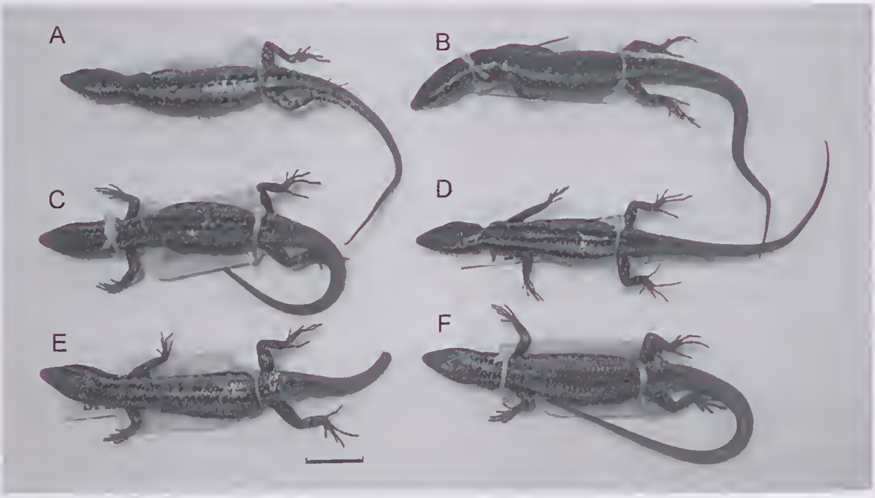

Fig. 40. *Cryptoblepharus australis*. NTM preserved material. **A**, R23448, Blackall, Qld; **B**, R25745, Camooweal, Qld; **C**, R22031, Copley, SA; **D**, R23454, Barcaldine, Qld; **E**, R22030, Copley, SA; **F**, R22029, Copley, SA. Scale bar = 10 mm.

half of body, subequal in width to the dark vertebral zone, tapering anteriorly into prominent narrow stripes extending to eye and posteriorly to form tail ground colour. Edges of pale laterodorsal zones usually ragged, interdigitating with broken dark paravertebral stripes and dark upper lateral zone. Laterodorsal zones usually uniform, but may contain fine pale speckling. Head concolorous with vertebral zone or coppery brown, usually with fine dark margins to scales. Laterally patterned with continuation of dark upper lateral zone, extending above ear, through eye to loreals. Pale grey lower temporal region flecked with dark spots and streaks. Labials and mental pale cream.

Flanks patterned with black upper lateral zone, variable in width, extending from loreals onto tail and forming ragged outer border to pale laterodorsal zone. Usually flecked with pale specks and short streaks, upper lateral zone may be represented by narrow broken black stripe but typically is 2–3 lateral scales wide and coalescing gradually into pale grey/pale grey-brown lower lateral zone. Lower lateral zone flecked with small pale spots and streaks and coalescing into pale venter. Tail concolorous with body, patterned with broken continuations of blackish vertebral and upper lateral zones. Limbs and toes concolorous with body, patterned with pale and dark speckling. Venter, including palmars and plantars, immaculate off-white.

Sex ratio and reproductive biology. Sex ratio favoured males (60:45), but was not significantly different from parity ($X^2 = 2.14$). Males mature at approximately 34 mm snout-vent length and females at 35 mm. Assessment of 71 reproductively active specimens indicated breeding is seasonal, with most being collected during spring and summer. Of 31 females, 25 were collected between December and January, and five between October and November. Of 40 males, 32 were collected between September and January.

Comparison with Australian congeners. Fixed allelic differences place *C. australis* in lineage 1 of Australian *Cryptoblepharus* and also distinguish it from most congeners within that lineage (as OTU carnD, Horner and Adams 2007). With no fixed allelic differences, *C. australis* is genetically similar to *C. metallicus* (as OTU plagA5, Horner and Adams 2007).

Morphologically distinguished from lineage 1 congeners *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus* and *C. wulbu* sp. nov. by ground colour and body pattern characteristics (greyish, longitudinally aligned pattern versus reddish, randomly speckled or blotched pattern), by being arboreal rather than saxicoline and by fewer mid-body scale rows (modally 24 versus 26), deeper head (mean 42.3 versus 32.5–36.0 % of SVL), and shorter hindlimbs (mean 41.1 versus 44.6–47.3 % of SVL). Distinguished from *C. buchananii*, *C. cygnatus* sp. nov., *C. metallicus* and *C. ruber* by having acute, instead of ovate, plantar scales.

Distinguished from most lineage 2 members (*C. adamsi* sp. nov., *C. fuhni*, *C. gurrmul* sp. nov., *C. litoralis*, *C. pulcher*, *C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov.) by usually having six, rather than five, supraciliary scales, acute instead of ovate plantar scales and a complex body pattern on a grey or brown ground colour. *Cryptoblepharus australis* is most similar to *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. in having combinations of complex body patterns, acute plantar scales and being arboreal. However it differs from all of these by usually having six, instead of five, supraciliary scales (modally 6 versus 5). Further differs from *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. by having smooth instead of keeled subdigital lamellae and from *C. exochus* sp. nov. by having fewer palmar scales (modally 9 versus 10) and more posterior temporal scales (modally 3 versus 2).

Not withstanding allozymic similarity (Horner and Adams 2007), comparison of 105 *C. australis* to 120 *C. metallicus* identified the following morphological differences: acute versus ovate plantar scales; wider head (mean 4.9 versus 4.7 % of head length); more fourth toe subdigital lamellae (modally 19 versus 18), plantar scales (modally 12 versus 10) and posterior temporal scales (modally 3 versus 2), providing evidence for specific designation.

Distribution. Arid inland Australia, extending north to vicinity of Barkly Highway in the Northern Territory and Queensland, east to the central plains of Queensland and New South Wales, and south to Eyre Peninsula in South Australia (Fig. 41). In Western Australia, known from Murchison and Great Victoria Desert bioregions, and probably also occurs in most bioregions adjoining southern Northern Territory and South Australia.

Sympatry. *Cryptoblepharus australis* occurs in sympatry with *C. buchananii* from lineage 1 and *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. pulcher* and *C. zoticus* sp. nov. from lineage 2 (Table 6).

Geographic variation. Geographic variation was investigated by separating specimens into four groups: *FLB*, a South Australian and south-eastern Western Australia group of 12 (4 ♂, 8 ♀), samples from bioregions COO, FLB, GAW, MUR and STP; *MAC*, a central northern group of 49 (33 ♂, 16 ♀) samples from bioregions BRT, GSD, MAC and TAN; *MGD*; a north-eastern group of 30 (14 ♂, 16 ♀) samples from bioregions MGD, CHC, DMR, MGD and MII; *ML*, a south-eastern group of 14 (9 ♂, 5 ♀) samples from bioregions BBS, DRP, ML and RIV.

Group pairs, where sexes were treated separately and combined, were subjected to tests of allometrically adjusted variables. Some variation in body proportions was detected, principally resulting from *MAC* (both sexes) being smaller than *FLB*, *MGD* and *ML* (SVL mean 39.6 versus 41.1, 41.0 and 41.6 mm; BL mean 16.5 versus 19.1, 19.1 and 18.3

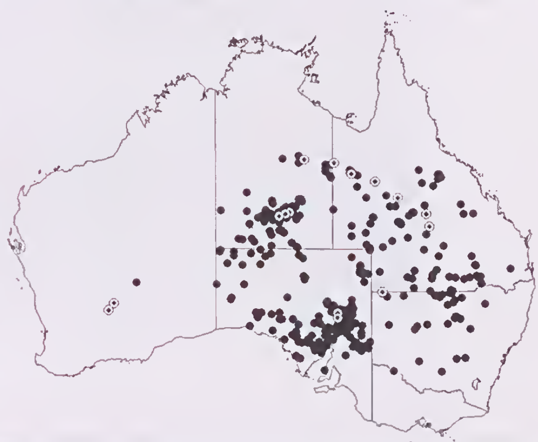

Fig. 41. Map of Australia showing distribution of *Cryptoblepharus australis*. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

Table 6. List of congeners sympatric with *Cryptoblepharus australis*, giving areas of sympatry.

Congeners sympatric with *Cryptoblepharus australis*	Area of sympatry
C. buchananii	WA: Comet Vale
C. pannosus sp. nov	Qld: Emerald, Blackall, Augathella, Roma, Alton Downs, Endfield Stn, Bellata. NSW: Sturt National Park, Byerawering Stn, Thurloo Downs, Cuddie Springs, Lightning Ridge, Brewarrina, Quambone, Mootwingee National Park, Wilcannia, Booligal, Yaneo, Warraderry State Forest. SA: Davenport Springs, Italowie Gap, Oraparinna Stn, Mutooroo Stn, Davies Ruins, 11 km SW of Clifton Hills Outstation, Mount Bryan, Loch Ness Well (Gammon Ranges)
C. pulcher clarus	SA: Eyre Peninsula, Wardang Island
C. zoticus sp. nov.	Qld: Mary Kathleen
Multiple sympatry	
C. ochrus sp. nov. + *C. pannosus* sp. nov.	SA: Clifton Hills

mm respectively) and having a deeper head (HD mean 3.3 versus 3.1, 3.2 and 3.1 mm respectively). Although these results indicate geographic variation in *C. australis*, both characters lost significance when sexes were combined. Though variable, southern groups *FLB* and *ML*, tended to have higher midbody scale rows counts (modally 26) than northern groups *MAC* and *MGD* (modally 24).

Habits and habitats. *Cryptoblepharus australis* occurs in a variety of habitats. Normally an arboreal species, museum records note its use of woodland associated with watercourses, flat plains, rocky hills and gorges, shrubland on hills and flat plains, and spinifex on hills. Connected with these records have been numerous tree and/or shrub species, including: *Acacia aneura, A. estrophiolata, A. kempeana, Callitris glaucophylla, Eucalyptus camaldulensis, E. coolibah, E. intertexta, E. microtheca, E. socialis* and *Triodia longiceps*. Individuals have been recorded from litter under *E. camaldulensis* and on rocks. In urban environments *C. australis* has been recorded on tree trunks, buildings, fences, rails or posts, in litter under citrus trees, under bark on dead pepper tree, on fig trees in park, on *Casuarina* trunks, on a 200 litre drum and on a footpath.

Taxonomic history. Sternfeld (1918) described *Ablepharus boutoni australis* from two Senckenberg Museum specimens, collected by Moritz von Leonhardi at Hermannsburg, Northern Territory in 1907. Sternfeld diagnosed the taxon by "..b) Schuppen in 24 Reihen. auffallend stark gestreift; Postnasale fehlend oder undeutlich; Oberseite hellbraun, mehr oder weniger dunkelbraun gefleckt; Dorsolateralstreifen sehr undeutlich. Schnauze sehr kurz ….. *A. b. australis* nov. subspec. West-Central-Australien, Mus. No. 6347, 1m, 2 Exempl., ("Scales in 24 series, remarkably strongly striped; postnasal missing or indistinct; dorsal surface light brown with more or less dark-brown spotting; dorsolateral stripe very indistinct. Snout very short"). Type locality was given as west Central Australia. Since that time, the syntypes have been allocated new SMF catalogue numbers and are now labelled SMF 15683 and 15684.

Mertens (1931) treated *C. australis* as a synonym of *A. b. metallicus,* using the two *A. b. australis* types as the basis of his *A. b. metallicus* description. He considered that Sternfeld described the *A. b. australis* subspecies unnecessarily, and noted that catalogue numbers indicated both specimens belonged to herpetological material collected at Hermannsburg. Sternfeld (1924) had already re-defined the type locality as Hermannsburg, upper Finke River, central Australia. Later, Mertens (1964) questioned the status of *C. metallicus*, stating that SMF 15683-84 displayed no *C. metallicus* features and should be considered faded examples of *C. plagiocephalus*, a designation followed by most subsequent authors. Mertens (1967) designated SMF 15683 as the lectotype of *A. b. australis*.

Cryptoblepharus buchananii (Gray, 1838)

Buchanan's snake-eyed skink

(Plate 1.3; Figs 42–45)

Tiliqua buchananii Gray, 1838: 291 (New Holland).

Ablepharus peronii var. *peronii* Duméril and Bibron, 1839. – Boulenger 1887: 347.

Ablepharus boutoni punctatus Sternfeld, 1918: 424.

Ablepharus boutoni plagiocephalus (Cocteau, 1836). – Mertens 1931: 116; Storr 1961: 176; Worrell 1963: 34; Mertens 1964: 107.

Ablepharus boutonii metallicus Boulenger, 1887. – Loveridge 1934: 375.

Cryptoblepharus plagiocephalus (Cocteau, 1836). – Storr, 1976: 56; Storr and Hanlon 1980: 431; Storr *et al.* 1999: 24, figs Plate 2 (3); Storr *et al.* 1983: 223; Cogger *et al.* 1983a: 142; Wilson and Knowles 1988: 120; Dudley 1989: 1; Ehmann 1992: 182; Storr *et al.* 1999: 24; Cogger 2000: 406; Brooker *et al.* 1995: 180; Bush *et al.* 1995: 112, fig. page 112; Maryan 1996: 9; Stanger *et al.* 1998: 23; Wilson and Swan 2003: 148.

Type material examined. *Tiliqua buchananii* Gray, 1838. SYNTYPES: BMNH 1946.8.19.73, W. Australia; BMNH 1946.8.19.74, W. Australia. *Ablepharus boutonii punctatus* Sternfeld, 1918. LECTOTYPE: SMF 15685, Yalgoo, W. Australia, coll. A. Görling, 1907.

Non-type material examined. See Appendix 4.

Diagnosis. A large (45–50 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from Australian congeners by combination of usually having: six supraciliary scales; 24 mid-body scale rows; 52 paravertebral scales; 19 smooth subdigital lamellae under the fourth toe; hindlimb length 41.1% of SVL; head depth 42.3% of head length; tail length 136% of SVL; rounded, usually callused plantar scales; greyish, longitudinally aligned body pattern and being arboreal.

Description (44 specimens). Postnasals absent; prefrontals usually in broad contact (93%), occasionally in narrow contact (3%) or separated (4%); supraciliaries 5–7 (mean 6.0), modally 6; enlarged upper ciliaries 3–4 (mean 3.0), modally 3; posterior loreal largest (98%), occasionally subequal (2%); supralabials 7–8 (mean 7.0), modally 7; fifth supralabial subocular (100%); infralabials 5–7 (mean 6.0), modally 6; nuchals usually 2 (96%), occasionally 3 (2%) or 7 (2%); bilateral posttemporals usually 3+3 (80%), occasionally 2+3 (10%), or 2+2 (10%).

Midbody scale rows 22–28 (mean 24.9), modally 24; paravertebrals 45–57 (mean 52.0), modally 52; subdigital lamellae smooth, 13–17 below fourth finger (mean 14.7) modally 14, 16–20 below fourth toe (mean 17.9), modally 18; 11–15 supradigital lamellae above fourth finger (mean 12.8) modally 13, 14–19 above fourth toe (mean 15.3), modally 15; palmar and plantar scales rounded (Fig. 42), occasionally capped with dark brown calli, skin usually visible between scales; plantars 8–13 (mean 9.7), modally 10; palmars 7–9 (mean 8.2), modally 8.

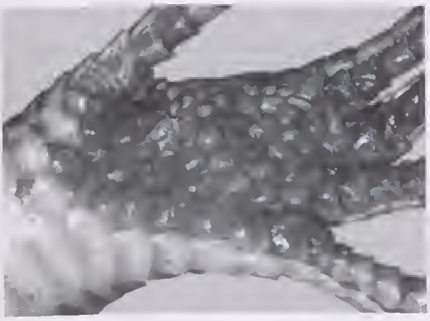

Fig. 42. Ventral surface of hind foot of *Cryptoblepharus buchananii*, showing light brown, ovate plantar scales (NTM R22061, Donnybrook, WA). Scale: x20.

Fig. 43. Lectotype of *Ablepharus boutoni punctatus*, SMF 15685, Yalgoo, WA.

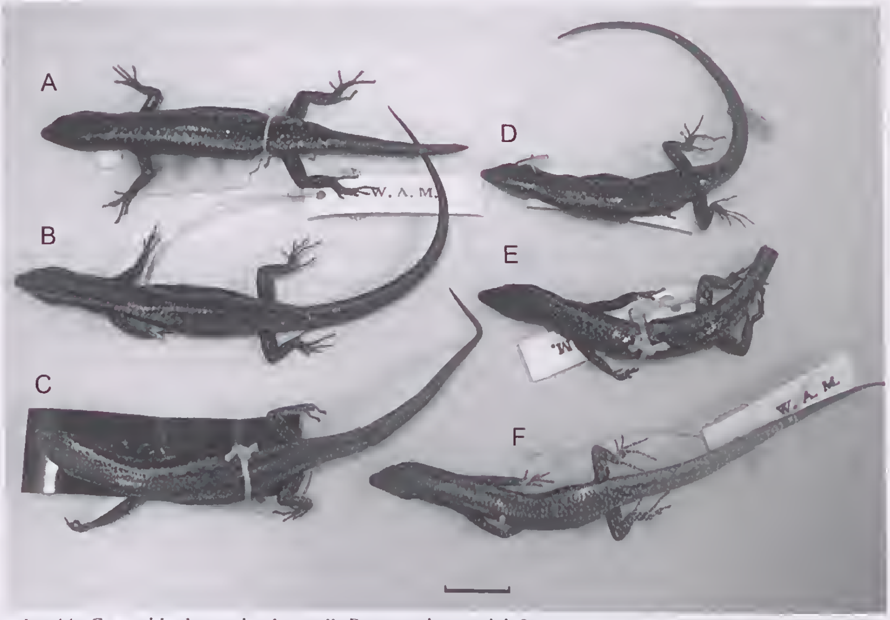

Fig. 44. *Cryptoblepharus buchananii*. Preserved material from Western Australia: **A**, NTM R22062, Donnybrook; **B**, WAM R68030, Lake Cronin; **C**, WAM R26521, Zanthus; **D**, R83755, Durba Gorge; **E**, WAM R42294, Jiggalong; **F**, WAM R84097, Coondil Pool, Mt Clere Station. Scale bar = 10 mm.

Snout-vent length to 49.3 mm (mean 41.1 mm). *Percentages of snout-vent length*: body length 47.0–55.8% (mean 51.0%); tail length 117.4–155.2% (mean 133.6%); forelimb length 30.2–37.1% (mean 34.1%); hindlimb length 35.9–45.9% (mean 41.5%); forebody length 38.3–46.8% (mean 42.2%); head length 19.7–22.8% (mean 21.2%). *Percentages of head length*: head depth 36.9–48.5% (mean 42.0%); head width 53.6–67.4% (mean 59.8%); snout length 41.5–47.5% (mean 44.4%). Paravertebral scale width 3.3–4.9% (mean 3.9%) of snout-vent length; dorsolateral scale width 75.1–107.6% (mean 89.7%) of paravertebral scale width.

Lenticular scale organs 2–5 (mean 4.0), modally 4. Premaxillary teeth 4–5 (mean 4.7), modally 5; maxillary teeth 20–21 (mean 20.2), modally 20; mandibular teeth 23–25 (mean 23.7), modally 23. Hemipenis: length 7.6% (n = 1) of snout-vent length; width 88.9% (n = 1) of hemipenis length; trunk 45.9% (n = 1) of hemipenis length.

Details of primary types. *Tiliqua buchananii* Gray, 1838. SYNTYPE: BMNH 1946.8.19.73. Postnasals absent; prefrontals in broad contact; supraciliaries 6; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 26; paravertebrals 51; subdigital lamellae smooth, 13 below fourth finger; 19 below fourth toe; supradigital lamellae 12 above fourth finger; 14 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 8; palmars 8. Snout-vent length 43.1 mm; body length 22.3 mm; tail not original; forelimb length 14.1 mm; hindlimb length 16.9 mm; forebody length 16.5 mm; head length 8.6 mm; head depth 3.6 mm; head width 5.7 mm; snout length 3.8 mm. SYNTYPE: BMNH 1946.8.19.74. Postnasals absent; prefrontals in broad contact; supraciliaries 6; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 7; nuchals 2. Midbody scale rows 24; paravertebrals 50; subdigital lamellae smooth, 14 below fourth finger; 18 below fourth toe; supradigital lamellae 13 above fourth finger; 16 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 8; palmars 8. Snout-vent length 41.2 mm; body length 19.2 mm; tail not original; forelimb length 14.0 mm; hindlimb length 17.2 mm; forebody length 17.8 mm; head length 8.6 mm; head depth 3.2 mm; head width 5.1 mm; snout length 3.1 mm.

Ablepharus boutonii punctatus Sternfeld, 1918. LECTOTYPE: SMF 15685 (Fig. 43). Postnasals absent; prefrontals in broad contact; supraciliaries 6; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 26; paravertebrals 53; subdigital lamellae smooth, 16 below fourth finger; 16 below fourth toe; supradigital lamellae 14 above fourth finger; 17 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 9; palmars 8. Snout-vent length 37.3 mm; body length 17.8 mm; tail not original; forelimb length 12.1 mm; hindlimb length 15.8 mm; forebody length 16.3 mm; head length 8.0 mm; head depth 3.4 mm; head width 5.2 mm; snout length 3.7 mm.

Colouration and pattern. Greyish, brownish or blackish, with longitudinally aligned, complex body pattern dominated by broad, dark vertebral zone and pale laterodorsal zones/stripes (Plate 1.3, Fig. 44). Intensity of body pigmentation and patterning is variable, both individually and geographically, ranging from pale and obscure (Fig. 44F) to dark and prominent (Fig. 44A). Most specimens conform to the following description.

Dorsal ground colour grey, grey-brown or grey-black, with broad, dark vertebral zone extending from above eye to hindlimb. Vertebral zone as wide as paired paravertebral scales, dark grey to dark brown, peppered with pale spots and/or specks and dotted with short longitudinal black streaks and spots. Latter most prominent on outer edges of paravertebral scales, forming two ragged, narrow black stripes from neck to tailbase, where they merge creating tapering, blackish median stripe on anterior third of tail. Pale grey to pale brown laterodorsal zones, or broad stripes, extending from above eye onto tail, broadest on posterior half of body, about half width of dark vertebral zone, tapering anteriorly into prominent narrow stripes to eye, and posteriorly to form tail ground colour. Edges of pale laterodorsal zones ragged, interdigitating with broken dark paravertebral stripes and dark upper lateral zone. Laterodorsal zones usually uniform, but may have fine pale and/or dark speckling. Head concolorous with vertebral zone, variegated with fine dark margins to scales. Laterally patterned with continuation of dark upper lateral zone, extending above ear, through eye to loreals. Pale lower temporal region flecked with dark spots and streaks. Labials pale cream.

Laterally, black upper zone, variable in width, extendingfrom loreals onto tail, forming ragged border to pale dorsolateral zone. Flecked with pale specks and short streaks, upper lateral zone may be represented by narrow broken black stripe but usually about two lateral scales wide and coalescing gradually into pale grey/pale grey-brown lower lateral zone. Lower lateral zone peppered with small pale and/or dark spots and streaks and coalescing into pale venter. Tail concolorous with body, patterned with broken continuations of blackish vertebral and upper lateral zones. Limbs and toes concolorous with body, patterned with pale and dark speckling. Ventral surface immaculate off-white. Palmar and plantar scales off-white, outer rows capped with dark brown calli.

Southern populations tend to be darker (Fig. 44A), with broader dark vertebral zones and speckled, pale blue/grey venter. Occasional specimens are obscurely patterned, with little indication of vertebral zones and pale dorsolateral stripes (Fig. 44F).

Sex ratio, sexual dimorphism and reproductive biology. Sex ratio favoured females (25:19), but was not significantly different from parity ($X^2 = 0.82$). Males mature at about 35 mm snout-vent length and females at 38 mm. Sample size of reproductively active animals was 17 and analysis suggested that breeding usually occurs in the spring/summer but may take place all year round. Eight reproductive females were recorded between January and March and five between September and November, one reproductive male in May and three between August and September.

At a study site near Perth, Western Australia, Davidge (1980) identified a spring/summer breeding season, with no gravid females being caught in autumn or winter. Davidge (1980) further determined a minimum snout-vent length at maturity of 30 mm, a modal clutch size of two eggs and a sex ratio that favoured males (49:30).

Comparison with Australian congeners. Fixed allelic differences place *C. buchananii* in lineage 1 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTU plagA4, Horner and Adams 2007).

Morphologically distinguished from lineage 2 members *C. adamsi*, *C. fuhni*, *C. gurrmul* sp. nov., *C. litoralis*, *C. pulcher*, *C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov. by usually having six, rather than five, supraciliary scales and complex body pattern on a grey or brown ground colour and from *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. by usually having six, rather than five, supraciliary scales and ovate, instead of acute, plantar scales.

Distinguished from lineage 1 congeners *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus* and *C. wulbu* sp. nov. by ground colour and body pattern characteristics (greyish, longitudinally aligned pattern versus reddish, randomly speckled or blotched pattern), by being arboreal rather saxicoline and by fewer mid-body scale rows (modally 24 versus 26), deeper head (mean 42.3 versus 32.5–36.0 % of SVL), and shorter hindlimbs (mean 41.1 versus 44.6–47.3 % of SVL.

Cryptoblepharus buchananii is most similar to *C. cygnatus* sp. nov., *C. metallicus* and *C. ruber* in having combinations of complex body patterns, flat ovate plantar scales, usually six supraciliary scales and being arboreal. However, it differs from *C. cygnatus* sp. nov. by having smooth instead of callused subdigital lamellae, more paravertebral scales (modally 52 versus 49), fewer subdigital lamellae (modally FTL 14 versus 16; HTL 18 versus 19), palmar and plantar scales (modally PAL 8 versus 9; PLN 10 versus 11), more posterior temporal scales (modally 3 versus 2) and larger size (mean SVL 41.1 instead of 37.5 mm). It differs from *C. metallicus* in having more paravertebral (modally 52 versus 48) and posterior temporal scales (modally 3 versus 2), plain instead of callused plantar scales and larger size (mean SVL 41.1 instead of 38.6 mm). Differs from *C. ruber* in having fewer fourth finger subdigital lamellae (modally 14 versus 16), more palmar scales (modally 10 versus 9) and a longer, narrower head (mean HL 21.2 instead of 20.8% of SVL; HW 59.8 instead of 61.5% of head length).

Distribution. Mid and southern Western Australia, from the Pilbara region to much of southern Western Australia (Fig. 45).

Sympatry. *Cryptoblepharus buchananii* occurs in sympatry with *C. australis* from lineage 1 and *C. plagiocephalus* and *C. ustulatus* sp. nov. from lineage 2. Sympatric with *C. australis* at Comet Vale; *C. plagiocephalus* at Greenough, and *C. ustulatus* sp. nov. at Dolphin Island and Weeli Wooli Spring.

Geographic variation. Geographic variation was investigated by separating specimens into three groups: *MW*, a mid-western group of 13 (8 ♂, 5 ♀) samples from bioregions GAS, LSD, MUR and PIL; *MWC*, a coastal group of 9 (2 ♂, 7 ♀) samples from bioregion GS; *VB*, a south-western group of 22 (9 ♂, 13 ♀) samples from bioregions AW, COO, ESP, GVD, JF, MAL, SWA and WAR.

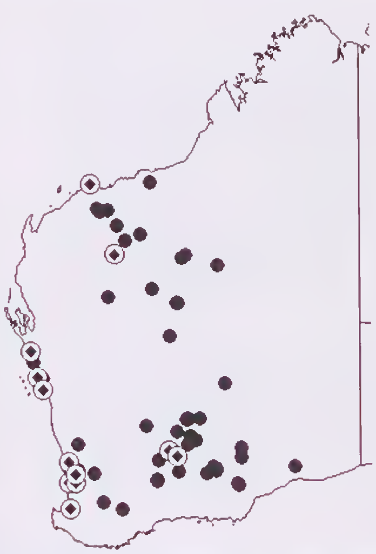

Fig. 45. Map of Western Australia showing distribution of *Cryptoblepharus buchananii*. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

Group pairs, where sexes were treated separately and combined, were analysed by tests of allometrically adjusted variables. Significant difference was detected only in snout-vent length of both sexes between groups *MWC* and *SW*, with *MWC* being slightly smaller than *SW* (maximum SVL 43.3 versus 45.1 mm). Thus geographic variation in *C. buchananii* appears limited to coastal populations on the Geraldton Sandplains (GS) being slightly smaller than those from more southern regions of Western Australia. Though not statistically analysed, assessment of ground colour suggests that south-western populations are more melanotic than those from other regions (Fig. 43a).

Habits and habitats. *Cryptoblepharus buchananii*'s broad geographic range encompasses a variety of habitats. Typically arboreal, museum records of the species note its occurrence in open woodland and urban environments. Within these it has been associated with tree trunks (including *Casuarina* sp.) and man-made structures such as garden sheds, fences and old railway sleepers. Bush *et al.* (1995) confirm *C. buchananii*'s use of rock surfaces, walls, fences and telegraph poles. Maryan (1996) recorded an individual from dead *Acacia* scrub. In the Geraldton region Storr *et al.* (1983) record it (as *C. plagiocephalus*) as uncommon, being found mainly on trees along water-courses and around lagoons, especially *Eucalyptus rudis* in southern parts of the region.

Taxonomic history. Gray (1838) described *Tiliqua buchananii* from two British Museum specimens collected in "New Holland". Gray diagnosed the taxon as, "Ears shallow, overlapped by 2 or 3 whitish superficial scales; scales smooth, olive, black lined; above black and olive varied; back with a broad black-edged silvery streak on each side; limbs, tail, and sides olive and black dotted, beneath silvery". The type locality was re-defined by Boulenger (1887), as originating from Western Australia. Mertens (1931) corroborated this finding, commenting that the two types of *T. buchananii* "obviously originate from west Australia". Examination of the types revealed 'W. Australia' written on the specimen label and confirmed Gray's description of a 'dark' animal. Indicated by the blackish ground colour, *T. buchananii*'s type locality is most likely to be south-west Western Australia.

Without reference to *T. buchananii*, Sternfeld (1918) described *Ablepharus boutoni punctatus*, diagnosing the taxon by 'scales in 26 series, strongly striped, black-brown colouration, brightly spotted, distinct dorsolateral stripes, snout moderately short'. Collection data was given as west Australia, two examples Mus. No. 6347. Post-description, these two syntypes were allocated new SMF catalogue numbers, being now labelled SMF 15685 and 15686 and the type locality restricted to Yalgoo, Western Australia. Mertens (1967) designated SMF 15685 as the lectotype of

A. b. punctatus (Fig. 43). Morphologically, the types of *A. b. punctatus* conform to *C. buchananii*.

Mertens (1922) considered *A. b. punctatus* to be a synonym of *A. b. plagiocephalus*, and later (Mertens, 1931) also included *T. buchananii* in the synonymy of *A. b. plagiocephalus*.

Cryptoblepharus cygnatus sp. nov.

Swanson's snake-eyed skink

(Plates 1.4–1.5; Figs 46–51)

Cryptoblepharus plagiocephalus (Cocteau, 1836). – Storr 1976: 56; Storr *et al.* 1981: 24; Gow 1981b; Cogger *et al.* 1983a: 142; James and Shine 1985: 466; Wilson and Knowles 1988: 120; Sadlier 1990: 26; Horner 1991: 18; Ehmann 1992,: 182; Woinarski and Gambold 1992: 111; Goodfellow 1993: 63; Griffiths *et al.* 1997: 95; Horner and Griffiths 1998: 48; Stanger *et al.* 1998: 23; Horner 1999: 60; Storr *et al.* 1999: 24; Cogger 2000: 406; Wilson and Swan 2003: 148.

Cryptoblepharus swansoni Wells and Wellington, 1985: 27 *(nomen nudum).*

Type material examined. *Cryptoblepharus cygnatus* Horner. HOLOTYPE: Adult male, NTM R.22887 (Tissue sample No. ABTC-AM6), Goose Creek, Melville Island, Northern Territory, 11°30'32"S 130°54'19"E. coll. P. Horner, 8 October 1996, open forest, on *Melaleuca* sp. trunk. PARATYPES (37 specimens): NORTHERN TERRITORY: NTM R10970-971, Jabiluka, 12°33'S 132°53'E, I. Archibald, 3 Jan 1983; NTM R13592, north road, Murgenella, 11°28'S 132°51'E, P. Horner, 15 Jul 1987, ABTC H25; NTM R13729, Swim Creek, Point Stuart Station, 12°34'S 131°53'E, P. Horner, 24 Apr 1988, ABTC H78; NTM R13770, Ja Ja, 12°31'S 132°49'E, M. King, 12 Jul 1988, ABTC H99; NTM R16117-118, Goomadeer River crossing, Arnhem Land, 12°07'S 133°41'E, P. Horner, 11 Jul 1989, ABTC K15-K16; NTM R18762-763, Bullocky Point, Darwin, 12°26'S 130°50'E, P. Horner, 12 Nov 1997, ABTC BT7-BT8; NTM R21028, Black Point, Cobourg Peninsula, 11°09'S 132°10'E, P. Horner, 28 Sep 1990, ABTC P24; NTM R21047, Black Point, Cobourg Peninsula, 11°10'S 132°10'E, P. Horner, 30 Sep 1990, ABTC P55; NTM R21174, Jabiluka Project Area, 12°33'S 132°55'E, J. Bywater, 6 Jun 1994, ABTC S19; NTM R21508-509, Bullocky Point, Darwin, 12°26'S 130°50'E, P. Horner, 26 May 1995, ABTC V02-VO3; NTM R21684, Shoal Bay, Military Reserve, 12°22'S 130°58'E, P. Horner, 25 Jul 1995; NTM R21740, R21744, Litchfield National Park, Tjaynera Falls area, 13°15'S 130°44'E, P. Horner, 18 Oct 1995, ABTC V56, V60; NTM R22098-099, Adelaide River Town, 13°14'S 131°08'E, P. Horner, 26 Jan 1996, ABTC Y67-Y68; NTM R22105, Howard Springs, 12°28'S 131°04'E, R. Horner, 11 Feb 1996, ABTC Y71; NTM R22451, Point Guy, Howard Island, 12°11'S 135°13'E, G. Brown, 1996, ABTC Z74; NTM R22854, R22867, Taracumbie Falls, Melville Island, 11°36'S 130°42'E, P. Horner, 4 Oct 1996, ABTC AH2, AJ4; NTM R22881, R22884-886, R22888, R22891-893, R22900, Goose Creek, Melville Island, 11°30'S 130°54'E, P. Horner, 8 Oct 1996, ABTC AL4, AM3-AM5, AM7, AN1-AN3, AO4; NTM R23025-026, Maxwell Creek Airstrip, Melville Island, 11°32'S 130°35'E, P. Horner, 16 Oct 1996, ABTC AX5-AX6; NTM R23734, Stuart Park, Darwin, 12°26'S 130°50'E, P. Horner, 17 Mar 1996, ABTC Y73; NTM R23927-928, The Crossing, Arafura Swamp, Arnhem Land, 12°24'S 135°00'E, P. Horner, 25 Jul 1998, ABTC DC6-DC7.

Non-type material examined. See Appendix 4.

Diagnosis. A medium sized (40–44 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of six supraciliary scales and 24 mid-body scale rows; mean values of hindlimb length 42.0% of SVL, head depth 43.3% of head length, hemipenis length 10.1% of snout-vent length; callused subdigital lamellae; rounded, plain plantar scales; greyish, longitudinally aligned body pattern and arboreal habits.

Description (71 specimens). Postnasals absent; prefrontals usually in broad contact (74%), occasionally in narrow contact (13%) or narrowly separated (13%); supraciliaries 5–7 (mean 6.0), modally 6; enlarged upper ciliaries 2–5 (mean 3.1), modally 3; posterior loreal usually largest (79%), occasionally subequal (21%); supralabials 7–8 (mean 7.1), modally 7; fifth supralabial usually subocular (90%), occasionally sixth (10%); infralabials 6–7 (mean 6.0), modally 6; nuchals 2–4 (mean 2.1), modally 2; bilateral posttemporals usually 2+2 (61%), occasionally 3+3 (23%), or 2+3 (16%).

Midbody scale rows 22–24 (mean 23.4), modally 24; paravertebrals 44–54 (mean 49.2), modally 49; subdigital lamellae with dark brown calli (Fig. 46B), 15–19 below fourth finger (mean 16.2) modally 16, 17–22 below fourth toe (mean 19.7) modally 19; 11–15 supradigital lamellae above fourth finger (mean 12.9) modally 13, 13–18 above fourth toe (mean 15.2) modally 15; palmar and plantar scales rounded, not capped with dark calli, skin usually visible between scales (Fig. 46A); plantars 9–15 (mean 10.9), modally 11; palmars 7–10 (mean 9.1), modally 9.

Snout-vent length to 44.6 mm (mean 37.5 mm). *Percentages of snout-vent length*: body length 42.7–58.6% (mean 50.6%); tail length 116.5–156.5% (mean 136.5%); forelimb length 29.0–38.4% (mean 33.5%); hindlimb length 36.7–47.8% (mean 42.0%); forebody length 35.8–47.4% (mean 42.0%); head length 18.8–24.0% (mean 21.1%). *Percentages of head length*: head depth 36.2–58.6% (mean 43.3%); head width 52.8–67.5% (mean 60.3%); snout length 42.6–49.9% (mean 46.1%). Paravertebral scale width 3.4–5.7% (mean 4.4%) of snout-vent length; dorsolateral scale width 72.1–99.4% (mean 86.4%) of paravertebral scale width.

Lenticular scale organs 4–20 (mean 11.0), modally 11. Premaxillary teeth 4–5 (mean 4.9), modally 5; maxillary teeth 17–20 (mean 18.7), modally 19; mandibular teeth 21–25 (mean 22.9), modally 22. Hemipenis: length 8.7–12.0%

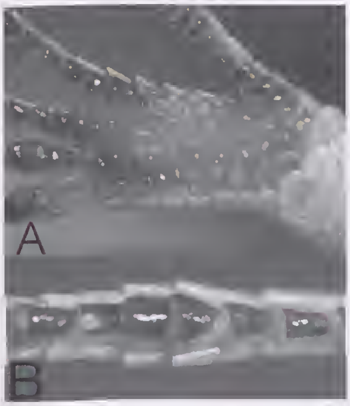

Fig. 46. Ventral surface of hind foot of *Cryptoblepharus cygnatus* sp. nov., showing (**A**) pale, ovate plantar scales and (**B**) callused fourth toe subdigital lamellae (NTM R22451, Point Guy, Howard Island, NT). Scale: A = x20; B = x70.

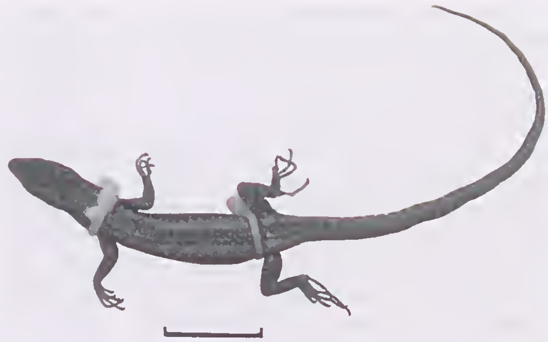

Fig. 47. Holotype of *Cryptoblepharus cygnatus* sp. nov. (NTM R22887, Goose Creek, Melville Island, NT. 11°30'S 130°54'E, ABTC AM6). Scale bar = 10 mm.

Fig. 48. Holotype of *nomen nudum Cryptoblepharus swansoni* Wells and Wellington, 1985 (NTM R2915, Smith Street, Darwin, NT). Scale bar = 10 mm.

Fig. 49. Hybrid of *Cryptoblepharus cygnatus* sp. nov. x *C. metallicus* (NTM R18837, Hi-way Inn, Daly Waters, NT). Scale bar = 10 mm.

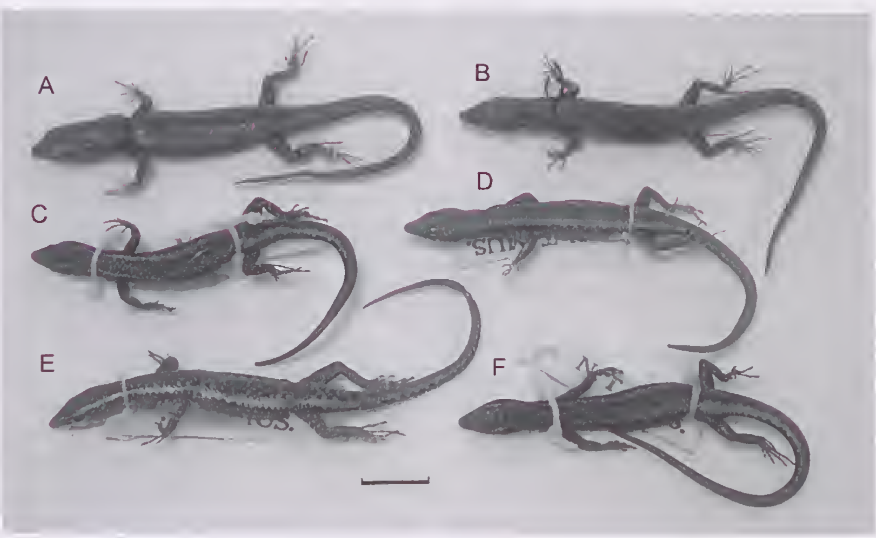

Fig. 50. *Cryptoblepharus cygnatus* sp. nov. NTM preserved material from the Northern Territory. **A** and **B**, R10970-971, Jabiluka; **C**, R22884, Melville Island; **D**, R16117, Goomadeer River; **E**, = R22451, Howard Island; **F**, R22885, Melville Island. Scale bar = 10 mm.

(mean 10.1%) of snout-vent length; width 66.6–103.3% (mean 86.0%) of hemipenis length; trunk 39.8–55.2% (mean 48.0%) of hemipenis length.

Details of holotype. NTM R.22887, adult male (Fig. 47). Postnasals absent; prefrontals in broad contact; supraciliaries 6; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 23; paravertebrals 48; subdigital lamellae callused, 16 below fourth finger; 19 below fourth toe; supradigital lamellae 14 above fourth finger; 16 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 11; palmars 10. Snout-vent length 31.8 mm; body length 15.7 mm; tail length 47.9 mm; forelimb length 11.2 mm; hindlimb length 13.2 mm; forebody length 13.9 mm; head length 7.2 mm; head depth 2.8 mm; head width 3.8 mm; snout length 3.2 mm.

Details of other primary types. *Cryptoblepharus swansoni* Wells and Wellington, 1985 (*nomen nudum*). HOLOTYPE: NTM R.2915 (Fig. 48). Smith Street, Darwin, Northern Territory. R. Pengilley, 17 January 1977. Postnasals absent; prefrontals in broad contact; supraciliaries 6; enlarged upper ciliaries 3; loreals subequal; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 24; paravertebrals 47; subdigital lamellae callused, 15 below fourth finger; 21 below fourth toe; supradigital lamellae 12 above fourth finger; 15 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 11; palmars 9. Snout-vent length 41.8 mm; body length 22.7 mm; tail length 54.0 mm; forelimb length 12.1 mm; hindlimb length 15.7 mm; forebody length 15.9 mm; head length 8.2 mm; head depth 4.0 mm; head width 5.0 mm; snout length 3.8 mm.

Colouration and pattern. A grey or brownish *Cryptoblepharus*, with longitudinally aligned, complex body pattern dominated by dark, broad vertebral zone and pale laterodorsal zones (Plate 1.4). Intensity of body pigmentation and patterning variable, ranging from pale and obscure (Fig. 50B) to dark and prominent (Fig. 50C). Melanism can occur in this taxon (Plate 1.5). Most specimens conform to the following description.

Dorsal ground colour grey to grey-brown, with broad, dark vertebral zone extending from above eye to hindlimb. Vertebral zone as wide as paired paravertebral scales, grey-brown to blackish, with pale spots/specks and dotted with short longitudinal blackish streaks and spots. Latter most prominent on outer edges of paravertebrals and usually forming two broken, narrow black stripes from neck to tailbase, where they merge creating blackish median, tapering stripe on anterior third of tail. Pale grey to pale brown laterodorsal zones extending from above eye onto tail, broadest on posterior half of body, about width of dark vertebral zone, tapering anteriorly into prominent narrow stripes extending to eye and posteriorly to form tail ground colour. Edges of pale laterodorsal zones usually ragged, interdigitating with broken dark paravertebral stripes and dark upper lateral zone. Laterodorsal zones usually uniform, but may contain fine pale and/or dark speckling. Head concolorous with vertebral zone or coppery brown, usually with fine dark margins to shields. Laterally, head patterned with continuation of dark upper lateral zone, extending above ear, through eye to loreals. Pale lower temporal region flecked with dark spots and streaks. Labials pale cream.

Laterally, a dark upper zone, variable in width, extendsing from loreals onto tail, forming ragged border to pale laterodorsal zone. Usually broken by pale spots and short streaks, upper lateral zone may be represented by narrow broken black stripe but typically about two lateral scales wide and coalescing gradually into pale grey/pale grey-brown lower lateral zone. Lower lateral zone peppered with small pale and/or dark spots and streaks and coalescing into pale venter. Tail concolorous with body, patterned with broken continuations of blackish vertebral and upper lateral zones. Limbs and toes concolorous with body, patterned with pale and dark speckling. Ventral surfaces immaculate off-white. Palmars and plantars finely speckled with dark brown, but not callused. Most subdigital lamellae capped with shiny dark brown calli (Fig. 46B).

Sex ratio, sexual dimorphism and reproductive biology. Sex ratio favoured males (41:30), but was not significantly different from parity ($X^2 = 1.70$). Males mature at approximately 32 mm snout-vent length and females at 35 mm. James and Shine (1985) determined that *C. cygnatus* sp. nov. (as *C. plagiocephalus*), from the Alligator Rivers region of the Northern Territory, was reproductive at most times of the year. This study supports their results, with 46 reproductively active animals being collected over virtually all months.

Comparison with Australian congeners. Fixed allelic differences place *C. cygnatus* sp. nov. in lineage 1 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTU plagB, Horner and Adams 2007).

Morphologically distinguished from lineage 2 members *C. adamsi, C. fuhni, C. gurrmul* sp. nov., *C. litoralis, C. pulcher, C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov. by usually having six, rather than five, supraciliary scales and complex body pattern on a grey or brown ground colour and from *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. by usually having six, rather than five, supraciliary scales and ovate, instead of acute, plantar scales.

Distinguished from lineage 1 congeners *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus* and *C. wulbu* sp. nov. by ground colour and body pattern characteristics (greyish, longitudinally aligned pattern versus reddish, randomly speckled or blotched pattern), by being arboreal rather saxicoline and by fewer mid-body scale rows (modally 24 versus 26), deeper head (mean 43.3 versus 32.5–36.0 % of SVL), and shorter hindlimbs (mean 42.0 versus 44.6–47.3 % of SVL).

Cryptoblepharus cygnatus sp. nov. is most similar to *C. buchananii, C. metallicus* and *C. ruber* in having combinations of complex body patterns, flat ovate plantar scales, usually six supraciliary scales and being arboreal. However, it differs from these in having callused instead of mostly smooth subdigital lamellae. It differs from *C. buchananii* by having fewer paravertebral scales (modally 49 versus 52), more subdigital lamellae (modally FTL 16 versus 14; HTL 19 versus 18), palmar and plantar scales (modally PAL 9 versus 8; PLN 11 versus 10), fewer posterior temporal scales (modally 2 versus 3) and smaller size (mean SVL 37.5 instead of 41.1 mm). It differs from *C. metallicus* by having smooth instead of callused plantar scales, more subdigital lamellae (modally FTL 16 versus 14; HTL 19 versus 18) and palmar and plantar scales (modally PAL 9 versus 8; PLN 11 versus 10). It differs from *C. ruber* by having smooth instead of callused plantar scales, fewer paravertebral scales (modally 49 versus 54), more plantar scales (modally 11 versus 9) and fewer posterior temporal scales (modally 2 versus 3).

Distribution. Far northern Northern Territory, from eastern Arnhem Land to west of Darwin (Fig. 51). The southern boundary of its known range is approximately 120 kilometres south of Darwin; however, a hybrid animal of *C. cygnatus* sp. nov. x *C. metallicus* origin was collected at Daly Waters, 500 km south of Darwin.

Sympatry. *Cryptoblepharus cygnatus* sp. nov. occurs in sympatry with lineage 1 co-members *C. metallicus* and *C. wulbu* sp. nov. sympatric with *C. metallicus* at Jabiluka and Jabiru in Kakadu National Park and with *C. wulbu* sp. nov. at Mount Borradaile, north-west Arnhem Land.

Fig. 51. Map of the Northern Territory showing distribution of *Cryptoblepharus cygnatus* sp. nov. Circled diamonds indicate genetically identified sample sites, star indicates collection site of *C. cygnatus* sp. nov. x *C. metallicus* hybrid (Horner and Adams 2007).

Geographic variation. Geographic variation was investigated by separating specimens into three groups: Arnhem, an eastern 'Top End' group of ten (7 ♂, 3 ♀) samples from bioregions ARC and ARP; Darwin, a western 'Top End' group of 45 (27 ♂, 18 ♀), from bioregions DAC and PCK, and Tiwi, a group of 16 (7 ♂, 9 ♀) from Melville Island.

Group pairs of each sex were subjected to tests of allometrically adjusted variables. Significant differences were detected between sexes of all groups, but significance was usually lost when combined sexes were analysed. Groups *Darwin* and *Tiwi* showed significant differences, both between sexes and combined, in head depth and head width with *Darwin* samples tending to have a larger head than *Tiwi* (combined sexes: HH, mean 3.5 versus 3.1 mm; HW, mean 4.8 versus 4.5 mm). Thus, Top End populations of *C. cygnatus* have a deeper, broader head than those from Melville Island.

Hybrid zone. NTM R18837 was identified by allozyme analysis as being of *C. cygnatus* sp. nov. x *C. metallicus* hybrid origin. *Cryptoblepharus cygnatus* sp. nov. and *C. metallicus* were genetically distinguished from each other by eight fixed allelic differences at loci Gada, Gpi, Guk, Hbdh, PepB, PepD-1, Pgk and Tpi (Horner and Adams 2007), with NTM R18837 being intermediate between them at those loci. Genetically determined *C. metallicus* (NTM R18838) occur at the same site as NTM R18837 (garden trees and fences by Hi-Way Inn, Daly Waters, NT), while the closest genetically (and morphologically) determined *C. cygnatus* sp. nov. were collected at Tjaynera Falls, Litchfield National Park (NTM R21740, R21744), about 450 kilometres north-west of Daly Waters. Illustrated in Fig. 49, NTM R18837 is an adult female, gravid with two well-developed eggs.

Extent of the hybrid zone is unknown, but could be restricted to a single event. Unequivocal *C. cygnatus* sp. nov. and *C. metallicus* are sympatric at many sites north of Daly Waters (example: Jabiru, 400 km north of Daly Waters). Morphologically, NTM R18837 cannot be reliably recognised from either parent stock, having weak calli on most subdigital lamellae and some plantars capped with brown calli.

Habits and habitats. *Cryptoblepharus cygnatus* occurs in a variety of habitats. Typically arboreal, museum records note its use of monsoon vine thickets, open forest, woodland, grassland, mangroves and urban environments. Within these it has been associated with numerous tree and/or shrub species, including *Avicennia marina*, *Callitris intratropica*, *Corypha elata*, *Eucalyptus miniata*, *Eucalyptus* spp., *Gronophyllum ramsayi*, *Melaleuca* spp., *Pseudoraphis spinescens* and *Terminalia grandifloris*. The species is not normally saxicoline, although some records note usage of sandstone in open forest. In urban environments it has been associated with buildings, walls, garden trees, fences and pine logs.

Locally abundant, *C. cygnatus* sp. nov. commonly occurs in large numbers on a single large tree (particularly *Melaleuca* spp.). Evidence of abundance is provided by Wells and Wellington (1985), who record 45 specimens (paratypes of the *nomen nudum C. swansoni*) collected over two consecutive days from building walls in Smith Street, central business district, Darwin.

Social behaviour of *C. cygnatus* sp. nov. has been observed in the Darwin area, NT (pers. obs.). An instance of male/male dominance or territorial behaviour occurred on a pine log fence rail. Activity involved close circling, punctuated by vicious biting and shaking of rivals hindquarters. Participants were unperturbed by observer's presence or a hand being placed near them. Outcome was not determined, being interrupted by capture of both specimens (NTM R21508-509) for accurate sex determination. The second instance was of mating behaviour and took place on a rough-barked tree trunk. Here, the male gripped the female immediately behind the forelimb with his jaws, positioned his hindquarters under hers and hung on until copulation was achieved.

Braithwaite (1987), in a study of lizards and tropical fire regimes, found that *C. cygnatus* sp. nov. (as *C. plagiocephalus*) was locally ubiquitous and probably little affected by annual dry season fires, although some individuals are killed by intense fires. The results of a second study on dietary pathways of lizards (James *et al.* 1984) showed that the diet of *C. cygnatus* sp. nov. (as *C. plagiocephalus*) contained 13% by volume prey of aquatic origin (midges and mosquitoes).

Taxonomic history. Wells and Wellington's (1985) controversial classification of Australian amphibians and reptiles described a large number of new species and resurrected numerous taxa from synonymy, usually without comment or justification. Many of the taxa described were of dubious status, and a large number have been determined *nomina nuda* (e.g. Shea and Sadlier 1999; Horner 1999). The description of one new species, *C. swansoni* (Fig. 48), was based on 46 specimens collected on stone walls of a building in Smith Street, Darwin NT (formerly housing the NTM natural science collection, now a ruin commemorating 'Cyclone Tracy'). It was diagnosed as "a member of the *Cryptoblepharus plagiocephalus* complex, believed confined to coastal Northern Territory where it inhabits savanna woodland and rock outcroppings. Its congener *Cryptoblepharus plagiocephalus* is believed restricted to mid coastal Western Australia (Shark Bay district)" (Wells and Wellington 1985). This diagnosis fails to "state in words characters that are purported to differentiate the taxon" or supply "bibliographic reference to such a published statement" (International Commission on Zoological Nomenclature 1999, Article 13, 13.1.1–13.1.2), simply being an unsubstantiated statement of habitat and distribution. On the above grounds, Horner (1999) considered the binomen, *C. swansoni,* to be *nomen nudum* and placed the name in the synonymy of *C. plagiocephalus* (= *C. metallicus*).

Etymology. From the Latin *cygnus*, meaning swan, and *natus*, a son; in reference to Stephen Swanson, herpetological author and photographer. Alludes to the Wells and Wellington (1985) *nomen nudum* '*swansoni*'.

Cryptoblepharus daedalos sp. nov.

Dappled snake-eyed skink

(Plates 1.6–1.7; Figs 52–55)

Cryptoblepharus megastictus Storr, 1976. – Storr *et al.*, 1981: 23; Gow 1981b; Cogger *et al.* 1983a: 141; Wilson and Knowles 1988: 119; Horner 1991: 17; Ehmann 1992: 182; Stanger *et al.* 1998: 23; Storr *et al.* 1999: 23; Cogger 2000: 405; Wilson and Swan 2003: 148.

Type material examined. *Cryptoblepharus daedalos* Horner. HOLOTYPE: Adult male, NTM R13615 (Tissue sample No. *ABTC* DO4), Victoria Highway roadside, 7 km west of Victoria River Bridge, Northern Territory, Australia, 15°35'S 131°05'E. coll. S. Donnellan and P. Baverstock. PARATYPES (15 specimens): NORTHERN TERRITORY: NTM R8293-297, Gregory National Park, 2 km west of Victoria River bridge, 15°35'S, 131°05'E, G. Armstrong, *et al.*, 12 Jan 1980; NTM R9473, Gregory National Park, 2 km west of Victoria River bridge, 15°37'S, 131°05'E, G. Armstrong, 18 Oct 1980; NTM R13168, Jasper Gorge, 16°02'S, 130°43'E, I. Archibald, 28 Aug 1985; NTM R13269-270, Gregory National Park, Victoria River bridge area, 15°35'S, 131°05'E, P. Edgar, 30 May 1986; NTM R13614, Gregory National Park, 7 km west of Victoria River bridge, 15°35'S, 131°05'E, S. Donnellan, 20 May 1986, *ABTC* D03; NTM R22474, Jasper Gorge, 16°01'S, 130°46'E, K. Claymore, 18 Apr 1996; NTM R24570, Joe Creek, Gregory National Park, 15°37'S, 131°04'E, D. Milne, 14 Oct 1998; NTM R25491, Jasper Gorge, 16°02'S, 132°48'E, K. Nash, 17 Nov 1999; NTM R25985, Jasper Gorge, 16°02'S, 130°48'E, K. Nash, 2 Apr 2000, *ABTC* EC5; AM R72765, Jasper Gorge, 16°02'S 130°40'E.

Diagnosis. A medium sized (40–44 mm SVL), very long-legged, very shallow-headed, saxicoline *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of six supraciliary scales, 26 mid-body scale rows, 48 paravertebral scales, 20 subdigital lamellae under fourth toe, 10 palmar scales, 15 plantar scales and two posttemporal scales; mean values of hindlimb length 46.8% of snout-vent length, head depth 36.0% of head length, paravertebral scale width 4.3% of snout-vent length, dorsolateral scale width 84.1% of paravertebral scale width; reddish, randomly speckled or blotched body pattern and saxicoline habits.

Description (16 specimens). Postnasals absent; prefrontals usually in broad contact (86%), occasionally in narrow contact (7%) or narrowly separated (7%); supraciliarics 5–7 (mean 6.0), modally 6; enlarged upper ciliaries 3–4 (mean 3.1), modally 3; posterior loreal largest (100%); supralabials 7–8 (mean 7.1), modally 7; fifth supralabial subocular (100%); infralabials 6–7 (mean 6.1), modally 6; nuchals 2–4

Fig. 52. Ventral surface of hind foot of *Cryptoblepharus daedalos* sp. nov. showing pale, ovate plantar scales (NTM R9473, Victoria River, NT). Scale: x20.

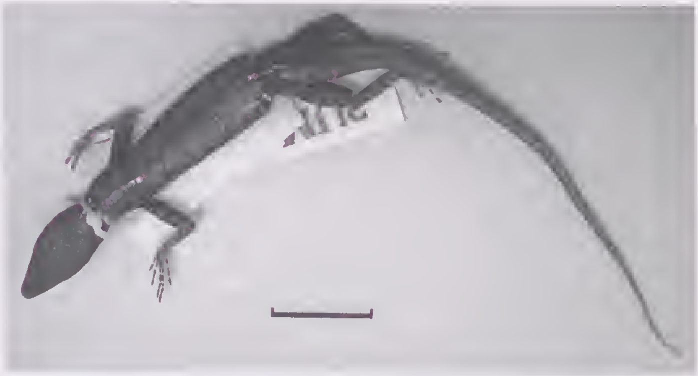

Fig. 53. Holotype of *Cryptoblepharus daedalos* sp. nov., NTM R13615, Victoria Highway, 7 km west of Victoria River bridge, Northern Territory, 15°35'S 13°05'E.

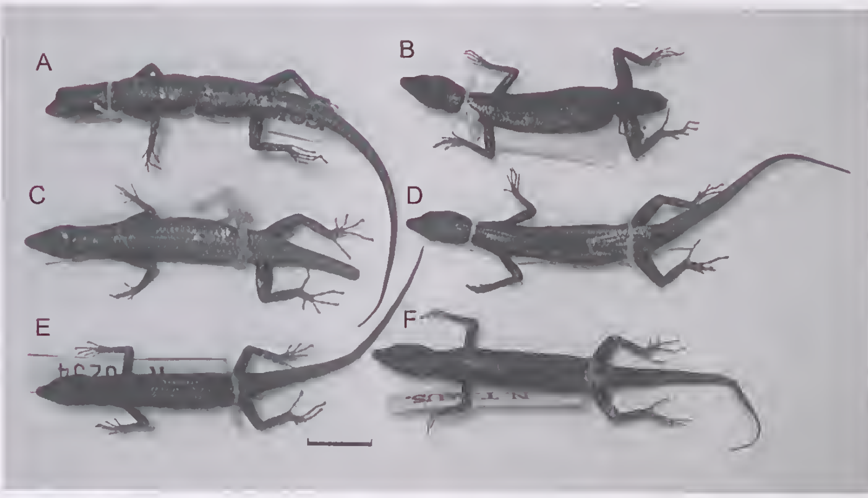

Fig. 54. *Cryptoblepharus daedalos* sp. nov. NTM preserved material from the Northern Territory: **A**, R24570, Joe Creek; **B**, R13614, Victoria River; **C**, R9473, Victoria River; **D**, R25985, Jasper Gorge; **E**, R8294, Victoria River; **F**, R8295, Victoria River. Scale bar = 10 mm.

(mean 2.4), modally 2; bilateral posttemporals usually 2+2 (53%), occasionally 2+3 (27%) or 3+3 (20%).

Midbody scale rows 24–26 (mean 25.7), modally 26; paravertebrals 45–54 (mean 48.9), modally 48; subdigital lamellae smooth, 15–18 below fourth finger (mean 16.2) modally 17, 18–23 below fourth toe (mean 20.3), modally 20; 12–15 supradigital lamellae above fourth finger (mean 13.2) modally 14, 14–18 above fourth toe (mean 15.6), modally 15; palmar and plantar scales rounded, without calli and skin not visible between scales (Fig. 52); plantars 11–15 (mean 13.4), modally 15; palmars 8–11 (mean 9.7), modally 10.

Snout-vent length to 40.8 mm (mean 35.7 mm). *Percentages of snout-vent length*: body length 46.1–52.7% (mean 49.0%); tail length 115.4–135.7% (mean 128.6%); forelimb length 33.9–42.4% (mean 37.8%); hindlimb length 43.7–49.3% (mean 46.8%); forebody length 39.4–48.1% (mean 42.9%); head length 20.1–24.0% (mean 21.6%). *Percentages of head length*: head depth 28.4–41.8% (mean 36.0%); head width 54.3–62.9% (mean 58.5%); snout length 42.1–48.5% (mean 44.9%). Paravertebral scale width 3.6–4.9% (mean 4.3%) of snout-vent length; dorsolateral scale width 74.5–100.6% (mean 84.1%) of paravertebral scale width.

Lenticular scale organs 3–17 (mean 8.1), modally 6. Premaxillary teeth 5–6 (mean 5.2), modally 5; maxillary teeth 19–22 (mean 20.5), modally 20; mandibular teeth 22–24 (mean 23.2), modally 24. Hemipenis proportions not measured.

Details of holotype. NTM R13615, adult male (Fig. 53). Postnasals absent; prefrontals in broad contact; supraciliaries 6; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 7; nuchals 2. Midbody scale rows 26; paravertebrals 51; subdigital lamellae smooth, 14 below fourth finger; 21 below fourth toe; supradigital lamellae 14 above fourth finger; 16 above fourth toe; palmars and plantars rounded, skin not visible between scales; plantars 14; palmars 8. Snout-vent length 37.4 mm; body length 18.5 mm; tail length 50.7 mm; forelimb length 14.4 mm; hindlimb length 18.1 mm; forebody length 16.0 mm; head length 8.0 mm; head depth 2.7 mm; head width 4.3 mm; snout length 3.5 mm.

Colouration and pattern. Dorsal ground colour russet to reddish, patterned with random, irregular brown-black spots, flecks and specks (Plates 1.6 and 1.7, Fig. 54). Dorsally and laterally, head concolorous with body but with fewer dark markings. Labials pale cream. Tail concolorous with body but with reduced speckling. Limbs concolorous with body, being patterned with dark streaks and spots. Venter immaculate off-white. Subdigital lamellae and palmar and plantar surfaces off-white, patterned with occasional dark flecks.

Sex ratio and reproductive biology. Sex ratio favoured females (9:7), but was not significantly different from parity ($X^2 = 0.25$). Of 16 animals only two females were reproductively active, these were collected in May and October suggesting that breeding could occur any time of the year.

Comparison with Australian congeners. Fixed allelic differences place *C. daedalos* sp. nov. in lineage 1 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTU megaA1, Horner and Adams 2007).

Morphologically distinguished from lineage 2 members (*C. adamsi* sp. nov., *C. exochus* sp. nov., *C. fuhni*, *C. gurrmul* sp. nov., *C. litoralis*, *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus*, *C. pulcher*, *C. tytthos* sp. nov., *C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov.) by usually having six, rather than five, supraciliary scales and (except for *C. ustulatus* sp. nov. and *C. zoticus* sp. nov.) speckled or blotched body pattern on reddish ground colour.

Distinguished from lineage 1 congeners: *C. australis*, *C. buchananii*, *C. cygnatus* sp. nov., *C. metallicus* and *C. ruber* by ground colour and body pattern characteristics (randomly speckled or blotched body pattern on reddish ground colour versus longitudinally aligned body pattern on greyish ground colour) and by being saxicoline rather than arboreal. Further distinguished from *C. australis*, *C. buchananii*, *C. cygnatus* sp. nov., *C. metallicus* and *C. ruber* by more mid-body scale rows (modally 26 versus 24), shallower head (mean 36.0 versus 41.1–43.3% of head length) and longer hindlimbs (mean 46.8 versus 40.9–42.0% of SVL).

Cryptoblepharus daedalos sp. nov. is most similar to *C. juno* sp. nov., *C. megastictus*, *C. ustulatus* sp. nov., *C. wulbu* sp. nov. and *C. zoticus* sp. nov. in having combinations of reddish ground colour and saxicoline habits. However, it differs from *C. ustulatus* sp. nov. and *C. zoticus* sp. nov. by having more supraciliary (modally 6 versus 5), paravertebral (modally 48 versus 46 and 45) and plantar scales (modally 15 versus 11 and 10), and longer hindlimbs (mean % of SVL, 46.8 versus 44.3 and 42.2). Differs from *C. wulbu* sp. nov. by having more paravertebral (modally 48 versus 39) and palmar scales (modally 10 versus 8) and a longer, narrower head (mean HL 21.6 versus 19.9% of SVL; HW 58.5 versus 65.4% of head length). Differs from *C. megastictus* by having more palmar (modally 10 versus 8) and plantar scales (modally 15 versus 10), fewer posterior temporal scales (modally 2 versus 3) and longer limbs (mean % of SVL, FL 37.8 versus 36.8; RL 46.8 versus 44.6). Most similar to *C. juno* sp. nov. but differs by having more plantar scales (modally 15 versus 12), fewer posterior temporal scales (modally 2 versus 3) and a deeper head (mean 36.0 versus 33.9% of head length).

Distribution. Stokes Range, north-western Northern Territory (Fig. 55). *Cryptoblepharus daedalos* sp. nov. has been recorded from several localities in the vicinity of the Victoria Highway bridge over the Victoria River and from Jasper Gorge, Victoria River.

Sympatry. *Cryptoblepharus daedalos* sp. nov. occurs in sympatry with *C. ruber*, a co-member of lineage 1, at 7 km south of Victoria Highway bridge, Victoria River.

Geographic variation. Small sample size and limited geographic range, prevented analysis of geographic variation.

Habits and habitats. *Cryptoblepharus daedalos* sp. nov. is saxicoline, with records placing it on rockfaces or on rocks. These habitats have been associated with open woodland vegetation, such as *Eucalyptus eliftonia*, *E. miniata*, *Livistonia* sp. and *Owenia vernicosa*, on rocky sandstone slopes and gullies. An interesting observation recorded for this taxon is "rapid vibration of the tail when aroused" (G. Armstrong, pers. comm.).

Specimen NTM R13269 (male, 34.8 mm SVL) contained a recently ingested autonomised tail from a conspecific in its gut. The tail was 28.3 mm in length, and was swallowed

Fig. 55. Map of the Northern Territory showing distribution of *Cryptoblepharus daedalos* sp. nov. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

base first leaving the tip extending from the buccal cavity. It is probable that immediately following an autonomy from another specimen, R13269 observed and interpreted the writhing tail as a live food item.

Etymology. From the Greek *daidalos*, meaning dappled, spotted or variegated; in reference to the taxon's random body pattern of dark spots and flecks.

Cryptoblepharus exochus sp. nov.

Noble snake-eyed skink

(Plate 1.8; Figs 56–60)

Type material examined. *Cryptoblepharus exochus* Horner. HOLOTYPE: Adult male, NTM R18669 (Tissue sample No. ABTC BR7), Mosquito Flat, Bradshaw Field Training Area, Northern Territory, 15°23'22"S 130°08'41"E. coll. P. Horner and S. Swanson, 29 September 1997. On *Excoecaria parvifolia* trunk, cracking blacksoil plain. PARATYPES (28 specimens): NORTHERN TERRITORY: NTM – R18568, R.18587, R.18589, R.18592, Mosquito Flat, Bradshaw Field Training Area, 15°23'S 130°08'E, L. Corbett and A. Hertog, 19–20 June 1997; R.18665-666, R.18667-668, R.18670-677, R.18679, R.18681-683, Mosquito Flat, Bradshaw Field Training Area, 15°23'S 130°08'E, P. Horner and S. Swanson, 28–29 September 1997; R.24787-788, R.24792, Mosquito Flat, Bradshaw Field Training Area, 15°23'S 130°08'E, P. Horner, L. Corbett and A. Hertog, 4–5 September 1999; R25930, Spirit Hills Station, 15°26'32"S 129°01'44"E, H. Puckey, 26 July 1999; WAM R137943, R137945-947, Spirit Hills Station (homestead), 15°26'S 129°01'E.

Diagnosis. A medium sized (40–44 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of five supraciliary scales; 24 mid-body scale rows, 51 paravertebral scales, 10 palmar and 12 plantar scales, 16 fourth finger subdigital lamellae, 20 fourth toe subdigital lamellae, 15 fourth toe supradigital scales; mean values of snout-vent length 37.1 mm, head depth 42.8% of head length, forelimb length 33.0% of snout-vent length, hindlimb length 40.7% of snout-vent length; pale, acute

Fig. 56. Ventral surface of hind foot of *Cryptoblepharus exochus* sp. nov. showing pale, acute plantar scales (holotype, NTM R18669, Mosquito Flat, Bradshaw Stn, NT). Scale: x20.

Fig. 57. Holotype of *Cryptoblepharus exochus* sp. nov. (NTM R18669, Mosquito Flat, Bradshaw Field Training Area, Northern Territory. 15°23'S 130°08'E, ABTC BR7). Scale bar = 10 mm.

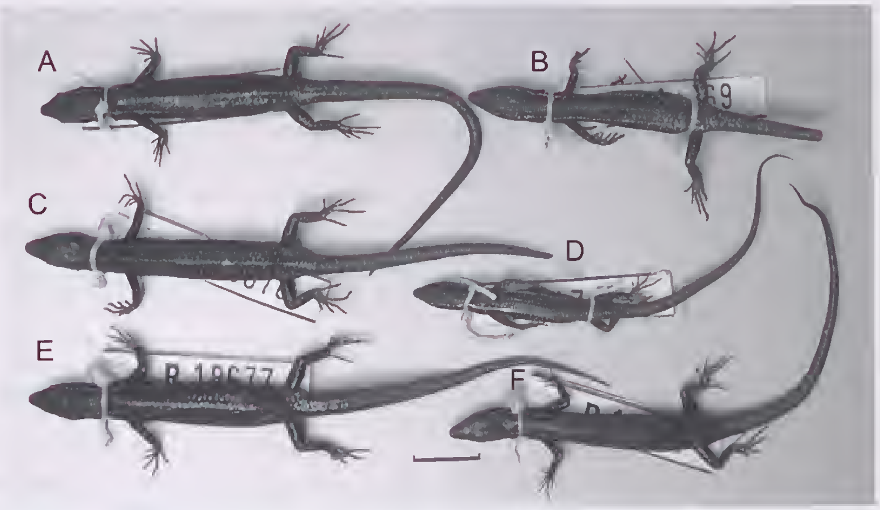

Fig. 58. *Cryptoblepharus exochus* sp. nov. NTM preserved material from the Northern Territory: **A**, R18682; **B**,R18669 [holotype]; **C**, R18676; **D**, R24792; **E**, R18677; **F**, R18679, Mosquito Flat, Bradshaw Stn, NT. Scale bar = 10 mm.

plantar scales; smooth subdigital lamellae; usually 2+2 posttemporal scales, and very narrow pale laterodorsal stripes.

Description (29 specimens). Postnasals absent; prefrontals in broad contact (100%); supraciliaries 5–6 (mean 5.0), modally 5; enlarged upper ciliaries 3 (100%); loreals usually subequal (81%), occasionally posterior (12%) or anterior (8%) loreal largest; supralabials 7; fifth supralabial subocular (100%); infralabials 6–7 (mean 6.0), modally 6; nuchals 2–4 (mean 2.2), modally 2; bilateral posttemporals usually 2+2 (72%), occasionally 2+3 (7%), or 3+3 (21%).

Midbody scale rows 24–26 (mean 24.8), modally 24; paravertebrals 48–57 (mean 50.9), modally 51; subdigital lamellae smooth, 15–17 below fourth finger (mean 15.9) modally 16, 17–22 below fourth toe (mean 19.5) modally 20; 12–15 supradigital lamellae above fourth finger (mean 13.2) modally 13, 14–17 above fourth toe (mean 15.2) modally 15; palmar and plantar scales acute, without calli and skin not visible between scales (Fig. 56); plantars 9–13 (mean 11.1), modally 12; palmars 8–11 (mean 10.2), modally 10.

Snout-vent length to 40.9 mm (mean 37.1 mm). *Percentages of snout-vent length*: body length 46.8–57.9% (mean 53.0%); tail length 131.5–161.4% (mean 146.2%); forelimb length 29.8–36.5% (mean 33.3%); hindlimb length 35.7–43.4% (mean 40.7%); forebody length 36.6–44.2% (mean 41.1%); head length 18.5–22.2% (mean 20.6%). *Percentages of head length*: head depth 36.9–48.4% (mean 42.8%); head width 55.6–67.5% (mean 60.5%); snout length 41.5–48.1% (mean 44.1%). Paravertebral scale width 3.2–4.5% (mean 3.9%) of snout-vent length; dorsolateral scale width 77.4–101.4% (mean 89.4%) of paravertebral scale width.

Lenticular scale organs 2–13 (mean 7.2), modally 5. Tooth counts not recorded. Hemipenis: length 6.0–8.9% (mean 6.8%) of snout-vent length; width 66.9–101.9% (mean 86.3%) of hemipenis length; trunk 41.6–59.2% (mean 51.0%) of hemipenis length.

Details of holotype. NTM R18669, adult male (Fig. 57). Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; loreals subequal; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 26; paravertebrals 49; subdigital lamellae smooth, 16 below fourth finger; 19 below fourth toe; supradigital lamellae 13 above fourth finger; 15 above fourth toe; palmars and plantars acute, skin not visible between scales; plantars 11; palmars 11. Snout-vent length 36.0 mm; body length 18.6 mm; tail not original (part missing); forelimb length 12.7 mm; hindlimb length 16.4 mm; forebody length 15.0 mm; head length 7.9 mm; head depth 3.1 mm; head width 4.6 mm; snout length 3.5 mm.

Colouration and pattern. Olive-brown, with longitudinally aligned, body pattern dominated by very narrow, pale laterodorsal stripes (Plate 1.8). Intensity of body pigmentation and patterning variable, ranging from obscure to prominent (Fig. 58). Most specimens conform to following description.

Dorsal ground colour olive-brown. Dorsum finely peppered with pale and dark specks and streaks. Broad vertebral zone, about four dorsal scales wide, extending from above eye to hindlimb. Narrow, dark dorsolateral stripes absent or obscure, if present, most prominent on anterior half of body. Very narrow, cream to white laterodorsal stripes extending from above eye to tailbase, most prominent on anterior half of body, about 0.75 width of laterodorsal scale. Edges of pale laterodorsal stripes usually smooth, but may be ragged on posterior half of body. Head concolorous with vertebral zone, heavily mottled with blackish flecks and specks. Laterally, head patterned with continuation of dark upper lateral zone, which extending above ear through eye to loreals. Pale lower temporal region flecked with dark spots and streaks. Labials cream, patterned with dark brown mottling.

Flanks have no distinct zonation, being olive-brown, flecked with dark streaks and pale flecks and coalescing into pale venter. Tail concolorous with body, lacking conspicuous markings. Limbs and toes concolorous with body, patterned with pale and dark speckling. Venter, including palmars and plantars, immaculate off-white. Subdigital lamellae brownish.

Sex ratio, sexual dimorphism and reproductive biology. Sex ratio favoured males (16:13), but was not significantly different from parity ($X^2 = 0.31$). Males mature at approximately 32 mm snout-vent length, females were indeterminate for maturity (smallest adult female examined was 38.6 mm SVL). Breeding biology was indeterminate, due to paucity of collection periods. However, of 23 adult specimens collected in June (4), July (1) and September (18), none were reproductively active, indicating that breeding may take place in the monsoonal wet season (summer).

Comparison with Australian congeners. Fixed allelic differences place *C. exochus* sp. nov. in lineage 2 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTU carnB, Horner and Adams 2007).

Morphologically distinguished from most lineage 1 members (except *C. australis*) by usually having five, rather than six, supraciliary scales and acute, instead of ovate, plantar scales.

Distinguished from lineage 2 congeners *C. adamsi* sp. nov., *C. fuhni, C. gurrmul* sp. nov., *C. litoralis, C. pulcher, C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov. by acute plantars (versus rounded). Further distinguished from: *C. gurrmul* sp. nov., *C. l. horneri* and *C. l. litoralis* by fewer mid-body scale rows (modally 24 versus 26–28) and paravertebral scales (modally 51 versus 55–57); from *C. fuhni, C. gurrmul* sp. nov. and *C. zoticus* sp. nov. by more paravertebral scales (modally 51 versus 45–46) and deeper head (mean 42.8 versus 32.5–36.1% of head length); from *C. virgatus* by more mid-body scale rows (modally 24 versus 22) and paravertebral scales (modally 51 versus 47); from *C. adamsi* sp. nov. and *C. pulcher* by pale plantar scales (versus darkly pigmented) and very narrow pale laterodorsal stripes.

Cryptoblepharus exochus sp. nov. is most similar to *C. australis, C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp.nov., *C. plagiocephalus* and *C. tytthos* sp. nov. in having combinations of complex body patterns, acute plantar scales and being arboreal. However, it differs from *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. (co-members of lineage 2) in having smooth, instead of keeled subdigital lamellae and usually more paravertebral scales (modally 51 versus 48–50). It differs from *C. australis* in having fewer supraciliary scales (modally 5 versus 6), more palmar scales (modally 10 versus 9) and fewer posterior temporal scales (modally 2 versus 3). Further distinguished from: *C. plagiocephalus* by narrow pale dorsolateral stripes, more palmar (modally 10 versus 9) and paravertebral scales (modally 51 versus 50), and by being larger (SVL, mean 37.1 versus 33.6 mm); from *C. mertensi* sp. nov. by more palmar scales (modally 10 versus 9), less distinct pale dorsolateral stripes and by being larger (SVL, mean 37.1 versus 34.3 mm); from *C. pannosus* sp. nov. by more plantar scales (modally 12 versus 10), usually 2+2 posttemporal scales (versus usually 3+3), narrow pale dorsolateral stripes and by being larger (SVL, mean 37.1 versus 34.4 mm); from *C. tytthos* sp. nov. by more subdigital lamellae (modally FTL 16 versus 15; HTL 20 versus 18) and by being larger (SVL, mean 37.1 versus 31.3 mm); from *C. ochrus* sp. nov. by usually 2+2 posttemporal scales (versus usually 3+3), fewer fourth toe supradigital scales (modally 15 versus 16), and shorter limbs (mean % of SVL: FL 33.0 versus 34.1%; RL, mean 40.7 versus 42.5%).

Additionally, of taxa examined for hemipenis proportions, *C. exochus* sp. nov. has a very short hemipenis (mean 6.8% of snout-vent length), all others except *C. mertensi* sp. nov. (6.1%) had mean hemipenis lengths above 7.0% of snout-vent length.

Distribution. The border region of far north-western Northern Territory and far north-eastern Western Australia (Fig. 59). Within this region it has been recorded from two sites, Mosquito Flat on the eastern bank of the Victoria River in the Bradshaw Field Training Area (formerly Bradshaw Station), and Spirit Hills Station which abuts the Western Australian border.

Sympatry. *Cryptoblepharus exochus* sp. nov. occurs in sympatry with *C. juno* sp. nov., *C. metallicus* and *C. ruber*. Sympatric with: *C. ruber* at Mosquito Flat, Bradshaw Field Training Area, NT and Spirit Hills Station, NT. Sympatry with more than one congener occurs at Bradshaw Field Training Area where, at Mosquito Flat, *C. exochus* sp. nov. and *C. ruber* can be found on *Excoecaria parvifolia* trunks, *C. metallicus* on *Eucalyptus* spp. in adjoining woodland and *C. juno* sp. nov. on nearby rock outcrops.

Geographic variation. Geographic variation was investigated by separating specimens, all from Victoria Bonaparte bioregion, into two groups, being 24 specimens from Mosquito Flat (east of the Victoria River) compared to five specimens from Spirit Hills (west of the Victoria River).

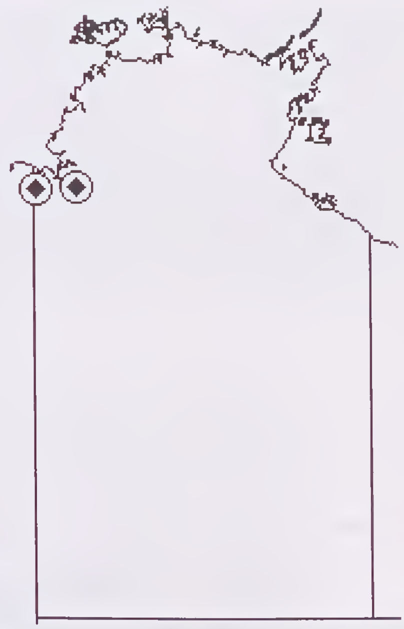

Fig. 59. Map of the Northern Territory showing distribution of *Cryptoblepharus exochus* sp. nov. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

Small sample size for one group limited analysis to both sexes combined. Tests of allometrically adjusted variables revealed some variation in body proportions. Mosquito Flat samples tended to be larger than those from Spirit Hills (mean SVL 37.3 versus 34.4 mm; mean body length 20.1 versus 18.8 mm), except in forebody length where Spirit

Fig. 60. Gutta-percha *Excoecaria parvifolia* on cracking blacksoil plain at Mosquito Flat, Bradshaw Field Training Area, NT. Type locality of *Cryptoblepharus exochus* sp. nov.

Hills samples were larger (mean SFL 16.1 versus 15.3 mm). These results indicate that geographic variation in *C. exochus* sp. nov. is limited to animals from Mosquito Flat being slightly larger than those from Spirit Hills.

Habits and habitats. *Cryptoblepharus exochus* sp. nov. appears to be the only arboreal *Cryptoblepharus* that is habitat specific. All specimens have been taken from the trunks and branches of Gutta-percha *Excoecaria parvifolia*, growing on the cracking blacksoil plains of the Victoria Bonaparte bioregion (Fig. 60). Deviating slightly from typical arboreal *Cryptoblepharus* behaviour, *C. exochus* sp. nov. if threatened and prevented from climbing, commonly jumps from tree trunks and seeks refuge in nearby deep, earth cracks. On Mosquito Flat *C. exochus* sp. nov. is abundant, greatly outnumbering the micro-sympatric *C. ruber*.

Etymology. From the Latin adjective *exochus*, meaning standing out or eminent; in reference to the distinctiveness of this taxon in comparison to closely related congeners.

Cryptoblepharus fuhni Covacevich and Ingram, 1978

Fuhn's snake-eyed skink

(Plate 1.9; Figs 61–64)

Cryptoblepharus fuhni Ingram and Covacevich, 1978:151; 1981: 295. – Cogger *et al.* 1983a: 141; Wells and Wellington 1985: 27; Wilson and Knowles 1988: 119; Covacevich and Couper 1991: 357; Ehmann 1992: 181; Roberts 1994: 234; Healey 1997: 329; Stanger *et al.* 1998: 23; Cogger 2000: 405; Wilson and Swan 2003: 148.

Non-type material examined. See Appendix 4.

Diagnosis. A large (45–50 mm SVL), very long-legged, very shallow-headed, saxicoline *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of five supraciliary scales, 24 mid-body scale rows, 45 paravertebral scales and 21, darkly callused, fourth toe subdigital lamellae; mean values of 41.6 mm snout-vent length, and hindlimb length 52.8% of snout-vent length; rounded, dark pigmented plantar scales; blackish ground colour with contrasting narrow, discontinuous pale dorsolateral stripes, and saxicoline habits. *Cryptoblepharus fuhni* differs from all congeners in having longer limbs (mean % of SVL: forelimb 40.7 versus 28.6–38.4; hindlimb 52.8 versus 38.8–47.3).

Description (13 specimens). Postnasals absent; prefrontals usually in broad contact (79%), occasionally in narrow contact (7%) or narrowly separated (14%); supraciliaries 5–6 (mean 5.2), modally 5; enlarged upper ciliaries 3–5 (mean 3.2), modally 3; posterior loreal usually largest (72%), occasionally subequal (14%) or anterior largest (14%); supralabials 7–8 (mean 7.1), modally 7; fifth supralabial subocular (100%); infralabials 6–7 (mean 6.2), modally 6; nuchals 2–3 (mean 2.2), modally 2; bilateral posttemporals 3+3 (n = 1).

Midbody scale rows 22–26 (mean 24.4), modally 24; paravertebrals 44–50 (mean 46.1), modally 45; subdigital lamellae with dark calli, 14–19 below fourth finger (mean 17.4) modally 18, 20–26 below fourth toe (mean 22.2) modally 21; 12–16 supradigital lamellae above fourth finger (mean 14.7) modally 14, 16–20 above fourth toe (mean 18.3) modally 18; palmar and plantar scales rounded, without calli and skin visible between scales (Fig. 61); plantars 9–12 (mean 10.6), modally 11; palmars 8–10 (mean 8.8), modally 9.

Snout-vent length to 47.0 mm (mean 41.6 mm). *Percentages of snout-vent length*: body length 46.4–54.5% (mean 50.5%); tail length 153.8% (n = 1); forelimb length 35.8–45.3% (mean 40.7%); hindlimb length 47.6–57.8% (mean 52.8%); forebody length 37.4–47.7% (mean 42.2%); head length 19.7–24.1% (mean 21.2%). *Percentages of head length*: head depth 32.0–41.4% (mean 36.1%); head width 54.3–65.1% (mean 60.1%); snout length 42.1–47.1% (mean 44.5%). Paravertebral scale width 3.7–4.9% (mean 4.2%) of snout-vent length; dorsolateral scale width 83.3–111.9% (mean 95.2%) of paravertebral scale width.

Lenticular scale organs 5–9 (mean 6.6), modally 6. Tooth counts not recorded. Hemipenis proportions not measured.

Details of holotype. QM J.20566, Melville Range, Cape Melville, Cape York, north-east Queensland (14°16'S 144°30'E), coll. J. Covacevich, C. Tanner and T. Tebble, 30 November 1970. Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; loreals subequal in size; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 24; paravertebrals 48; subdigital lamellae callused, 18 below fourth finger; 25 below fourth toe; supradigital lamellae 15 above fourth finger; 20 above fourth toe; palmars and plantars rounded, without calli, skin visible between scales; plantars 11; palmars 9. Snout-vent length 47.0 mm; body length 25.5 mm; tail not original; forelimb length 16.8 mm; hindlimb length 24.2 mm; forebody length 19.1 mm; head length 9.4 mm; head depth 3.9 mm; head width 6.0 mm; snout length 4.2 mm. Type series illustrated by paratype QM J20567 (Fig. 62) collected with the holotype.

Colouration and pattern. A blackish-brown *Cryptoblepharus*, with a longitudinally aligned body pattern dominated by narrow, discontinuous, silvery laterodorsal stripes (Plate 1.9, Figs 62, 63). Most specimens conform to the following description.

Dorsal ground colour blackish-brown, with broad, dark brown vertebral zone extending from above eye to hindlimbs. Vertebral zone slightly narrower than paired paravertebral scales and dotted with short blackish streaks and spots. Spotting is most prominent on outer edges of paravertebrals and forms two, broken narrow black stripes from neck to hindlimbs. Narrow, discontinuous, silvery white laterodorsal stripes extend from above eye onto tail, about half width of laterodorsal scales, these are broken into regular series of silvery white streaks by intrusions of dark pigment. Margins of pale laterodorsal stripes straight-edged. Head concolorous with body, patterned with blackish blotches and speckling. Labials light brown, with dark margins to scales.

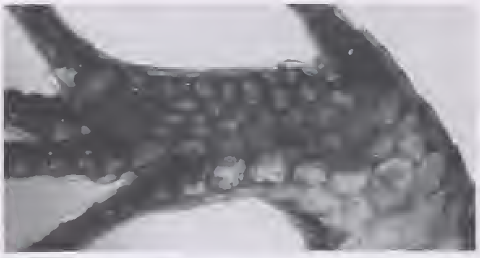

Fig. 61. Ventral surface of hind foot of *Cryptoblepharus fuhni* showing dark, ovate plantar scales (NTM R26965, Cape Melville, Qld). Scale: x20.

Fig. 62. Paratype of *Cryptoblepharus fuhni* Covacevich and Ingram, 1978. Melville Range, Cape Melville, Cape York, northeast Qld, 14°16'S 144°30'E.

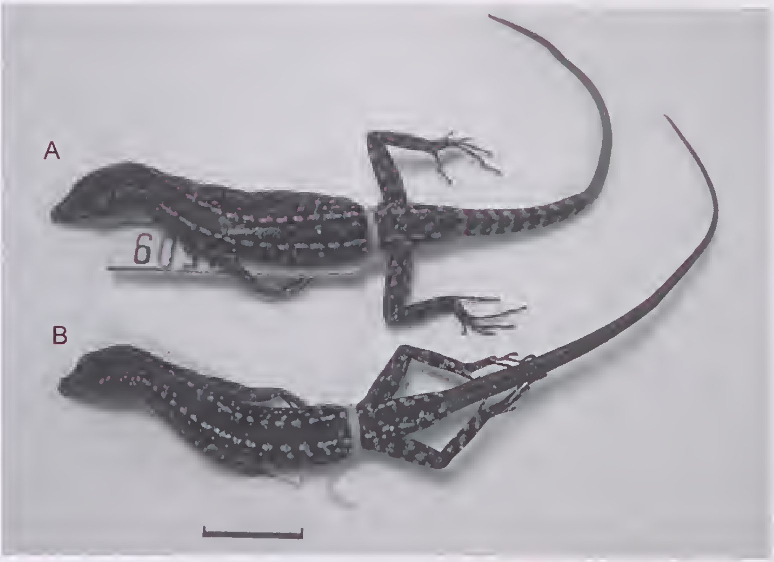

Fig. 63. *Cryptoblepharus fuhni*. NTM preserved material from Queensland. **A**, R26965; **B**, R26967, Cape Melville, Qld. Scale bar = 10 mm.

Flanks dark brown, speckled with blackish spots and streaks and occasional silvery spots and coalesce into pale venter. Tail concolorous with body, being blackish and patterned with broad, broken continuations of silvery white dorsolateral stripes. Limbs and toes concolorous with body, patterned with dark and pale speckling. Ventral surfaces immaculate off-white. Palmars and plantars blackish or dark grey (Fig. 61).

Roberts (1994) noted that *C. fuhni*, although retaining the distinctive body pattern, have a pale, greyish ground colour where Cape Melville juts into the sea and the granite boulders are also pale grey.

Sex ratio, sexual dimorphism and reproductive biology. Sex ratio of 12 specimens favoured females (7:5), but was not significantly different from parity ($X^2 = 0.33$). Reproductive data not recorded.

Comparison with Australian congeners. Fixed allelic differences place *C. fuhni* in lineage 2 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTU fuhn, Horner and Adams 2007).

Morphologically distinguished from lineage 1 members (*C. australis*, *C. buchananii*, *C. cygnatus* sp. nov., *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus*, *C. metallicus*, *C. ruber* and *C. wulbu* sp. nov.) by usually having five, rather than six, supraciliary scales, reduced melanistic body pattern and saxicoline, littoral habits.

Distinguished from lineage 2 congeners (*C. adamsi* sp. nov., *C. exochus* sp. nov., *C. fuhni*, *C. gurrmul* sp. nov., *C. litoralis*, *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus*, *C. pulcher*, *C. tytthos* sp. nov., *C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov.) by unique combination of blackish ground colour and contrasting narrow, discontinuous, pale dorsolateral stripes. Further distinguished from: *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. by having rounded, dark pigmented plantars instead of pale acute pale plantars; from *C. adamsi* sp. nov., *C. pulcher*, *C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov. by having callused (instead of smooth) and more numerous fourth toe subdigital lamellae (modally 21 versus 18–19), longer hindlimbs (mean 52.8 versus 40.5–42.2 % of SVL), and by being larger (mean SVL 41.6 versus 33.4–35.6 mm). *Cryptoblepharus fuhni* is most similar to *C. gurrmul* sp. nov. and *C. litoralis* in having combinations of complex body patterns on blackish ground colour, flat, ovate plantar scales and saxicoline habits, however it differs from both by having fewer midbody scale rows (modally 24 versus 26–28) and paravertebral scales (modally 45 versus 55–57).

Cryptoblepharus fuhni is a unique taxon that is easily distinguished from all congeners by having longer limbs (mean % of SVL, forelimb 40.7 versus 28.6–38.4; hindlimb 52.8 versus 38.8–47.3) and unique narrow laterodorsal stripes that are broken into regular alternating pale streaks.

Distribution. Melville Range, Cape Melville, northeast Queensland (Fig. 64).

Sympatry. At Melville Range, *C. fuhni* is micro-sympatric with *C. virgatus* (Covacevich and Ingram 1978), a co-member of lineage 2.

Geographic variation. Taxon known from a single locality.

Habits and habitats. *Cryptoblepharus fuhni* is a saxicoline species, endemic to the bare, 'black' granite boulders of the Melville Range. Locally abundant, they shelter in crevices and cracks among boulders (Covacevich and Ingram 1978; Roberts 1994). Roberts (1994) records occupation of 'wave-washed' boulders where Cape Melville juts into the sea.

Taxonomic history. Recognised and described in 1978, *C. fuhni* has not been affected by nomenclatural change.

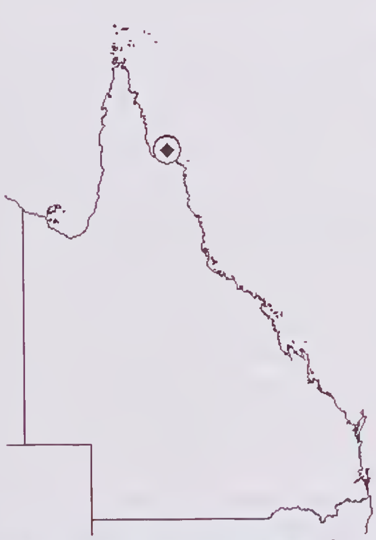

Fig. 64. Map of Queensland showing distribution of *Cryptoblepharus fuhni*. Circled diamond indicates genetically identified sample sites (Horner and Adams 2007).

Cryptoblepharus gurrmul sp. nov.

Arafura snake-eyed skink

(Plate 1.10; Figs 65–69)

Cryptoblepharus litoralis (Mertens, 1958). – Horner 1984: 7.

Cryptoblepharus horneri Wells and Wellington, 1985: 27 (in part).

Type material examined. *Cryptoblepharus gurrmul* Horner. HOLOTYPE: Adult male, NTM R10900, New Year Island, Northern Territory, Australia, 10°55'S 133°02'E, coll. P. Horner, 1400 hours, 14 October 1982. Active amongst beach debris (driftwood and broken coral boulders). PARATYPES (13 specimens): NORTHERN TERRITORY: NTM R7679-681, same data as holotype, except collected by P. Horner and G. Gow, 10 October 1979; NTM R10901-904, same data as holotype; NTM R10923-927, Oxley Island, Northern Territory, Australia, 10°59'S 132°50'E, collected by P. Horner, 21 October 1982; NTM R28475, North Goulburn Island, 11°33'S 133°23'E, collected by K. Brennan, 24 September 2006.

Diagnosis. A medium sized (40–44 mm SVL), long-legged, shallow-headed, littoral *Cryptoblepharus*, distinguished from Australian congeners by combination of presence of postnasal scale; modal values of five supraciliary scales, 28 mid-body scale rows, 55 paravertebral scales, seven palmar, seven plantar scales, and maximum snout-vent length of 44.3 mm.

Description (13 specimens). Postnasals present (100%); prefrontals in broad contact (100%); supraciliaries 5–6 (mean 5.0), modally 5; enlarged upper ciliaries 3–4 (mean 3.1), modally 3; loreals usually subequal (69%), occasionally posterior is largest (31%); supralabials 6–8 (mean 6.9), modally 7; fifth supralabial usually subocular (89%), occasionally fourth (11%); infralabials 6–7 (mean 6.1), modally 6; nuchals 2–7 (mean 4.0), modally 2; bilateral posttemporals usually 3+3 (50%), occasionally 2+3 (25%), or 2+2 (25%).

Midbody scale rows 27–30 (mean 28.2), modally 28; paravertebrals 49–57 (mean 53.5), modally 55; subdigital lamellae smooth, 11–15 below fourth finger (mean 13.0) modally 13, 16–19 below fourth toe (mean 17.7) modally 18; 10–13 supradigital lamellae above fourth finger (mean 11.6) modally 11, 14–17 above fourth toe (mean 15.2) modally 15; palmar and plantar scales rounded, without calli and dark skin visible between scales (Fig. 65); plantars 6–9 (mean 7.5), modally 7; palmars 6–9 (mean 7.2), modally 7.

Snout-vent length to 44.3 mm (mean 37.8 mm). *Percentages of snout-vent length*: body length 47.6–57.8% (mean 52.3%); tail length 149.5–180.2% (mean 161.7%); forelimb length 30.9–37.5% (mean 34.6%); hindlimb length 37.9–47.9% (mean 44.1%); forebody length 37.0–43.7% (mean 40.0%); head length 19.0–22.5% (mean 21.2%). *Percentages of head length*: head depth 38.7–49.3% (mean 43.3%); head width 58.6–66.1% (mean 62.4%); snout length 42.6–48.5% (mean 45.8%). Paravertebral scale width

Fig. 65. Ventral surface of hind foot of *Cryptoblepharus gurrmul* sp. nov. showing dark, ovate plantar scales (NTM R10901, New Year Island, NT). Scale: x20.

Fig. 66. Holotype of *Cryptoblepharus gurrmul* sp. nov. (NTM R10900, New Year Island, Northern Territory, Australia, 10°55'S 133°02'E). Scale bar = 10 mm.

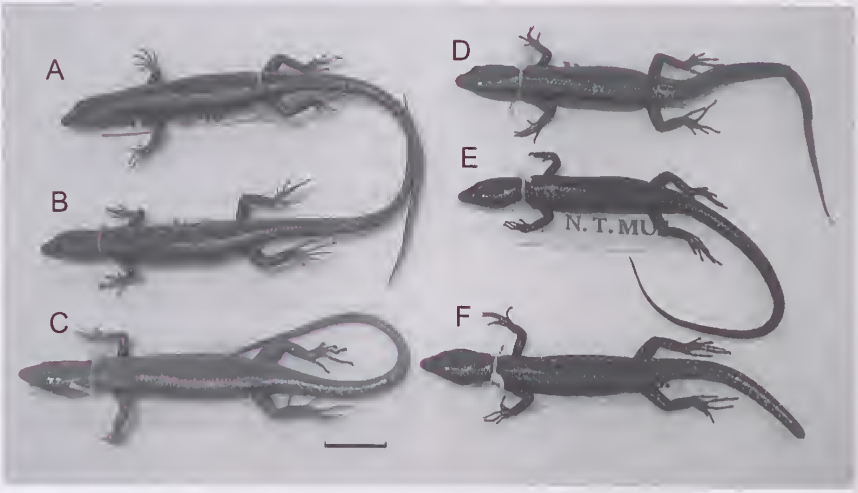

Fig. 67. *Cryptoblepharus gurrmul* sp. nov. NTM preserved material from the Northern Territory: **A–C**, R10900- R10902, New Year Island (R10900 is holotype); **D**, R7679, New Year Island; **E–F**, R10925, R10927, Oxley Island. Scale bar = 10 mm.

3.5–4.2% (mean 3.8%) of snout-vent length; dorsolateral scale width 77.6–102.1% (mean 92.8%) of paravertebral scale width.

Lenticular scale organs 3–10 (mean 6.1), modally 5. Premaxillary teeth 4–5 (mean 4.8), modally 5; maxillary teeth 17–18 (mean 17.8), modally 18; mandibular teeth 24. Hemipenis proportions not measured.

Details of holotype. Adult male (Fig. 66), NTM R10900. Postnasals present; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; loreals subequal; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 27; paravertebrals 53; subdigital lamellae smooth, 14 below fourth finger; 17 below fourth toe; supradigital lamellae 12 above fourth finger; 15 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 8; palmars 9. Snout-vent length 37.8 mm; body length 19.5 mm; tail not original; forelimb length 13.0 mm; hindlimb length 16.8 mm; forebody length 15.0 mm; head length 7.9 mm; head depth 3.9 mm; head width 5.0 mm; snout length 3.4 mm.

Body pattern longitudinally aligned (conforms to species description above).

Colouration and pattern. A grey-brown to blackish *Cryptoblepharus*, with longitudinally aligned, complex body pattern dominated by dark, broad vertebral zone and obscure, pale laterodorsal stripes (Plate 1.10). Intensity of body pigmentation and patterning is variable, ranging from obscure to prominent (Fig. 67). Most specimens conform to the following description.

Dorsal ground colour grey, grey-brown to black with broad, dark vertebral zone extending from above eye to hindlimb. Vertebral zone as wide as, or slightly wider than, paired paravertebral scales, grey-brown to blackish, speckled with dark and pale flecks and spots. Latter most prominent on outer edges of paravertebral scales, forming two broken, narrow black stripes from neck to hindlimbs. Pale grey laterodorsal stripes obvious or obscure, extend from above eye onto tail, broadest on posterior half of body, about 1–2 laterodorsal scales wide, tapering anteriorly into narrow stripes extending to eye and posteriorly to form tail ground colour. Edges of pale laterodorsal stripes usually ragged but occasionally smooth. Laterodorsal stripes uniform or may contain dark and/or pale speckling. Head concolorous with vertebral zone or brownish, usually patterned with dark margins to head shields. Laterally patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Pale lower temporal region flecked with dark spots and streaks. Labials pale grey, patterned with dark margins to scales.

Flanks patterned with dark grey to blackish upper lateral zone, variable in width, extending from loreals onto tail and forming outer border to pale laterodorsal stripes. Usually peppered with dark and/or pale specks and short streaks, upper lateral zone may be represented by narrow broken black stripe but typically is about two lateral scales wide and coalesces gradually into pale grey lower lateral zone. Lower lateral zone peppered with small pale and/or dark spots and streaks and coalesces into pale venter. Tail concolorous with body, patterned with broken continuations of blackish vertebral and upper lateral zones. Limbs and toes concolorous with body, patterned with pale and dark speckling. Ventral surfaces blue-grey to off-white. Palmar and plantar scales dark grey to dark brown, with darker skin clearly visible between scales.

One of the known populations differs in intensity of body pattern. New Year Island specimens are generally pale, with indistinct patterning (Fig. 67 A–D), while samples from Oxley and North Goulburn Islands are blackish with distinct patterning (Plate 1.10, Fig. 67 E–F).

Sex ratio and reproductive biology. Sex ratio favoured males (7:6), but was not significantly different from parity ($X^2 = 0.06$). Though sample sizes are small, they indicate both sexes mature at approximately 34 mm snout-vent length. Adults average 37.8 mm snout-vent length and females grow larger than males (maximum SVL = 44.3 versus 40.8 mm). Breeding biology was indeterminate, as most specimens were collected in October. Of the 14 samples, four were reproductively active, three males and one female.

Comparison with Australian congeners. Allozymic differentiation unknown. Morphologically distinguished from Australian congeners by presence of postnasal scales, (absent in all others except a single *C. l. horneri*), high number of mid-body scale rows (modally 28 versus 22–26) and few palmar and plantar scales (PAL, modally 7 versus 8–11, PLN, modally 7 versus 9–15).

Further distinguished from lineage 1 members (*C. australis, C. buchananii, C. cygnatus* sp. nov., *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus, C. metallicus, C. ruber* and *C. wulbu* sp. nov.) by usually having usually having five, rather than six, supraciliary scales, reduced body pattern and saxicoline, littoral habits and from most lineage 2 members (*C. adamsi* sp. nov., *C. exochus* sp. nov., *C. fuhni, C. gurrmul* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus, C. pulcher, C. tytthos* sp. nov., *C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov.) (except *C. litoralis*) by having more paravertebral scales (modally 55 versus 45–51). Further distinguished from *C. litoralis* by being smaller (maximum snout-vent length: 44.3 versus 51.0 mm).

Distribution. Known only from Oxley, New Year and North Goulburn islands off the north-east Arnhem Land coast, Arafura Sea, Northern Territory (Fig. 68). Oxley Island (ca. 3.7 km^2) is located 30 km east of inhabited Croker Island, and New Year Island (1.6 km^2) is about 23 km further north-east from Oxley Island. New Year Island is approximately 50 km from the Australian mainland. North Goulburn Island (36 km^2) is approximately 16 km off the mainland in north-west Arnhem Land.

Sympatry. Occurs in sympatry with *C. cygnatus* sp. nov. and *C. litoralis horneri* on New Year Island, Northern Territory.

Geographic variation. Geographic variation was investigated by dividing specimens into two groups, based on distribution: a group of eight from New Year Island, and a group of five from Oxley Island. Small sample sizes prevented analysis of separate sexes.

Tests of allometrically adjusted variables revealed only minor differences between these two populations. Samples from New Year Island had more fourth finger subdigital lamellae (mean 13.6 versus 12.0) and usually subequal loreal scales (versus posterior loreal usually largest), while Oxley Island samples usually had darkly pigmented plantar scales. Two samples from North Goulburn Island shared the dark pigmentation of the Oxley Island population.

Habits and habitats. *Cryptoblepharus gurrmul* sp. nov. is a littoral species which at New Year Island (Fig. 69) was found among beach debris (driftwood and coral litter), and at Oxley Island and North Goulburn Island on and under low beach rocks, close to the high water mark.

Fig. 68. Map of the Northern Territory showing distribution of *Cryptoblepharus gurrmul* sp. nov.

Fig. 69. Beach on New Year Island, Northern Territory, type locality of *Cryptoblepharus gurrmul* sp. nov.

Horner (1984) recorded the following behavioural observations on Oxley Island specimens (as *C. litoralis*). Agile, fast-moving skinks which, in suitable habitat, tend to aggregate in small groups. Forage amongst rocks in intertidal zone, and retreat to fringing vegetation when confronted by an incoming tide. Some specimens, when trapped on rocks completely surrounded by water, leapt into the sea and rapidly swam to a nearby rock or shore. Upon collection, one specimen disgorged a polychaete worm of the family Nereidae.

Etymology. From the Margu Aboriginal language, *Gurrmul* being the name given to New Year Island, the type locality. Used as a noun in apposition.

Cryptoblepharus juno sp. nov.

Juno's snake-eyed skink

(Plate 2.1; Figs 70–73)

Cryptoblepharus megastictus Storr, 1976. – Storr *et al.* 1981: 23; Gow 1981b; Cogger *et al.*, 1983: 141; Wilson and Knowles 1988: 119; Horner 1991: 17; Ehmann 1992: 182; Gambold 1992: 99; Stanger *et al.* 1998: 23; Storr *et al.* 1999: 23; Cogger 2000: 405; Wilson and Swan 2003: 148.

Type material examined. *Cryptoblepharus juno* Horner. HOLOTYPE: Adult female, NTM R24789 (Tissue sample No. *ABTC* DS2), Lobby Creek, Bradshaw Station, Northern Territory, Australia, 15°19'48"S 130°06'15"E. coll. P. Horner, T. Hertog and L. Corbett, 5 September 1999. Rocky slope, on base of tree trunk surrounded by boulders. PARATYPES (36 specimens): NORTHERN TERRITORY: AM R72691, R72960, 6 km northwest of Bullo River crossing of Victoria Hwy, 15°40'S 129°39'E, 21–22 June 1978; AM R73030, R73039, 31 km northwest of Bullo River crossing of Victoria Hwy (station road), 15°42'S 129°39'E, 21 June 1978; AM R117118, R117122, 31 km northwest of Bullo River crossing of Victoria Hwy (station road), 15°42'S 129°39'E, 22 August 1985; NTM R18637, R18639, Bradshaw Station, 15.20'S 130.06'E, A. Fisher, 7 June 1997; NTM R18640, Bradshaw Station, 15.22'S 130.07'E, A. Fisher, 7 June 1997; NTM R22353-354, R22356-357, Jarrnarm Escarpment, Keep River National Park, 15.46'S 129.05'E, P. Horner, 24 April 1996, *ABTC* Y87-Y88, Y90-Y91; NTM R22363-365, Jarrnarm Escarpment, Keep River National Park, 15.46'S 129.05'E, P. Horner, 29-30 April 1996, *ABTC* Y97-Y99; NTM R22367, Jarrnarm Escarpment, Keep River National Park, 15.465'S 129.05'E, P. Horner, 24 April 1996; NTM R23204, Spirit Hills Station, 15.28'S 129.21'E, T. Griffths and Survey team, 18 August 1996; NTM R24125, North Kollendong Swamp, Bradshaw Station, 15.00'S 130.03'E, P. Horner and Survey Team, 4 November 1998; NTM R24793-795, Lobby Creek, Bradshaw Station, 15.20'S 130.06'E, P. Horner and Survey team, 5 September 1999, *ABTC* DT8-DT9, DU1; NTM R26837-838, Bradshaw Station, 15.14'S 130.23'E, J. Woinarski and A. Fisher, 11 March 2002; NTM R5626, R5643, Keep River National Park, 15.45'S 129.05'E, Survey team, 4 November 1981; NTM R5677-678, Keep River National Park, 15.45'S 129.05'E, Survey team, 31 October 1981; NTM R9144, Keep River National Park, 15.45'S 129.05'E, Survey team, September 1980. WESTERN AUSTRALIA: NTM R16784-787, Dead Horse Spring, Lake Argyle, 16.06'S 128.45'E, P. Horner, 31 March 1991, *ABTC* R66-R69; NTM R26008, near Bellburn Camp, Purnululu National Park, 17.27'S 128.18'E, P. Horner, 6 July 2000, *ABTC* EX1; WAM R47637, Lake Argyle, 16°15'S 128°45'E, 9 January 1972; WAM R32361, Wyndham, 15°29'S 128°07'E, 1968.

Diagnosis (37 specimens). A medium sized (40–44 mm SVL), very long-legged, very shallow-headed, saxicoline *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of six supraciliary scales, 26 mid-body scale rows, 49 paravertebral scales, 19 subdigital lamellae under fourth toe, nine palmar scales, 12 plantar scales and three posttemporal scales; mean values of hindlimb length 46.5% of snout-vent length, head depth 33.9% of head length, paravertebral scale 4.3% of snout-vent length, dorsolateral scale 84.3% of paravertebral scale width; reddish, randomly speckled or blotched body pattern and saxicoline habits.

Description. Postnasals absent; prefrontals usually in broad contact (82%), occasionally in narrow contact (5%) or narrowly separated (13%); supraciliaries 6–7 (mean 6.0), modally 6; enlarged upper ciliaries 2–4 (mean 3.1), modally 3; posterior loreal usually largest (92%), occasionally subequal (8%); supralabials 7; fifth supralabial subocular (100%): infralabials 6–7 (mean 6.0), modally 6; nuchals 2–4 (mean 2.3), modally 2; bilateral posttemporals usually 3+3 (52%), occasionally 2+3 (34%), or 2+2 (14%).

Midbody scale rows 24–28 (mean 25.4), modally 26; paravertebrals 44–54 (mean 48.8), modally 49; subdigital lamellae smooth, 13–19 below fourth finger (mean 16.0) modally 16, 17–23 below fourth toe (mean 19.9) modally 19; 11–14 supradigital lamellae above fourth finger (mean 13.1) modally 13, 13–18 above fourth toe (mean 15.9) modally 15; palmar and plantar scales rounded, without calli and skin not visible between scales (Fig. 70); plantars 10–15 (mean 12.1), modally 12; palmars 7–12 (mean 9.1), modally 9.

Fig. 70. Ventral surface of hind foot of *Cryptoblepharus juno* sp. nov. showing pale, ovate plantar scales (NTM R26008, Purnululu National Park, WA.). Scale: x20.

Fig. 71. Holotype of *Cryptoblepharus juno* sp. nov., NTM R24789, Lobby Creek, Bradshaw Station, Northern Territory, 15°19'48"S 130°06'15"E. Scale bar = 10 mm.

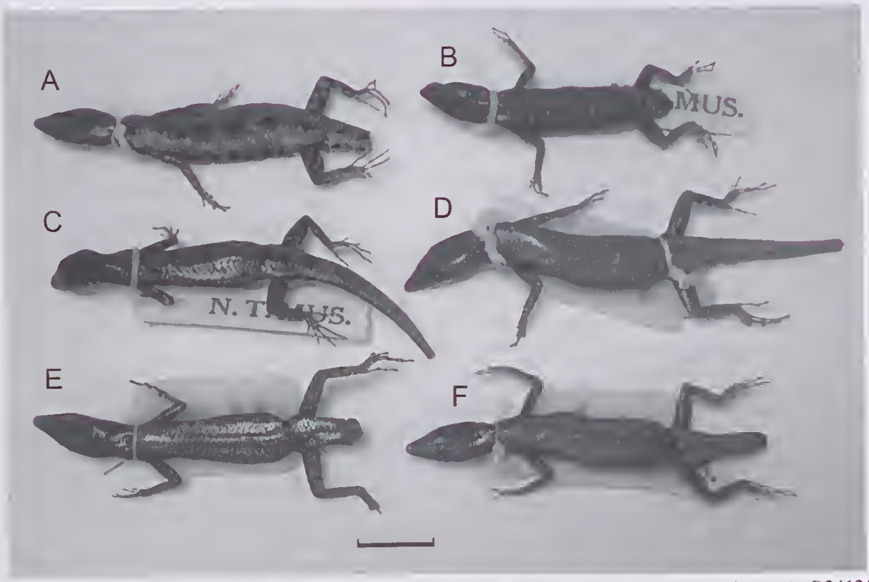

Fig. 72. *Cryptoblepharus juno* sp. nov. NTM preserved material from the Northern Territory: **A**, R24125, Bradshaw Station; **B**, R22367, Keep River; **C**, R23204, Spirit Hills Station; **D**, R22365, Keep River; **E**, R22363, Keep River; **F**, R22364, Keep River. Scale bar = 10 mm.

Snout-vent length to 43.1 mm (mean 36.7 mm). *Percentages of snout-vent length*: body length 41.5–55.5% (mean 49.7%); tail length 122.0–138.8% (mean 131.3%); forelimb length 33.2–41.9% (mean 37.7%); hindlimb length 40.9–52.2% (mean 46.5%): forebody length 38.7–49.0% (mean 42.8%); head length 19.6–24.0% (mean 21.3%). *Percentages of head length*: head depth 26.3–41.1% (mean 33.9%); head width 53.2–65.7% (mean 58.2%); snout length 42.0–50.1% (mean 45.4%). Paravertebral scale width 3.4–5.2% (mean 4.3%) of snout-vent length; dorsolateral scale width 64.0–102.9% (mean 84.3%) of paravertebral scale width.

Lenticular scale organs 2–17 (mean 7.2), modally 6. Premaxillary teeth 4–5 (mean 4.5); maxillary teeth 20–23 (mean 21.8), modally 23; mandibular teeth 21–24 (mean 23.0), modally 24. Hemipenis: length 6.8–9.1% (mean 8.4%) of snout-vent length; width 70.3–112.5% (mean 81.8%) of hemipenis length; trunk 45.1–64.4% (mean 54.2%) of hemipenis length.

Details of holotype. NTM R24789, adult female (Fig. 71). Postnasals absent; prefrontals in broad contact; supraciliaries 6; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 4. Midbody scale rows 26; paravertebrals 47; subdigital lamellae smooth, 15 below fourth finger; 18 below fourth toe; supradigital lamellae 11 above fourth finger; 14 above fourth toe; palmars and plantars rounded, skin not visible between scales; plantars 11; palmars 8. Snout-vent length 39.5 mm; body length 20.4 mm; tail not original; forelimb length 13.8 mm; hindlimb length 16.8 mm; forebody length 16.4 mm; head length 7.8 mm; head depth 2.8 mm; head width 4.5 mm; snout length 3.6 mm.

Colouration and pattern. A reddish *Cryptoblepharus*, patterned with random dark spots and flecks and/or blotches (Plate 2.1). Intensity of body pigmentation and patterning is variable, ranging from pale and obscure (Fig. 72 D and F) to dark and prominent (Fig. 72 A, B and C). Most specimens conform to the following description.

Dorsal ground colour russet to reddish, patterned with random, irregular brown-black spots, flecks, specks and/or blotches. Head and tail concolorous with body, but with reduced dark markings. Labials pale cream. Limbs concolorous with body, patterned with dark streaks and spots. Venter immaculate off-white. Subdigital lamellae, palmar and plantar surfaces off-white, patterned with occasional dark flecks.

Sex ratio and reproductive biology. Sex ratio favoured males (20:17), but was not significantly different from parity ($X^2 = 0.24$). Maturity is reached at approximately 34 mm snout-vent length. Adults average 36.7 mm snout-vent length and males reach a larger maximum size (SVL = 43.1 mm versus 42.2 mm). Small sample size of ten reproductive animals indicates breeding is seasonal, with all being collected between July and November.

Comparison with Australian congeners. Fixed allelic differences place *C. juno* sp. nov. in lineage 1 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTU megaA2, Horner and Adams 2007).

Morphologically distinguished from lineage 2 members (*C. adamsi* sp. nov., *C. exochus* sp. nov., *C. fuhni*, *C. gurrmul* sp. nov., *C. litoralis*, *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus*, *C. pulcher*, *C. tytthos* sp. nov., *C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov.) by usually having six, rather than five, supraciliary scales and (except for *C. ustulatus* sp. nov. and *C. zoticus* sp. nov.) speckled or blotched body pattern on reddish ground colour.

Distinguished from lineage 1 congeners: *C. australis*, *C. buchananii*, *C. cygnatus* sp. nov., *C. metallicus* and *C. ruber* by ground colour and body pattern characteristics (randomly speckled or blotched body pattern on reddish ground colour versus longitudinally aligned body pattern on greyish ground colour) and by being saxicoline rather than arboreal. Further distinguished from *C. australis*, *C. buchananii*, *C. cygnatus* sp. nov., *C. metallicus* and *C. ruber* by more mid-body scale rows (modally 26 versus 24), shallower head (mean 33.9 versus 41.1–43.3% of head length) and longer hindlimbs (mean 46.5 versus 40.9–42.0% of SVL).

Cryptoblepharus juno sp. nov. is most similar to *C. daedalos* sp. nov., *C. megastictus*, *C. ustulatus* sp. nov., *C. wulbu* sp. nov. and *C. zoticus* sp. nov. in having combinations of reddish ground colour and saxicoline habits. However, it differs from *C. ustulatus* sp. nov. and *C. zoticus* sp. nov. by having more supraciliary (modally 6 versus 5), paravertebral (modally 49 versus 46 and 45) and plantar scales (modally 12 versus 11 and 10), and longer hindlimbs (mean % of SVL, 46.5 versus 44.3 and 42.2). Differs from *C. wulbu* sp. nov. by having more paravertebral scales (modally 49 versus 39), fewer plantar scales (modally 12 versus 13) and fourth finger subdigital lamellae (modally 16 versus 17) and a longer, narrower head (mean HL 21.3 versus 19.9% of SVL; HW 58.2 versus 65.4% of head length). Differs from *C. megastictus* by having more palmar scales (modally 9 versus 8), wider paravertebral scales (mean 4.3 versus 3.7% of SVL) and speckled rather than blotched body pattern. Most similar to *C. daedalos* sp. nov. but differs by having fewer plantar scales (modally 12 versus 15), more posterior temporal scales (modally 3 versus 2) and a shallower head (mean 33.9 versus 36.0% of head length).

Distribution. *Cryptoblepharus juno* is found in the region where far northern Western Australia meets northwestern Northern Territory. Occurs from Bradshaw Station in the NT, west to Wyndham WA, and south to the Bungle Bungle Range WA (Fig. 73).

Sympatry. Sympatric with *C. ruber* at Lake Argyle (Dead Horse Spring) WA and Bradshaw Station (Koolendong Valley) NT. With *C. metallicus* at Wyndham WA and Bradshaw Station (Lobby Creek) NT, where *C. exochus* sp. nov. also occurs on nearby Mosquito Flat.

Geographic variation. Small sample size and limited distribution, prevented analysis of geographic variation.

Habits and habitats. Saxicolous, *C. juno* inhabits sandstone escarpment, rock outcrops, rocky hills and sandstone/limestone outliers. Associated with these habitats were open woodland and dry rainforest vegetation, such as *Celtis phillipenensis*. One record notes use of a tree trunk surrounded by boulders. Ian Morris (pers. comm.) observed this species pirating food from ants in a cave-like overhang at Keep River. Three or four individuals were dispersed about the ant trail where, when an ant burdened with a morsel of food approached, a skink would straddle the ant trail (holding its body arched) and when the ant passed underneath, snatch the food morsel. The skinks could accomplish this manoeuvre from any angle, even while hanging upside down from the cave roof. Gambold (1992) found *C. juno* sp. nov. to be moderately common on sandstone of the Osmand Ranges and Bungle Bungle massif.

Etymology. Named for Juno who, in Roman religion and mythology, was principal goddess of the Pantheon and the patroness primarily of marriage and the well-being of women.

Fig. 73. Map of north-western Australia showing distribution of *Cryptoblepharus juno* sp. nov. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

Cryptoblepharus litoralis (Mertens, 1958)
Coastal snake-eyed skink

(Plates 2.2–2.3; Figs 74–82; Table 7)

Ablepharus boutonii litoralis Mertens 1964: 106. – Worrell 1963: 35.

Cryptoblepharus litoralis Mertens, 1958. – Gow 1981b; Cogger *et al*. 1983a: 141; Horner 1984: 7; Wells and Wellington 1985: 27; Wilson and Knowles 1988: 119; Greer 1989: 146; Covacevich and Couper 1991: 357; Horner 1991: 16; Ehmann 1992: 181; Woinarski *et al*. 1996: 75; Healey 1997: 329; Stanger *et al*. 1998: 23; Horner 1999: 60; Cogger 2000: 405; Wilson and Swan 2003: 148.

Cryptoblepharus horneri Wells and Wellington, 1985: 27 (in part).

Diagnosis. A very large (>50 mm SVL), long-legged, shallow-headed, saxicoline, littoral *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of five supraciliary scales, 26 mid-body scale rows, 51–57 paravertebral scales, 20–22 fourth toe subdigital lamellae, 9–11 palmar scales; 11–16 plantar scales; mean values of 39.0–41.0 mm snout-vent length, smooth to narrowly callused subdigital lamellae; rounded, dark pigmented plantar scales, and lack of postnasal scales.

Description (53 specimens). Postnasals usually absent; prefrontals usually in broad contact (88%), occasionally narrowly separated (4%) or fused (8%); supraciliaries 5–6 (mean 5.1), modally 5; enlarged upper ciliaries 2–4 (mean 3.0), modally 3; anterior loreal usually largest (60%), occasionally subequal (38%) or posterior largest (2%); supralabials 6–8 (mean 7.1), modally 7; fifth supralabial usually subocular (90%), occasionally fourth (2%) or sixth (8%); infralabials 6–7 (mean 6.0), modally 6; nuchals 2–6 (mean 3.2), modally 2; bilateral posttemporals usually 2+2 (74%), occasionally 2+3 (20%), or 3+3 (6%).

Midbody scale rows 24–28 (mean 26.0), modally 26; paravertebrals 47–62 (mean 55.4), modally 57; subdigital lamellae smooth to broadly callose, 13–19 below fourth finger (mean 16.0) modally 16, 17–24 below fourth toe (mean 20.2) modally 20; 11–16 supradigital lamellae above fourth finger (mean 13.2) modally 13, 12–18 above fourth toe (mean 15.6) modally 16; palmar and plantar scales rounded, without calli and skin visible between scales; plantars 9–16 (mean 12.0), modally 11; palmars 7–14 (mean 10.7), modally 11.

Snout-vent length to 51.0 mm (mean 40.5 mm). *Percentages of snout-vent length*: body length 45.0–57.1% (mean 52.0%): tail length 116.1–176.8% (mean 144.5%); forelimb length 30.3–40.3% (mean 35.3%); hindlimb length 38.5–51.0% (mean 45.1%); forebody length 37.5–47.6% (mean 41.7%); head length 18.3–23.2% (mean 20.7%). *Percentages of head length*: head depth 36.6–53.3% (mean 42.2%); head width 50.7–69.7% (mean 59.7%); snout length 40.7–49.2% (mean 45.3%). Paravertebral scale width 2.8–4.3% (mean 3.5%) of snout-vent length; dorsolateral scale width 80.0–111.3% (mean 94.6%) of paravertebral scale width.

Lenticular scale organs 1–13 (mean 5.8), modally 5. Following teeth counts are from Queensland specimens only: Premaxillary teeth 5–6 (mean 5.3), modally 5; maxillary teeth 23–25 (mean 24.0), modally 24; mandibular teeth 29–31 (mean 30.5), modally 31. Following hemipenis proportions are from Queensland specimens only: length 6.8–9.6% (mean 7.9) of snout-vent length; width 87.3–104.7% (mean 97.5) of hemipenis length; trunk 27.8–48.3% (mean 37.1) of hemipenis length.

Colouration and pattern. Grey-brown to grey- black skink, with longitudinally aligned, complex body pattern dominated by dark, broad vertebral zone and pale laterodorsal stripes. Intensity of body pigmentation and patterning is variable, ranging from obscure to prominent. Most specimens conform to the following description.

Dorsal ground colour grey-brown to grey-black with broad, dark vertebral zone extending from above eye to hindlimb. Vertebral zone as wide as paired paravertebral scales, dark grey with pale grey speckling and dotted with short longitudinal black streaks and spots. The latter most prominent on outer edges of paravertebrals and usually form two broken, narrow black stripes from neck to hindlimbs. Pale grey laterodorsal stripes may be obvious or obscure, extend from above eye onto tail, broadest on posterior half of body, about width of laterodorsal scales, tapering anteriorly into narrow stripes extending to eye and posteriorly to form tail ground colour. Edges of pale laterodorsal stripes usually ragged but occasionally smooth. Laterodorsal stripes usually uniform, but may contain dark and/or pale speckling. Head concolorous with vertebral zone or brownish, usually immaculate, occasionally with darker mottling. Laterally, head is patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Pale lower temporal region flecked with dark spots and streaks. Labials pale grey, often with dark margins to scales.

Flanks patterned with blackish upper lateral zone, variable in width, extending from loreals onto tail and forming a border to pale laterodorsal stripe. Usually flecked with pale specks and short streaks, upper lateral zone may be represented by a narrow, broken, black stripe but typically is about two lateral scales wide and coalesces gradually into pale grey lower lateral zone. Lower lateral zone peppered with small pale streaks and/or dark spots and coalesces into pale venter. Tail concolorous with body, patterned with broken continuations of blackish vertebral and upper lateral zones. Limbs and toes concolorous with body, patterned with pale and dark speckling. Ventral surfaces blue-grey to off-white. Palmar and plantar scales dark grey to dark brown.

Comparison with Australian congeners. Fixed allelic differences place *C. litoralis* in lineage 2 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTUs horn and litor, Horner and Adams 2007).

Morphologically distinguished from lineage 1 members *C. australis, C. buchananii, C. cygnatus* sp. nov., *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus, C. metallicus, C. ruber* and *C. wulbu* sp. nov. by usually having five, rather than six, supraciliary scales, reduced melanistic body pattern and saxicoline, littoral habits. Distinguished from lineage 2 congeners by the following combinations of morphological characters: Distinguished from *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus,* and *C. tytthos* sp. nov. by having rounded, dark pigmented plantar scales (versus acute, pale plantars); from *C. adamsi* sp. nov., *C. fuhni, C. pulcher, C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov. by having more mid-body scale rows (modally 26 versus 22–24) and paravertebral scales (modally 57 versus 45–50). Further distinguished from *C. pulcher, C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov. by being larger (mean SVL, 40.5 versus 33.4–35.6 mm); from *C. gurrmul* sp. nov. by having fewer mid-body scale rows (modally 26 versus 28), fewer plantar scales (modally 11 versus 7), more fourth toe subdigital lamellae (modally 20 versus 18) and by lack of postnasal scales (versus present).

Distribution. Coastal mid-north and north-eastern Australia to southern New Guinea (Fig. 74).

Habits and habitats. A saxicoline, coastal taxon, which frequents beach rocks, rocky headlands and breakwaters. Usually abundant in suitable habitat.

Subspecies. *Cryptoblepharus litoralis* is a polytypic taxon comprised of three allopatric subspecies: *Cryptoblepharus litoralis horneri*; *Cryptoblepharus litoralis litoralis*; *Cryptoblepharus litoralis vicinus* ssp. nov.

Fig. 74. Map of northern Australia and New Guinea showing distribution of *Cryptoblepharus litoralis*. Note disjunct ranges of (**A**) *C. l. horneri* (Arnhem Land coast), (**B**) *C. l. litoralis* (Queensland coast), (**C**) *C. l. vicinus* ssp. nov. (Port Moresby, PNG). Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

Cryptoblepharus litoralis horneri Wells and Wellington, 1985

Horner's snake-eyed skink

(Plate 2.2; Figs 74A, 75–78)

Cryptoblepharus horneri Wells and Wellington, 1985: 27 (in part).

Type material examined. *Cryptoblepharus litoralis horneri* Wells and Wellington, 1985. HOLOTYPE: NTM R7762, Cape Wessel island (= Rimbija Island), Wessel Islands, Northern Territory, 11°00'S 136°45'E, coll. P. Horner, 16 October 1979.

Non-type material examined. See Appendix 4.

Diagnosis. As given above for species. Distinguished from conspecific *C. l. litoralis* by having fewer paravertebral (mean 54.5 versus 56.6), palmar (mean 9.5 versus 11.0) and plantar scales (mean 10.9 versus 11.8), more broadly callose subdigital lamellae (versus narrowly callose) and loreal scales usually subequal (versus anterior usually largest). Distinguished from conspecific *C. l. vicinus* ssp. nov. by more paravertebrals (mean 54.5 versus 50.8) and fewer plantar scales (modally 11 versus 16). In addition, *C. l. horneri* has an allopatric distribution apparently restricted to the islands and coast of Arnhem Land.

With no fixed allelic differences, *C. l. horneri* is genetically similar to *C. l. litoralis*.

Description (14 specimens). As described above for species, except for the following variation. Prefrontals usually in broad contact (90%), occasionally narrowly separated (10%); supraciliaries 5–6 (mean 5.1), modally 5; enlarged upper ciliaries 3); loreals usually subequal (57%), often anterior largest (43%); supralabials 6–7 (mean 6.9), modally 7; fifth supralabial usually subocular (93%), occasionally fourth (7%); infralabials 6; nuchals 2–6 (mean 3.4), modally 2; bilateral posttemporals usually 2+2 (57%), occasionally 2+3 (43%).

Midbody scale rows 24–28 (mean 25.6), modally 26; paravertebrals 50–58 (mean 54.5), modally 55; subdigital lamellae broadly callused, 13–18 below fourth finger (mean 15.8) modally 16, 17–22 below fourth toe (mean 19.5) modally 20; 11–15 supradigital lamellae above fourth finger (mean 12.8) modally 13, 12–17 above fourth toe (mean 15.1) modally 15; plantars 9–12 (mean 10.9) (Fig. 75), modally 11; palmars 7–11 (mean 9.5), modally 9.

Snout-vent length to 51.0 mm (mean 38.9 mm). *Percentages of snout-vent length*: body length 45.0–55.8% (mean 50.3%); tail length 135.1–171.9% (mean 152.1%); forelimb length 31.3–39.2% (mean 35.1%); hindlimb length 41.0–47.7% (mean 45.1%); forebody length 37.5–47.6% (mean 43.0%); head length 18.9–23.2% (mean 21.1%). *Percentages of head length*: head depth 36.6–43.6% (mean 40.1%); head width 50.7–69.7% (mean 59.1%); snout length 40.7–47.8% (mean 44.4%). Paravertebral scale width 2.8–4.3% (mean 3.7%) of snout-vent length; dorsolateral scale width 80.0–103.9% (mean 89.3%) of paravertebral scale width.

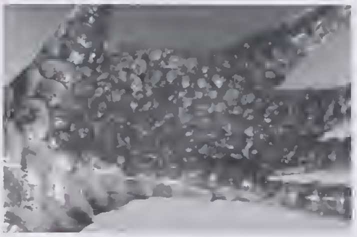

Fig. 75. Ventral surface of hind foot of *Cryptoblepharus litoralis horneri*, showing dark, ovate plantar scales (NTM R7762, Rimbija Island, Wessel Islands, NT). Scale: x20.

Fig. 76. Holotype of *Cryptoblepharus litoralis horneri* Wells and Wellington, 1985. NTM R7762, Cape Wessel Island (= Rimbija Island), Northern Territory, Australia, 11°00'S 136°45'E. Scale bar = 10 mm.

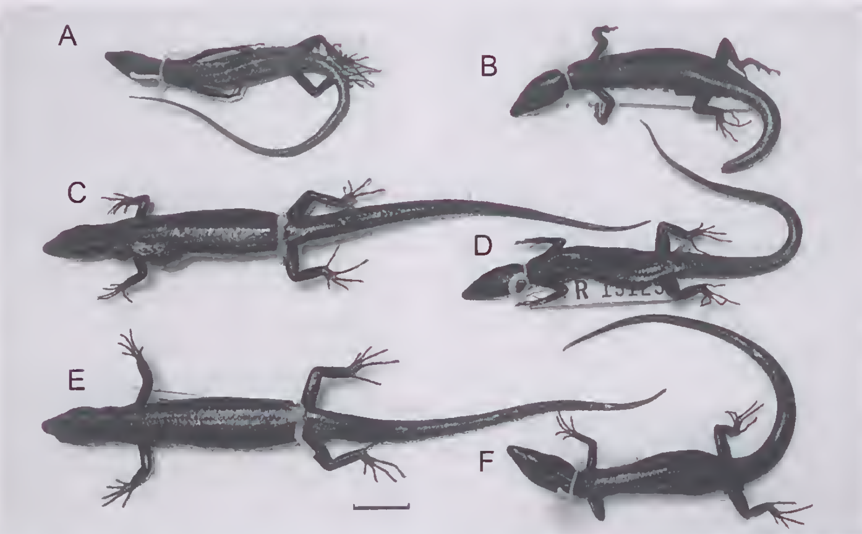

Fig. 77. *Cryptoblepharus litoralis horneri.* NTM preserved material from the Northern Territory. **A**, R17066, Murgenella; **B**, R19040, Jensen Island; **C**, R7761, Rimbija Island; **D**, R19129, Wessel Islands; **E**, R7762 [holotype], Rimbija Island; f = R19128, Wessel Islands. Scale bar = 10 mm.

Lenticular scale organs 1–13 (mean 5.8), modally 7.

Details of holotype. NTM R7762 (Fig. 76). Postnasals absent; left prefrontal fused to frontal; supraciliaries 5; enlarged upper ciliaries 3; loreals subequal; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 4. Midbody scale rows 26; paravertebrals 58; subdigital lamellae broadly callused, 16 below fourth finger; 21 below fourth toe; 12 supradigital lamellae above fourth finger; 14 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 12; palmars 11. Snout-vent length 51.0 mm; body length 28.1 mm; tail not original; forelimb length 16.1 mm; hindlimb length 21.6 mm; forebody length 19.6 mm; head length 9.8 mm; head depth 4.3 mm; head width 6.4 mm; snout length 4.5 mm.

Colouration and pattern. As described above for species (see Plate 2.2 and Fig. 77).

Sex ratio and reproductive biology. Sex ratio favoured males (8:6), but was not significantly different from parity (X2 = 0.29). Small sample size of four reproductive animals limited analysis. However, the data indicates males mature at approximately 39 mm snout-vent length and females at 43 mm. Adults average 38.9 mm snout-vent length and females grow larger than males (maximum SVL = 51.0 mm versus 41.1 mm).

Distribution. Coastal Arnhem Land, Northern Territory (Fig. 74A). Occurring mainly on off-shore islands (Rimbija, Emu, Jensen and islet 'L' in the Wessel group; Elcho, Truant and New Year Islands). Recorded from the mainland coast near Murgenella. All records are located within the Arnhem Coast (ARC) bioregion.

Sympatry. *Cryptoblepharus l. horneri* is sympatric with *C. metallicus* (lineage 1) on the Wessel islands, and with *C. gurrmul* sp. nov. (lineage 2) and *C. cygnatus* sp. nov. (lineage 1) on New Year Island.

Geographic variation. Small sample size and limited distribution prevented analysis of geographic variation.

Habits and habitats. A poorly known, saxicoline, coastal *Cryptoblepharus*. Museum records note its use of wave-washed rocks, rocks at base of headlands, rocks at high tide mark, under log on a beach, and in crevice of small coral chunk embedded in sand.

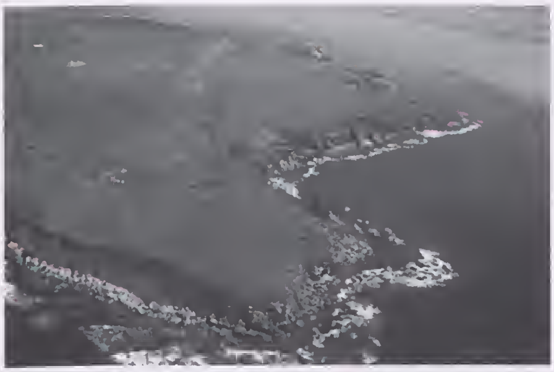

Fig. 78. Cape Wessel on Rimbija Island, Northern Territory, Australia. Type locality of *Cryptoblepharus litoralis horneri*.

Taxonomic history. Gow (1981b) first drew attention to the occurrence of *C. l. horneri* (as *C. litoralis*) on "Cape Wessel Island" (= Rimbija Island) (Fig. 78), Northern Territory. Collection of further specimens from islands off the Arnhem Land coast prompted Horner (1984) to publish information on comparative morphology (Queensland versus Northern Territory populations of '*C. litoralis*') and distribution of the taxon. Wells and Wellington (1985) cited data published in Horner (1984) and without examination of specimens, described the taxon as a new species applying the binomen *C. horneri*. Wells and Wellington's (1985) description of *C. horneri* distinguished the new taxon from *C. litoralis* by stating the taxon could be identified by "its higher mid-body scale count, shorter body and fewer sub-digital lamellae" (Wells and Wellington 1985). By designating NTM R7762 (illustrated in Horner 1984) as the holotype, and stating "characters that are purported to differentiate the taxon" and supplying "bibliographic reference to such a published statement" (International Commission on Zoological Nomenclature 1999, Article 13: 13.1.1–13.1.2), Wells and Wellington validated the binomen. However, their failure to personally examine material listed in Horner (1984) was unfortunate. Of the eight specimens Horner analysed, only two are referable to *C. l. horneri*, the other six are now known to represent *C. gurrmul* sp. nov. Thus, the 'diagnostic' characters given by Wells and Wellington (1985) do not differentiate between *C. l. horneri* and *C. l. litoralis*, but do between *C. litoralis* and *C. gurrmul* sp. nov.

Pending this more detailed comparison with congeners, Horner (1999) synonymised *C. horneri* with *C. litoralis*. This work involves first usage of the trinomen *Cryptoblepharus litoralis horneri*.

Cryptoblepharus litoralis litoralis (Mertens, 1958)
Coastal snake-eyed skink

(Plate 2.3; Figs 74B, 79–82; Table 7)

Ablepharus boutonii litoralis Mertens, 1958: 54.

Type material examined. HOLOTYPE: SMF 53219, Flying Fish Point, 6 miles east of Innisfail, Queensland, Australia, coll. R. Mertens and H. Felten, 24 April 1957.

Non-type material examined. See Appendix 4.

Diagnosis. As given above for species. Distinguished from conspecific *C. l. horneri* by having more paravertebral (mean 57.6 versus 54.3), palmar (mean 11.0 versus 9.5) and plantar scales (mean 11.8 versus 10.9), more narrowly callose subdigital lamellae (versus broadly callose) and anterior loreal scale usually largest (versus usually subequal). Distinguished from conspecific *C. l. vicinus* ssp. nov. by having more paravertebral (mean 56.6 versus 50.8) and fewer plantar scales (modally 11 versus 16). In addition, *C. l. litoralis* has an allopatric distribution apparently restricted to islands of Torres Strait and the Queensland coast.

With no fixed allelic differences, *C. l. litoralis* is genetically similar to *C. l. horneri*.

Description (33 specimens). As described above for species, except for the following variation. Prefrontals in broad contact (100%); supraciliaries 5–6 (mean 5.1), modally 5; enlarged upper ciliaries 3–4 (mean 3.0), modally 3; anterior loreal usually largest (79%), occasionally subequal (18%) or posterior largest (3%); supralabials 7–8 (mean 7.1), modally 7; fifth supralabial subocular (100%); infralabials 6–7 (mean 6.0), modally 6; nuchals 2–6 (mean 3.4), modally 2; bilateral posttemporals usually 2+2 (86%), occasionally 2+3 (5%), or 3+3 (9%).

Midbody scale rows 24–28 (mean 26.0), modally 26; paravertebrals 48–62 (mean 56.6), modally 57; subdigital lamellae narrowly callose, 13–17 below fourth finger (mean 15.9) modally 16, 18–23 below fourth toe (mean 20.1) modally 20; 12–14 supradigital lamellae above fourth finger (mean 13.4) modally 14, 14–17 above fourth toe (mean 15.7) modally 16; plantars 10–14 (mean 11.8), modally 11 (Fig. 79); palmars 9–13 (mean 11.0), modally 11.

Snout-vent length to 51.0 mm (mean 41.0 mm). *Percentages of snout-vent length*: body length 48.1–56.3% (mean 52.3%); tail length 116.1–176.8% (mean 142.0%); forelimb length 30.6–38.7% (mean 35.4%); hindlimb length 38.5–48.9% (mean 45.0%); forebody length 37.7–45.7% (mean 41.6%); head length 18.3–22.5% (mean 20.6%). *Percentages of head length*: head depth 37.1–53.3% (mean 42.2%); head width 53.1–64.4% (mean 59.4%); snout length 42.9–49.2% (mean 45.6%). Paravertebral scale width 2.9–4.1% (mean 3.4%) of snout-vent length; dorsolateral scale width 83.2–111.3% (mean 98.2%) of paravertebral scale width.

Lenticular scale organs 2–9 (mean 5.8), modally 5.

Details of holotype. *Ablepharus boutonii litoralis* Mertens, 1958. SMF 53219 (Fig. 80). Postnasals absent; right prefrontal fused to frontal; supraciliaries 5; enlarged upper ciliaries 3; loreals subequal; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 24; paravertebrals 53; subdigital lamellae narrowly callused, 16 below fourth finger; 21 below fourth toe; supradigital lamellae 13 above fourth finger; 16 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 11; palmars 11. Snout-vent length 42.4 mm; body

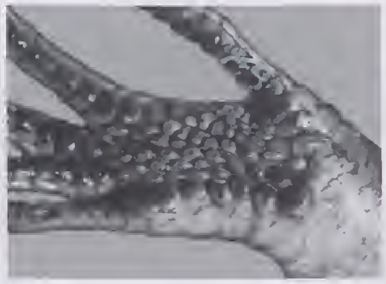

Fig. 79. Ventral surface of hind foot of *Cryptoblepharus litoralis litoralis* showing dark, ovate plantar scales (NTM R18901, Flying Fish Point, Qld). Scale: x20.

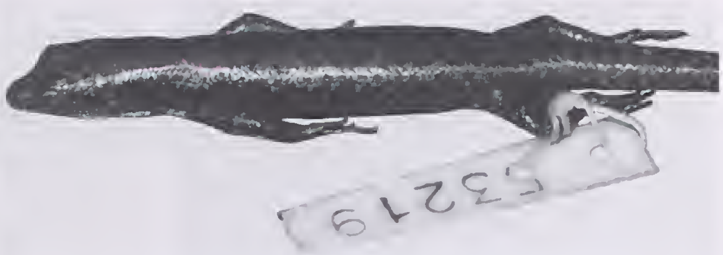

Fig. 80. Holotype of *Ablepharus boutonii litoralis* Mertens, 1958. SMF 53219, Flying Fish Point, 6 miles east of Innisfail, Queensland, Australia.

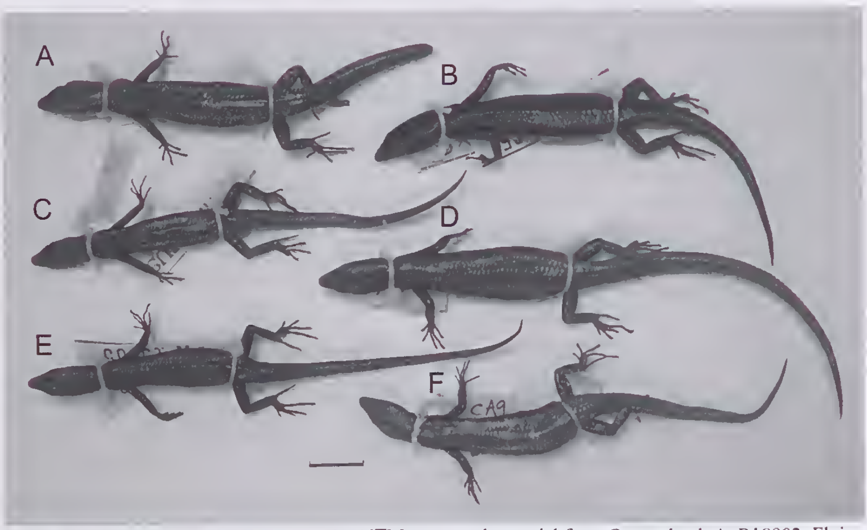

Fig. 81. *Cryptoblepharus litoralis litoralis.* NTM preserved material from Queensland. **A**, R18902, Flying Fish Point; **B**, R18865, Cooktown; **C**, R18897, Flying Fish Point; **D**, R18901, Flying Fish Point; **E**, R18905 Mourilyan; **F**, R19128, Flying Fish Point. Scale bar = 10 mm.

length 21.7 mm; tail not original; forelimb length 14.1 mm; hindlimb length 19.3 mm; forebody length 17.3 mm; head length 9.1 mm; head depth 4.4 mm; head width 5.9 mm; snout length 4.4 mm.

Colouration and pattern. As described above for species (see Plate 2.3 and Fig. 81).

Sex ratio and reproductive biology. Sex ratio favoured females (21:12), but was not significantly different from parity ($X^2 = 2.46$). Males mature at approximately 37 mm snout-vent length and females at 38 mm. Adults average 41.0 mm snout-vent length and females grow larger than males (maximum SVL = 51.0 versus 44.0 mm). Reproduc-

Table 7. List of congeners sympatric with *Cryptoblepharus l. litoralis*, giving areas of sympatry.

Congeners sympatric with *Cryptoblepharus l. litoralis*	Area of sympatry
C. p. pulcher	Qld: Airlie Beach, Cape Hillsborough, Dingo Beach, Emu Park, Hayman Island. Hinchinbrook Island, North Keppel Island, Townsville
C. virgatus	Qld: Cooktown, Dauar Island, Flying Fish Point, Hammond Island, King Island, Lizard Island, Moa Island, Murray Island, Purtaboi Island, Somerset, Stoney Point, Temple Bay, Thursday Island, Tip of Cape York, Warraber Island, Yam Island
Multiple sympatry	
C. metallicus + *C. pannosus* sp. nov.	Qld: Townsville
C. metallicus + *C. p. pulcher*	Qld: Magnetic Island, Townsville
C. metallicus+ *C. virgatus*	Qld: Horn Island

tive animals were collected in December and January, but data for other months is unavailable.

Distribution. Coastal eastern Queensland, from Torres Strait islands south to the vicinity of Gladstone (Fig. 74B).

Sympatry. *Cryptoblepharus l. litoralis* occurs in sympatry with *C. metallicus* from lineage 1 and *C. pannosus* sp. nov., *C. pulcher* and *C. virgatus* from lineage 2 (Table 7).

Geographic variation. Geographic variation was investigated by dividing specimens into three disparate groups: *CMC*, a south coastal Queensland group of 5 (2 ♂, 3 ♀) samples from bioregion CMC; *SWT*, a mid-north coastal Queensland group of 16 (7 ♂, 9 ♀), from the type locality, Flying Fish Point (Fig. 82), and *NWT*, a far north coastal Queensland group of 12 (3 ♂, 9 ♀), being samples from north of the type locality.

Group pairs, where sexes were treated separately and combined, were subjected to tests of all allometrically adjusted variables. Significant differences were detected between females of each group, but not males. Differentiation was due to *NWT* females having a deeper head than *SWT* and *CMC* (mean 3.5 versus 3.0 and 3.2 mm), and *CMC* females having longer forebodies than *SWT* (mean 15.9 mm versus 15.3).

These results indicate that geographic variation in *C. l. litoralis* is limited to females of northern populations having deeper heads and females of southern populations having slightly longer forebodies.

Habits and habitats. As for species.

Taxonomic history. Recognised and described in 1958 by Robert Mertens, *Ablepharus boutonii litoralis* has a relatively uneventful taxonomic history. Placed in *Cryptoblepharus* by Fuhn (1969a), who excised the large *boutonii* – Rassenkreis from *Ablepharus*. Cogger *et al.* (1983a) treated the taxon as a full species. This study involves first usage of the trinomen *Cryptoblepharus litoralis litoralis*.

Fig. 82. Flying Fish Point, Queensland, Australia. Type locality of *Cryptoblepharus litoralis litoralis*.

Cryptoblepharus litoralis vicinus ssp. nov.

Papuan coastal snake-eyed skink

(Fig. 74C)

Type material examined. *Cryptoblepharus litoralis vicinus* Horner. HOLOTYPE: QM J32823, Ela Beach, Port Moresby, Central Province, Papua New Guinea, 09°29'S 147°09'E, 10 October 1976. PARATYPES: NEW GUINEA: QM J32824-825, same data as holotype; QM J32857-859, same data as holotype, except 27 December 1976.

Diagnosis. A large (45–50 mm SVL), long-legged, deep-headed, coastal *Cryptoblepharus*, distinguished from Indo-Pacific congeners by combination of: modal values of five supraciliary scales, 26 midbody scale rows, 51 paravertebral scales, 22 subdigital lamellae under the fourth toe, 16 plantar scales and 2 nuchal scales; mean value of: 41.3 mm snout-vent length; loreals subequal in size; semi-melanotic colouration and absence of a pale midlateral stripe. Distinguished from Australian conspecifics (*C. l. horneri* and *C. l. litoralis*) by fewer paravertebral (modally 51 versus 57 and 55) and more plantar scales (modally 16 versus 11).

Description (6 specimens). Postnasals absent; prefrontals usually in broad contact; supraciliaries 5; enlarged upper ciliaries 2–4 (mean 3.1), modally 3; loreals usually subequal; supralabials 7–8 (mean 7.3), modally 7; fifth supralabial usually subocular; infralabials 6; nuchals 2.

Midbody scale rows 26–28 (mean 26.3), modally 26; paravertebrals 47–55 (mean 50.8), modally indeterminate; subdigital lamellae smooth, 16–19 below fourth finger (mean 17.3) modally 16, 20–24 below fourth toe (mean 22.2) modally 22; 13–16 supradigital lamellae above fourth finger (mean 13.5) modally 13, 15–18 above fourth toe (mean 16.3) modally 16; palmar and plantar scales rounded; plantars 15–16 (mean 15.5), modally 16; palmars 11–14 (mean 12.0), modally 11.

Snout-vent length to 45.7 mm (mean 41.3 mm). *Percentages of snout-vent length*: body length 51.2–57.1% (mean 54.3%); tail length indeterminate; forelimb length 30.3–40.3% (mean 35.3%); hindlimb length 39.9–51.0% (mean 45.2%); forebody length 37.9–42.5% (mean 39.3%); head length 19.3–22.0% (mean 20.5%). *Percentages of head length*: head depth 42.8–51.3% (mean 47.1%); head width 58.2–66.1% (mean 62.6%); snout length 44.1–48.6% (mean 45.8%). Paravertebral and dorsolateral scale widths not measured.

Details of holotype. Adult specimen, QM J32823. Postnasals absent; prefrontals in narrow contact; supraciliaries 5; enlarged upper ciliaries 3 on left side, 4 on right side; loreals subequal; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 28; paravertebrals 53; subdigital lamellae smooth, 16 below fourth finger; 22 below fourth toe; supradigital lamellae 13 above fourth finger; 16 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 16; palmars 12. Snout-vent length 41.5 mm; body length 22.4 mm; tail not original; forelimb length 14.8 mm; hindlimb length 18.5

mm; forebody length 16.1 mm; head length 8.5 mm; head depth 3.6 mm; head width 4.9 mm; snout length 3.8 mm.

Colouration and pattern. As described above for species.

Distribution. Type series collected at Ela Beach, Port Moresby, Central Province, Papua New Guinea (Fig. 74C).

Sympatry and geographic variation. Cases of sympatry unknown. Samples from a single locality.

Comparison with congeners. *Cryptoblepharus l. vicinus* ssp. nov. is distinguished from Australian congeners by characters given in the above species description and subspecies diagnosis.

Among Indo-Pacific congeners, *C. l. vicinus* ssp. nov. is distinguished from *C. C. cursor, C. keiensis, C. novaeguineae, C. novocaledonicus, C. novohebridicus, C. renschi, C. rutilus* and *C. yulensis* sp. nov. by more midbody scale rows (modally 26 versus 24 or less); from *C. burdeni* and *C. p. poecilopleurus* by fewer midbody scale rows (modally 26 versus 28 or more); from *C. baliensis, C. intermedius* and *C. leschenault* by fewer supraciliary scales (modally 5 versus 6) and sombre pattern (versus boldly striped); from *C. egeriae* and *C. p. paschalis* by fewer midbody scale rows (modally 26 versus 28) and fewer supraciliary scales (modally 5 versus 6); from *C. nigropunctatus* by more midbody scale rows (modally 26 versus 24) and fewer paravertebral scales (modally 51 versus 57); from *C. c. larsonae* ssp. nov. by more fourth toe subdigital lamellae (modally 22 versus 19) and greater size (mean SVL, 41.3 versus 36.8 mm); from *C. eximius* by greater size (mean SVL, 41.3 versus 34.9 mm) and lack of pale mid-lateral stripe (versus present); from *C. schlegelianus* by more paravertebral scales (modally 51 versus 46) and fourth toe subdigital lamellae (modally 22 versus 16); from *C. xenikos* sp. nov. and *C. richardsi* sp. nov. by wider head (mean 62.6 versus 57.8% or less of head length), more plantar scales (modally 16 versus 14 or less), further differs from *C. xenikos* sp. nov. by more midbody scale rows (modally 26 versus 22), and from *C. richardsi* sp. nov. by fewer paravertebral scales (modally 51 versus 53). Most similar to *C. furvus* sp. nov., but distinguished by mean number of paravertebrals (51 versus 58), nuchal scales (2 versus 4), plantar scales (16 versus 15) and relative size of loreals (subequal versus anterior largest).

Habits and habitats. A coastal species, presumed similar in habits to Australian conspecifics.

Etymology. From the Latin adjective *vicinus*, meaning near or neighbouring; in reference to the geographic relationship of this taxon with Australian subspecies of *C. litoralis.*

Cryptoblepharus megastictus Storr, 1976

Blotched snake-eyed skink

(Plate 2.4; Figs 83–86)

Cryptoblepharus megastictus Storr, 1976:61.– Smith and Johnstone 1978: 43; Smith and Johnstone 1981: 222; Storr *et al.* 1981: 23; Cogger *et al.* 1983a: 141; Wilson and Knowles 1988: 119; Greer 1989: 146; Kendrick and Rolfe 1991: 350; Ehmann 1992: 182; Healey 1997: 329; Stanger *et al.* 1998:23; Storr *et al.* 1999: 23; Cogger 2000: 405; Wilson and Swan 2003: 148.

Type material examined. *Cryptoblepharus megastictus* Storr, 1976. HOLOTYPE: WAM R43245, Mitchell Plateau, Western Australia, 14°52'S 125°50'E. coll. L. Smith and R. Johnstone, 24 January 1973.

Non-type material examined. See Appendix 4.

Diagnosis. A medium sized (40–44 mm SVL), long-legged, very shallow-headed, saxicoline *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of six supraciliary scales, 26 mid-body scale rows, 45 paravertebral scales, 19 subdigital lamellae under fourth toe, 8 palmar and 10 plantar scales; mean values of hindlimb length 44.6% of snout-vent length, head depth 32.5% of head length, paravertebral scale width 3.7% of snout-vent length, dorsolateral scale width 92.3% of paravertebral scale width; reddish, randomly blotched body pattern and saxicoline habits.

Description (9 specimens). Postnasals absent; prefrontals in broad contact; supraciliaries 6; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2–3 (mean 3.0), modally 2; bilateral posttemporals 3+3.

Midbody scale rows 24–28 (mean 26.2), modally 26; paravertebrals 44–51 (mean 47.2), modally 45; subdigital lamellae smooth, 14–18 below fourth finger (mean 16.7) modally 16, 18–21 below fourth toe (mean 19.4), modally 19; 12–14 supradigital lamellae above fourth finger (mean 13.1) modally 13, 15–17 above fourth toe (mean 15.6), modally 15; palmar and plantar scales rounded, without calli (Fig. 83), skin visible between scales; plantars 9–13 (mean 10.8), modally 10; palmars 6–10 (mean 8.2), modally 8.

Snout-vent length to 40.5 mm (mean 34.6 mm). *Percentages of snout-vent length*: body length 45.3–52.7% (mean 48.9%); tail length 106.2–129.6% (mean 122.3%); forelimb length 34.7–39.2% (mean 36.8%); hindlimb length 43.1–45.8% (mean 44.6%); forebody length 41.1–44.7% (mean 42.7%); head length 21.3–22.9% (mean 21.9%). *Percentages of head length*: head depth 27.7–38.2% (mean 32.5%); head width 55.5–65.6% (mean 59.9%); snout length 42.4–47.7% (mean 44.6%). Paravertebral scale width 3.4–4.2% (mean 3.7%) of snout-vent length; dorsolateral scale width 83.3–103.6% (mean 92.3%) of paravertebral scale width.

Lenticular scale organs 5–10 (mean 8.0), modally 7. Tooth counts and hemipenis proportions not measured.

Details of holotype. WAM R43245 (Fig. 84). Postnasals absent; prefrontals in broad contact; supraciliaries 6; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 26; paravertebrals 47; subdigital lamellae smooth, 16 below fourth finger; 20 below fourth toe; supradigital lamellae 14 above fourth finger; 17 above fourth toe; palmars and plantars rounded, skin visible be-

Fig. 83. Ventral surface of hind foot of *Cryptoblepharus megastictus*, showing pale, ovate plantar scales (NTM R22788, Kalumburu, WA). Scale: x20.

Fig. 84. Holotype of *Cryptoblepharus megastictus* Storr, 1976. WAM R43245, Mitchell Plateau, Western Australia, 14°52'S 125°50'E. Scale bar = 10 mm.

Fig. 85. *Cryptoblepharus megastictus*. NTM preserved material from Western Australia: **A** and **B**, R22788-22789, Kalumburu. Scale bar = 10 mm.

tween scales; plantars 10; palmars 12. Snout-vent length 26.4 mm; body length 11.9 mm; tail length 34.2 mm; forelimb length 9.35 mm; hindlimb length 12.1 mm; forebody length 11.8 mm; head length 6.0 mm; head depth 1.7 mm; head width 3.4 mm; snout length 2.7 mm.

Colouration and pattern. A reddish *Cryptoblepharus*, patterned with random, irregular dark blotches (Plate 2.4, Fig. 85).

Dorsal ground colour russet, reddish or mauve, patterned with random, irregular brown-black blotches. Occasionally, scattered whitish spots are randomly interspersed among the dark blotches. Head concolorous with body, but with occasional dark streaks rather than blotches. Labials pale cream. Tail and limbs concolorous with body but with blotches reduced in size. Venter immaculate off-white. Subdigital lamellae and palmar and plantar surfaces off-white, patterned with occasional dark flecks.

Sex ratio and reproductive biology. Sex ratio favoured females (6:3), but was not significantly different from parity ($X^2 = 1.00$). Small sample size prevented analysis of reproductive biology.

Comparison with Australian congeners. Fixed allelic differences place *C. megastictus* in lineage 1 of Australian *Cryptoblepharus* and also distinguish it from most congeners within that lineage (as OTU megaA4, Horner and Adams 2007). With no fixed allelic differences, *C. megastictus* is genetically similar to *C. ruber* (as OTU plagA2, Horner and Adams 2007).

Morphologically distinguished from lineage 2 members (*C. adamsi* sp. nov., *C. exochus* sp. nov., *C. fuhni*, *C. gurrmul* sp. nov., *C. litoralis*, *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus*, *C. pulcher*, *C. tytthos* sp. nov., *C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov.) by usually having six, rather than five, supraciliary scales and (except for *C. ustulatus* sp. nov. and *C. zoticus* sp. nov.) blotched body pattern on reddish ground colour.

Distinguished from lineage 1 congeners: *C. australis*, *C. buchananii*, *C. cygnatus* sp. nov., *C. metallicus* and *C. ruber* by ground colour and body pattern characteristics (blotched body pattern on reddish ground colour versus longitudinally aligned body pattern on greyish ground colour) and by being saxicoline rather than arboreal. Further distinguished from *C. australis, C. buchananii, C. cygnatus* sp. nov., *C. metallicus* and *C. ruber* by more mid-body scale rows (modally 26 versus 24), fewer paravertebral scales (modally 45 versus 48–54), shallower head (mean 32.5 versus 41.1–43.3 % of head length) and longer hindlimbs (mean 44.6 versus 40.9–42.0 % of SVL).

Cryptoblepharus megastictus is most similar to *C. daedalos* sp. nov., *C. juno* sp. nov., *C. ustulatus* sp. nov., *C. wulbu* sp. nov. and *C. zoticus* sp. nov. in having combinations of reddish ground colour and saxicoline habits. However, it differs from *C. ustulatus* sp. nov. and *C. zoticus* sp. nov. by having more supraciliary scales (modally 6 versus 5) and midbody scale rows (modally 26 versus 22 and 24) and longer head (mean % of SVL, 21.9 versus 20.9 and 21.1). Differs from *C. wulbu* sp. nov. by having more paravertebral scales (modally 45 versus 39), fewer plantar scales (modally 10 versus 13), shorter limbs (mean % of SVL: FL 36.8 versus 38.4; RL 44.6 versus 47.3) and a longer head (mean 21.9 versus 19.9% of SVL). Differs from *C. daedalos* sp. nov. by having fewer palmar (modally 8 versus 10) and plantar scales (modally 10 versus 15), more posterior temporal scales (modally 3 versus 2) and shorter limbs (mean % of SVL: FL 36.8 versus 37.8; RL 44.6 versus 46.8). Differs from *C. juno* sp. nov. by having fewer palmar scales (modally 8 versus 9), narrower paravertebral scales (mean 3.7 versus 4.3% of SVL) and blotched rather than speckled body pattern.

Not withstanding allozymic similarity (Horner and Adams 2007), comparison of nine *C. megastictus* to 31 *C. ruber* identified the following morphological differences: more mid-body scale rows (modally 26 versus 24); fewer paravertebral scales (modally 45 versus 54), smaller size (mean SVL, 35 versus 41 mm), shallower head (mean 32 versus 41 % of head length) and condition of plantar scales (plain instead of callused), they also differ in ground colour and body pattern characters. Together these differences provide evidence for specific designation.

Distribution. North Kimberley region of Western Australia. Recorded from Mitchell Plateau, Kalumburu and Soela Falls (Fig. 86).

Fig. 86. Map of north-western Australia showing distribution of *Cryptoblepharus megastictus*. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

Sympatry. Macro-sympatric with *C. ruber* at Mitchell Plateau, Western Australia.

Geographic variation. Small sample size and limited geographic range prevented analysis of geographic variation.

Habits and habitats. A poorly known, saxicoline species, associated with sandstone massifs and outliers of the Mitchell Plateau (pers. obs.). Kendrick and Rolfe (1991) record its use of sandstone associated with rainforest patches, while Smith and Johnstone (1978) note its presence on off-shore islands (Middle Osborn and South West Osborn) and record the taxon from basalt, and its use of the tidal splash zone and creek margins.

Taxonomic history. Recognised and described in 1976 by Glen Storr, of the Western Australian Museum.

Cryptoblepharus mertensi sp. nov.

Mertens's snake-eyed skink

(Plate 2.5; Figs 87–90)

Type material examined. *Cryptoblepharus mertensi* Horner. HOLOTYPE: Adult female, NTM R22943 (Tissue sample No. ABTC BC4), Roper River, junction with Sherwin Creek, Northern Territory, Australia, 14°39'29"S 134°21'32"E. coll. J. Wombey, 27 October 1996. PARATYPES (22 specimens): NORTHERN TERRITORY: NTM – R16352, R16357, R16359, R16365, Nathan River Station, 15°32'S,135°25'E, Operation Raleigh volunteers, 23 June 1990; R21873, R21876-877, R21890, Junction of Sherwin Creek and Roper River, 14°40'S,134°22'E, J. Wombey, 4–7 November 1995; R22589-590, Junction of Sherwin Creek and Roper River, 14°40'S,134°22', T. Hertog and M. Burt, 11–13 May 1996; R22450, Junction of Sherwin Creek and Roper River, 14°39'29"S 134°21'32"E, P. Horner, 24 May 1996; R22941-942, R22944-945, Junction of Sherwin Creek and Roper River, 14°39'29"S 134°21'32"E, J. Wombey, 27 November 1996; R22449, Wadamunga Lagoon, Roper River, 14°48'16"S 134°56'35"E, P. Horner, 23 May 1996; R22640, R22644-645, R22649, Roper River, 14°48'00"S 134°56'42"E, P. Horner, 23 May 1996.

Diagnosis. A small (<40 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of five supraciliary scales, 24 mid-body scale rows and 49 paravertebral scales; mean values of 34.0 mm snout-vent length, head depth 43.4% of head length, forelimb length 34.0% of snout-vent length, hemipenis length 6.1% of snout-vent length; pale, acute plantar scales; weakly keeled subdigital lamellae and usually 2+2 posttemporal scales.

Description (23 specimens). Postnasals absent; prefrontals in broad contact (100%); supraciliaries 5–6 (mean 5.3), modally 5; enlarged upper ciliaries 3–4 (mean 3.0), modally 3; loreals usually subequal (85%), occasionally anterior largest (15%); supralabials 6–7 (mean 7.0), modally 7; fifth supralabial subocular (100%); infralabials 6–7 (mean 6.1), modally 6; nuchals 2; bilateral posttemporals usually 2+2 (86%), occasionally 2+3 (5%), or 3+3 (9%).

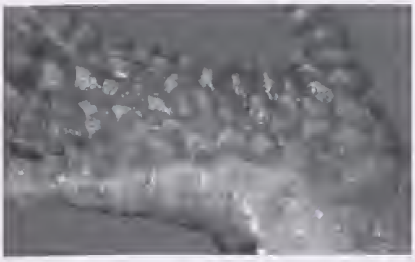

Fig. 87. Ventral surface of hind foot of *Cryptoblepharus mertensi* sp. nov. showing pale, acute plantar scales (NTM R22644, Roper River, NT). Scale: x20.

Fig. 88. Holotype of *Cryptoblepharus mertensi* sp. nov. (NTM R22943, Sherwin Creek junction with Roper River, Northern Territory, Australia. 14°39'29"S 134°21'32"E, *ABTC* BC4). Scale bar = 10 mm

Fig. 89. *Cryptoblepharus mertensi* sp. nov. NTM preserved material from the Northern Territory. **A** and **B**, R21877 and R22945, Sherwin Creek; **C–F**, R22644, R22649, R22645, R22640, Roper River. Scale bar = 10 mm.

Midbody scale rows 22–24 (mean 23.9), modally 24; paravertebrals 45–49 (mean 47.4), modally 49; subdigital lamellae weakly keeled, 14–18 below fourth finger (mean 15.8) modally 16, 17–21 below fourth toe (mean 18.7) modally 18; 12–14 supradigital lamellae above fourth finger (mean 12.7) modally 13, 13–16 above fourth toe (mean 15.2) modally 16; palmar and plantar scales acute, without calli and skin not visible between scales (Fig. 87); plantars 9–12 (mean 10.4), modally 10; palmars 9–10 (mean 9.5), modally 9.

Snout-vent length to 38.5 mm (mean 34.3 mm). *Percentages of snout-vent length*: body length 44.7–54.9% (mean 50.5%); tail length 136.9–156.8% (mean 144.9%); forelimb length 28.4–39.8% (mean 34.0%); hindlimb length 38.0–47.2% (mean 42.0%); forebody length 35.0–44.4% (mean 40.6%); head length 19.1-23.8% (mean 21.0%). *Percentages of head length*: head depth 36.8–48.1% (mean 43.4%); head width 57.9–67.3% (mean 63.2%); snout length 41.9–49.7% (mean 45.1%). Paravertebral scale width 3.3–4.9% (mean 4.0%) of snout-vent length; dorsolateral scale width 75.2–110.7% (mean 90.2%) of paravertebral scale width.

Lenticular scale organs 5–15 (mean 7.8), modally 5. Tooth counts not recorded. Hemipenis: length 5.7–7.1% (mean 6.1%) of snout-vent length; width 86.8–106.5% (mean 96.5%) of hemipenis length; trunk 32.5–41.6% (mean 37.7%) of hemipenis length.

Details of holotype. Adult female, NTM R22943 (Fig. 88). Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; loreals subequal; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 24; paravertebrals 49; subdigital lamellae weakly keeled, 15 below fourth finger; 18 below fourth toe; supradigital lamellae 13 above fourth finger; 15 above fourth toe; palmars and plantars acute, skin not visible between scales; plantars 10; palmars 10. Snout-vent length 35.7 mm; body length 18.2 mm; tail not original; forelimb length 11.8 mm; hindlimb length 14.5

mm; forebody length 14.5 mm; head length 7.3 mm; head depth 3.0 mm; head width 4.6 mm; snout length 3.2 mm.

Colouration and pattern. A brownish-grey *Cryptoblepharus*, with longitudinally aligned, complex body pattern dominated by broad vertebral zone and pale laterodorsal stripes (Plate 2.5). Intensity of body pigmentation and patterning is variable, ranging from pale to prominent (Fig. 89). Most specimens conform to the following description.

Dorsal ground colour brown-grey, with broad vertebral zone extending from above eye to hindlimb. Vertebral zone about four scales wide, brown-grey, finely flecked with short longitudinal blackish streaks and spots. The latter are most prominent on outer edges of dorsolateral scales and usually form narrow black stripes from neck to mid-body, where they become ragged and discontinuous. Cream laterodorsal stripes extend from above eye to tailbase, most prominent on anterior half of body, about width of laterodorsal scale, becoming less pronounced on posterior half of body. Edges of pale laterodorsal stripes smooth anteriorly to ragged posteriorly. Head concolorous with vertebral zone, mottled with blackish flecks and specks. Patterned with continuation of dark lateral zone, which extends above ear, through eye to loreals. A vague, pale lower temporal stripe extends from supralabials to ear. Labials pale cream, patterned with occasional dark flecks.

Flanks patterned with narrow, black-brown upper lateral stripe, about width of upper lateral scale, extending from eye to tailbase. Posteriorly flecked with pale spots and streaks, upper lateral stripe forms distinct outer border to pale laterodorsal stripe. Mid- to lower lateral zone brown-grey, peppered with small pale and/or dark spots and streaks and coalesces into pale venter. Tail concolorous with body, patterned with vague, broken continuations of vertebral and upper lateral zones. Limbs and toes concolorous with body, patterned with pale and dark speckling. Venter, including palmars and plantars, immaculate off-white.

Sex ratio and reproductive biology. Sex ratio favoured females (16:7), but was not significantly different from parity ($X^2 = 3.52$). Males mature at approximately 30 mm snout-vent length and females at 32 mm. Adults average 34.3 mm snout-vent length and females grow larger than males (maximum SVL = 38.5 versus 35.1 mm). Breeding biology was indeterminate, of 22 adult samples examined only three were reproductively active, two males (June and July) and a female (October).

Comparison with Australian congeners. Fixed allelic differences place *C. mertensi* sp. nov. in lineage 2 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTU carnC, Horner and Adams 2007).

Morphologically distinguished from most lineage 1 members (except *C. australis*) by usually having five, rather than six, supraciliary scales and acute, instead of ovate, plantar scales.

Distinguished from lineage 2 congeners *C. adamsi* sp. nov., *C. fuhni, C. gurrmul* sp. nov., *C. litoralis, C. pulcher, C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov. by acute plantars (versus rounded). Further distinguished from: *C. gurrmul* sp. nov., *C. l. horneri* and *C. l. litoralis* by fewer mid-body scale rows (modally 24 versus 26–28) and paravertebral scales (modally 49 versus 55–57); from *C. fuhni, C. gurrmul* sp. nov. and *C. zoticus* sp. nov. by more paravertebral scales (modally 49 versus 45–46) and deeper head (mean 43.4 versus 32.5–36.1 % of head length); from *C. virgatus* by more mid-body scale rows (modally 24 versus 22) and paravertebral scales (modally 49 versus 47); from *C. adamsi* sp. nov. and *C. pulcher* by pale plantar scales (versus darkly pigmented) and obscure pale laterodorsal stripes.

Cryptoblepharus mertensi sp. nov. is most similar to *C. australis, C. exochus* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp.nov., *C. plagiocephalus* and *C. tytthos* sp. nov. in having combinations of complex body patterns, acute plantar scales and being arboreal. However it differs from *C. australis* and *C. exochus* sp. nov. by having keeled, instead of smooth subdigital lamellae, fewer paravertebral (modally 49 versus 52 and 51) and plantar scales (modally 10 versus 12), further differs from *C. australis* by having fewer supraciliary scales (modally 5 versus 6) and from *C.exochus* sp. nov. by smaller size (mean SVL 34.3 instead of 37.1 mm). Differs from *C. ochrus* sp. nov., *C. pannosus* sp. nov. and *C. plagiocephalus* by having shorter forebody (mean % of SVL 40.6 instead of 41.8 or more) but deeper head (mean % of head length 43.4 instead of 40.3 or less), further differs from *C. ochrus* sp. nov. and *C. plagiocephalus* by having fewer paravertebral scales (modally 49 versus 50) and from *C. pannosus* sp. nov. by having narrow, smooth edged pale laterodorsal stripes (if present) instead of moderately broad, ragged edged stripes. Differs from *C. tytthos* sp. nov. by having deeper head (mean % of head length 43.4 instead of 40.6), more fourth finger subdigital lamellae (modally 16 versus 15), fewer plantar scales (modally 10 versus 11) and larger size (mean SVL 34.3 instead of 31.3 mm).

Additionally, of taxa able to be examined for hemipenis proportions, *C. mertensi* sp. nov. has the shortest hemipenis length (mean 6.1 versus 6.8–10.1 % of snout-vent length), all others except *C. exochus* sp. nov. had mean hemipenis lengths above 7.0% of snout-vent length.

Distribution. Gulf region of the Northern Territory; from near Roper Bar, on the lower reaches of the Roper River, southwards to Batten Creek, a tributary of the McArthur River (Fig. 90).

Sympatry. *Cryptoblepharus mertensi* sp. nov. occurs in sympatry with *C. ruber* and *C. metallicus*. It is sympatric with *C. metallicus* at the junction of Sherwin Creek and the Roper River, Nathan River Station and 3 km south of Batten Point. Sympatry with more than one congener occurs by the Roper River at 14°48'00"S 134°56'42"E (*C. ruber* and *C. metallicus*).

Geographic variation. Geographic variation was investigated by dividing specimens into two groups, being 19

Fig. 90. Map of the Northern Territory showing distribution of *Cryptoblepharus mertensi* sp. nov. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

specimens from the Roper River area (6 ♂, 13 ♀) and four specimens from the Nathan River area (1 ♂, 3 ♀).

Small sample size for one group limited analysis to both sexes combined. Tests of allometrically adjusted variables revealed only minor variation in head proportions. Roper River samples tended to have wider heads and longer snouts than those from Nathan River (mean head width 4.99 versus 4.67 mm; mean snout length 3.53 versus 3.35 mm). These results indicate that geographic variation in *C. mertensi* sp. nov. is limited to more northern populations having slightly larger heads.

Habits and habitats. *Cryptoblepharus mertensi* sp. nov. is arboreal, with museum records noting its use of low open woodland. Specimens have usually been found close to waterways, on either *Melaleuca* or *Casuarina* trunks.

Etymology. Named for the late Professor Robert Mertens, former curator at the Senckenberg Museum, Frankfurt, in recognition of his outstanding contributions to *Cryptoblepharus* taxonomy.

Cryptoblepharus metallicus (Boulenger, 1887)

Metallic snake-eyed skink

(Plates 2.6–2.7; Figs 91–93; Table 8)

Ablepharus boutoni metallicus Boulenger, 1887: 347 ("North Australian Exped."). – Mertens 1931: 119; Loveridge 1934: 375; Mitchell 1964: 337; Worrell 1963: 35; Mertens 1964: 106.

Cryptoblepharus boutonii metallicus (Boulenger, 1887). – Cogger and Lindner 1974: 83.

Cryptoblepharus metallicus (Boulenger, 1887) . – Wells and Wellington 1985: 27.

Cryptoblepharus plagiocephalus (Cocteau, 1836). – Cogger *et al.* 1983a: 142; Wilson and Knowles 1988: 120; Horner 1991: 18; Covacevich and Couper 1991: 357; Ehmann 1992: 182; Stanger *et al.* 1998: 23; Cogger 2000: 406; Wilson and Swan 2003: 148.

Type material examined. *Ablepharus boutoni metallicus* Boulenger, 1887. LECTOTYPE: BMNH 57.10.24.38, North Australian Expedition, J. Elsey.

Non-type material examined. See Appendix 4.

Diagnosis. A large (45–50 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of six supraciliary scales, 24 mid-body scale rows and 48 paravertebral scales; mean values of hindlimb length 41.4% of snout-vent length, head depth 41.7% of head length, tail length 144.2% of snout-vent length; smooth subdigital lamellae; rounded, usually callused plantar scales; greyish, longitudinally aligned body pattern and being arboreal.

Description (119 specimens). Postnasals absent; prefrontals usually in broad contact (97%), occasionally in narrow contact (2%) or narrowly separated (1%); supraciliaries 5–7 (mean 6.0), modally 6; enlarged upper ciliaries 3–4 (mean 3.0), modally 3; usually posterior loreal largest (84%), occasionally subequal (16%); supralabials 6–8 (mean 7.1), modally 7; fifth supralabial usually subocular (98%), occasionally sixth (2%); infralabials 5–7 (mean 6.0), modally 6; nuchals 2–4 (mean 2.0); bilateral posttemporals usually 2+2 (57%), occasionally 3+3 (29%) or 2+3 (14%).

Midbody scale rows 22–26 (mean 24.1), modally 24; paravertebrals 45–56 (mean 49.7), modally 48; subdigital lamellae smooth, 12–18 below fourth finger (mean 15.0) modally 14, 15–21 below fourth toe (mean 18.1), modally 18; 10–14 supradigital lamellae above fourth finger (mean 12.9) modally 13, 13–18 above fourth toe (mean 15.2), modally 15; palmar and plantar scales rounded, usually with dark brown calli (Fig. 91) and skin visible between scales; plantars 7–13 (mean 9.6), modally 10; palmars 6–10 (mean 7.7), modally 8.

Snout-vent length to 47.9 mm (mean 38.6 mm). *Percentages of snout-vent length*: body length 43.7–60.3% (mean 50.0%); tail length 128.0–168.7% (mean 144.2%); forelimb length 29.1–40.0% (mean 33.6%); hindlimb length 35.8-47.7% (mean 41.4%); forebody length 37.7–47.6% (mean 42.4%); head length 19.1–23.9% (mean 21.4%). *Percentages of head length*: head depth 31.6–51.9% (mean 41.7%); head width 52.4–70.0% (mean 59.9%); snout length 40.2–50.5% (mean 45.0%). Paravertebral scale width 3.0–5.1% (mean 4.0%) of snout-vent length; dorsolateral scale width 72.5–107.2% (mean 88.3%) of paravertebral scale width.

Lenticular scale organs 5–20 (mean 9.5), modally 6. Premaxillary teeth 4–5 (mean 4.5), modally 4; maxillary teeth 19–22 (mean 20.5), modally 20; mandibular teeth 22–24 (mean 23.5), modally 24. Hemipenis: length 6.8–10.3% (mean 8.6%) of snout-vent length; width 67.4–105.0% (mean 85.2%) of hemipenis length; trunk 41.0–63.1% (mean 51.3%) of hemipenis length.

Details of lectotype. BMNH 57.10.24.38. Postnasals absent; prefrontals in broad contact; supraciliaries 6; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody

Fig. 91. Ventral surface of hind foot of *Cryptoblepharus metallicus* showing callused, pale, ovate plantar scales (NTM R22096, Timber Creek, NT). Scale: x20.

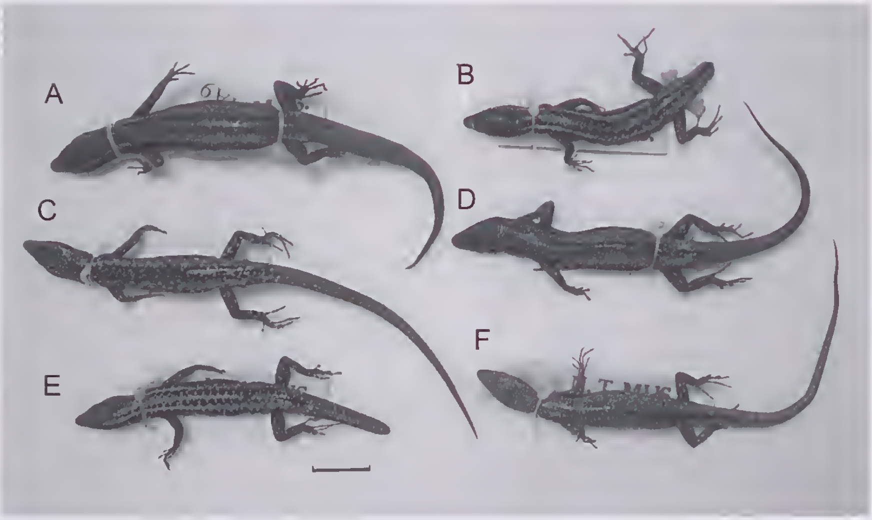

Fig. 92. *Cryptoblepharus metallicus*. NTM preserved material. **A**, R22732, English Company Islands, NT; **B**, R22728, Nhulunbuy, NT; **C**, R23483, Elliot, NT; **D**, R22525, Mt. Elizabeth Station, WA; **E**, R16127, Cadell River, NT; **F**, R18845, Leichhardt Falls, Qld. Scale bar = 10 mm.

scale rows 22; paravertebrals 52; subdigital lamellae smooth, 14 below fourth finger; 19 below fourth toe; supradigital lamellae 12 above fourth finger; 15 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 12; palmars 8. Snout-vent length 40.6 mm; body length 20.2 mm; tail not original; forelimb length 12.5 mm; hindlimb length 15.3 mm; forebody length 14.8 mm; head length 8.1 mm; head depth 3.7 mm; head width 4.6 mm; snout length 3.5 mm.

Colouration and pattern. A greyish or brownish *Cryptoblepharus*, with longitudinally aligned, complex body pattern dominated by dark, broad vertebral zone and pale laterodorsal zones/stripes (Plates 2.6 and 2.7). Intensity of body pigmentation and patterning is variable, ranging from pale and obscure to dark and prominent (Plates 2.6 and 2.7, Fig. 92). Most specimens conform to the following description.

Dorsal ground colour grey to grey-brown, with broad, dark vertebral zone extending from above eye to hindlimb. Vertebral zone as wide as paired paravertebral scales, grey-brown to blackish, with pale spots/specks and dotted with short longitudinal blackish streaks and spots. The latter are most prominent on outer edges of paravertebral scales and usually form two broken, narrow black stripes from neck to tailbase, where they merge creating a blackish median, tapering stripe on anterior third of tail. Pale grey to pale brown laterodorsal zones extend from above eye onto tail, broadest on posterior half of body, about half width of dark vertebral zone, tapering anteriorly into prominent narrow stripes extending to eye and posteriorly to form tail ground colour. Edges of pale laterodorsal zones usually ragged, interdigitating with broken dark paravertebral stripes and dark upper lateral zone. Laterodorsal zones usually uniform, but may contain fine pale and/or dark speckling. Head concolorous with vertebral zone or coppery brown, usually with fine dark margins to scales, and patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Pale lower temporal region is flecked with dark spots and streaks. Labials pale cream.

Flanks patterned with dark upper lateral zone, variable in width, extending from loreals onto tail and forming a ragged, outer border to pale laterodorsal zone. Usually broken by pale spots and short streaks, upper lateral zone may be represented by narrow broken black stripe but typically is about two lateral scales wide and coalesces gradually into pale grey/pale grey-brown lower lateral zone. Lower lateral zone peppered with small pale and/or dark spots and streaks and coalesces into pale venter. Tail concolorous with body, patterned with broken continuations of blackish vertebral and upper lateral zones. Limbs and toes concolorous with body, patterned with pale and dark speckling. Venter immaculate off-white. Palmar and plantar scales off-white, most usually capped with dark brown calli.

Sex ratio and reproductive biology. Sex ratio favoured males (70:49), but was not significantly different from parity ($X^2 = 3.7$). Both males and females mature at approximately 34 mm snout-vent length. Adults average 38.6 mm snout-vent length and females grow larger than males (maximum SVL = 47.9 versus 44.9 mm). Breeding occurs year-round, with reproductively active animals collected in all months except February, however spikes of reproductive activity for both sexes occur between December/January and July/August indicating breeding maybe a twice yearly event.

Comparison with Australian congeners. Fixed allelic differences place *C. metallicus* in lineage 1 of Australian *Cryptoblepharus* and also distinguish it from most congeners within that lineage (as OTU plagA5, Horner and Adams 2007). With no fixed allelic differences, *C. metallicus* is genetically similar to *C. australis* (as OTU earnD, Horner and Adams 2007).

Morphologically distinguished from lineage 2 members *C. adamsi* sp. nov., *C. fuhni*, *C. gurrmul* sp. nov., *C. litoralis*, *C. pulcher*, *C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov. by usually having six, rather than five, supraciliary scales and complex body pattern on a grey or brown ground colour and from *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. by usually having six, rather than five, supraciliary scales and ovate, instead of acute, plantar scales.

Distinguished from lineage 1 congeners *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus* and *C. wulbu* sp. nov. by ground colour and body pattern characteristics (greyish, longitudinally aligned pattern versus reddish, randomly speckled or blotched pattern), by being arboreal rather than saxicoline and by fewer mid-body scale rows (modally 24 versus 26), deeper head (mean 41.7 versus 32.5–36.0% of SVL), and shorter hindlimbs (mean 41.4 versus 44.6–47.3% of SVL.

Cryptoblepharus metallicus is most similar to *C. buchananii*, *C. cygnatus* sp. nov. and *C. ruber* in having combinations of complex body patterns, flat ovate plantar scales, usually six supraciliary scales and being arboreal. However, it differs from *C. cygnatus* sp. nov. in having smooth instead of callused subdigital lamellae, callused instead of smooth plantar scales, fewer subdigital lamellae (modally FTL 14 versus 16; HTL 18 versus 19) and palmar and plantar scales (modally PAL 8 versus 9; PLN 10 versus 11). It differs from *C. buchananii* in having fewer paravertebral (modally 48 versus 52) and posterior temporal scales (modally 2 versus 3), callused instead of plain plantar scales and smaller size (mean SVL 38.6 instead of 41.1 mm). Differs from *C. ruber* in having fewer paravertebral (modally: 48 versus 54) and posterior temporal scales (modally: 2 versus 3), longer tail (mean % of SVL: 144.2 instead of 132.6) and smaller size (mean SVL 38.6 instead of 40.9 mm).

Notwithstanding allozymic similarity (Horner and Adams 2007), comparison of 120 *C. metallicus* to 105 *C. australis* identified the following morphological differences: narrower head (mean 4.7 versus 4.9% of head length), fewer fourth toe subdigital lamellae (modally 18 versus 19), fewer plantar scales (modally 10 versus 12), fewer posterior temporal scales (modally 2 versus 3) and ovate versus acute plantar scales.

Distribution. Northern and north-eastern Australia; from inland south-eastern Queensland, through eastern and northern Queensland, the northern half of the Northern Territory to the Kimberley region of Western Australia (Fig. 93).

Sympatry. *Cryptoblepharus metallicus* occurs in sympatry with *C. ruber*, *C. cygnatus* sp. nov. and *C. juno* sp. nov. from lineage 1, and *C. adamsi* sp. nov., *C. exochus* sp. nov., *C. l. horneri*, *C. l. litoralis*, *C. mertensi* sp. nov., *C. pannosus* sp. nov., *C. pulcher*, *C. tytthos* sp. nov., *C. virgatus* and *C. zoticus* sp. nov. from lineage 2 (Table 8).

Geographic variation. Geographic variation was investigated by dividing specimens into four disparate groups: *eastQ*, an eastern Queensland group of eight (5 ♂, 3 ♀) samples from bioregions BBS, BBN, CMC, EIU and CYP; *midnorth*, a north-eastern Northern Territory group of 43 (25 ♂, 18 ♀), from bioregions GUC, GFU, STU, DAB, ARP, ARC and PCK; *norwest*, a north-western Northern Territory/ north-eastern Western Australia group of 38 (27 ♂, 11 ♀), from bioregions CK, NK, OVP and VB, and *souGulf*, a group of 30 (13 ♂, 17 ♀) from southern Gulf Of Carpentaria bioregions DMR, GUP, MII and MGD. Group pairs, where sexes were treated separately and combined,

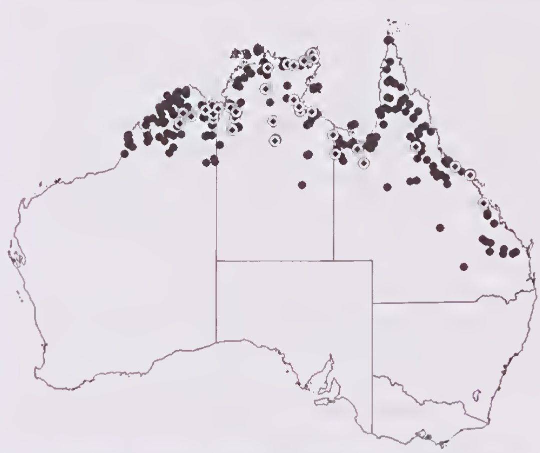

Fig. 93. Map of Australia showing distribution of *Cryptoblepharus metallicus*. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

Table 8. List of congeners sympatric with *Cryptoblepharus metallicus*, giving areas of sympatry.

Congeners sympatric with *Cryptoblepharus metallicus*	Area of sympatry
C. adamsi sp. nov.	Qld: Ayr, Chillagoe, Mount Molloy, Warrawee Stn
C. cygnatus sp. nov.	NT: Jabiru, Jabiluka
C. juno sp. nov.	WA: Wyndham
C. l. horneri	NT: Raragala Island
C. l. litoralis	Qld: Horn Island
C. mertensi sp. nov.	NT: Battern Point, Nathan River Stn, Sherwin Creek, Wadamunga Lagoon
C. pannosus sp. nov.	Qld: Amber Stn, Battery Stn, Brannigan Creek, Charters Towers, Doomadgee, Flinders River, Floraville Stn, Glen Garland Stn, Karumba, Hells Gate, Leichhardt Falls, Lynd River, Shelfer crossing (Mitchell River), Moranbah, Mt. Surprise, Normanton, Oriners Outstation (Mosquito Waterhole), Red Falls (west of Charters Towers), Springfield, Strathgordon Stn, Walker's Creek
C. p. pulcher	Qld: Bluff Mtn nr Biggenden, Clairview, Dingo Beach, Magnetic Island, Moura, Powlathanga Stn, Theodore, Warrawee Stn, Rowes Bay
C. ruber	WA: Kununurra
C. virgatus	Qld: Coen, Horn Island, Townsville
C. zoticus sp. nov.	Qld: Lawn Hill
Multiple sympatry	
C. exochus sp. nov. + *C. juno* sp. nov. + *C. ruber*	NT: Bradshaw Stn
C. l. litoralis + *C. p. pulcher*	Qld: Magnetic Island, Townsville
C. pannosus sp. nov. + *C. tytthos* sp. nov.	Qld: Mornington Island
C. pannosus sp. nov. + *C. zoticus* sp. nov.	Qld: Hells Gate

were subjected to tests of allometrically adjusted variables. Some variation was detected between sexes in all groups, however significance was mostly lost when group pairs of combined sexes were tested. Significant geographical difference was detected between groups *souGulf* and *midnorth* due to variation in snout-vent length, between groups *souGulf* and *norwest* due to variations in snout-vent length and hindlimb length and between groups *eastQ* and *norwest* due to variation in paravertebral scale width.

These results indicate that geographic variation in *C. metallicus* consists of populations from the southern Gulf of Carpentaria (*souGulf* group) being larger than western populations (groups *midnorth* and *norwest*), but similar to eastern populations (group *eastQ*) (mean snout-vent lengths: *souGulf*, 41.0 mm; *eastQ*, 40.3 mm; *midnorth*, 37.8 mm; *norwest*, 37.1 mm). Further size difference between *souGulf* and far western populations (*norwest*) is found in hindlimb length, with *norwest* having longer hindlimbs (mean 15.1 versus 16.0 mm). Eastern populations (*eastQ*) have slightly wider paravertebral scales than do far western (*norwest*) populations (mean 1.71 versus 1.42 mm).

Habits and habitats. *Cryptoblepharus metallicus* occurs in a variety of habitats. Normally arboreal, museum records note its use of vine thickets, open forest, woodland, shrubland, grassland, riparian and urban environments. Within these it has been associated with numerous tree and/or shrub species, including *Acacia* spp., *Brachychiton* sp., *Casuarina* sp., *Eucalyptus camaldulensis*, *Eucalyptus* spp., *Melaleuca* spp., *Xanthorrhoea* sp., as well as mangroves and driftwood. Though not usually saxicoline, some records note usage of beach rocks, rocky slopes and outcrops, and trees associated with sandstone outcrops. In urban environments has been associated with old buildings, palms and trees in gardens, fence rails, walls, sign posts and wooden structures.

Edgar (1987) in describing the results of a herpetofauna survey in Gregory National Park, Northern Territory, noted that *C. metallicus* (as *C. plagiocephalus*) was very abundant and ubiquitous, used trees that ranged from 5 to 50 cm diameter at breast height, favoured tree species with textured bark (such as paperbark and corkbark) and were not observed on smooth-barked *Eucalyptus* species.

Taxonomic history. Boulenger (1887) described *Ablepharus boutoni metallicus* from four British Museum specimens (BMNH 57.10.24. 38, 39,40 a + b) collected by J.R. Elsey on the "North Australian Expedition" of 1855–56, led by A.C. Gregory. Boulenger diagnosed the taxon as having "22 or 24 scales around the body. Four anterior labials. Yellowish or greenish above, strongly metallic, with small dark brown spots forming a more or less irregular band on each side". No type locality was given, though the general area can be determined from the expedition's journal (Gregory and Gregory 1884). The expedition's base campsite was on the bank of the Victoria River, near the present-day town of Timber Creek, Northern Territory. As determined by Shea and Horner (1996), Elsey did not accompany Gregory's exploring parties to the south-west between October 1855 and June 1856, but remained at base camp. Thus, it is most likely that the type locality is the vicinity of the expedition's Victoria River campsite.

The taxon was regarded as valid by Mertens (1931), however his research was based on examination of two individuals of *C. australis* (SMF 15683-84, types of *A. b. australis*) which he had placed in the synonymy of *A. b. metallicus*. Storr (1976) synonymised *A. b. metallicus* with *C. plagiocephalus*, a designation followed by most subsequent authors. Wells and Wellington (1985), without justification, elevated the taxon to species status, naming it *C. metallicus*, and designated BMNH 57.10.24.38 as lectotype.

Cryptoblepharus ochrus sp. nov.

Pale snake-eyed skink

(Figs 94–99)

Type material examined. *Cryptoblepharus ochrus* Horner. HOLOTYPE: Adult female, NTM R22025 (Tissue sample No. *ABTC* YO6), Coward Springs Siding, South Australia, 29°24'S 136°49'E. coll. P. Horner, 17 December 1995. Shrubland, on outhouses and *Casuarina* trees, 1800 hours. PARATYPES (21 specimens): SOUTH AUSTRALIA: NTM R22024, R22026–028, Coward Springs Siding, 29°24'S 136°49'E, P. Horner, 17 December 1995, *ABTC* YO5-YO9; SAM R28169, Coward Springs homestead and rail siding, 29°24'S 136°48'E, T. Schwaner *et al*., 18 August 1985; SAM R28216, Dalhousie Ruins, 26°31'S 135°28'E, T. Schwaner *et al*, 20 August 1985, *ABTC* TDS471; SAM R35875-876, Finke River, campsite area, 26°02'S 135°31'30"E, M. Hutchinson and G. Armstrong, 4 June 1990; SAM R35917, Alka Seltzer Bore, 26°18'S 136°01'E, G. Armstrong, 11 June 1990; SAM R35921-922, old stockyard, 6 km NE of Camp 1, 26°01'S 135°35'E, M. Hutchinson, 7 June 1990; SAM R35944, Everglade Bore, 26°09'S 135°57'E, M. Hutchinson and G. Armstrong, June 1990; SAM R35976, 7 km SW of Camp 1, 26°06'S 135°30'E, M. Hutchinson and G. Armstrong, 5 June 1990; SAM R36364, southern inflow of Lake Bulpanie, 27°46'S 139°35'E, H. Ehmann, 16 May 1990; SAM R36576, Coward Springs rail siding, 29°24'S 136°49'E, W. Head, 30 September 1990; SAM R40234, Horse Creek waterhole, 26°43'S 134°54'E, H. Owens, 28 May 1992, *ABTC* NP2518; SAM R40537, Mount Dean, 26°42'S 134°42'E, M. Hutchinson *et al*., 22 September 1992, *ABTC* NP3262; SAM R43942, 7.1 km N of Yelpawaralinna Waterhole, 27°07'37"S 138°42'29"E, 23 November 1993, *ABTC* GL129; SAM R46193, 9.5 km SE of Wares Peak, 29°38'43"S 135°45'21"E, H. Owens, 3 October 1995, *ABTC* LES111; SAM R46208, 10.5 km SE of Wares Peak, 29°39'18"S 135°46'00"E, H. Owens, 2 October 1995, *ABTC* LES098; SAM R47536, Coward Springs Bore, 29°24'01"S 136°48'50"E, H. Owens, 27 April 1996.

Diagnosis. A medium sized (40–44 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of five supraciliary scales, 24 mid-body scale rows, 50 paravertebral scales, 20 fourth toe subdigital lamellae and 13 lenticular scale organs; mean values of 39.0 mm snout-vent length, head depth 39.2% of head length, forelimb length 34.1% of snout-vent length, hindlimb length 42.5% of snout-vent length; weakly keeled fourth toe subdigital lamellae; pale, acute plantar scales; usually 3+3 posttemporal scales, and narrow, pale dorsolateral stripes.

Description (22 specimens). Postnasals absent; prefrontals usually in broad contact (95%), occasionally narrowly separated (5%); supraciliaries 5–6 (mean 5.1), modally 5; enlarged upper ciliaries 3–4 (mean 3.2), modally 3; loreals usually subequal (57%), often anterior is largest (43%); supralabials 7–8 (mean 7.0), modally 7; fifth supralabial subocular (100%); infralabials 6; nuchals 2–4 (mean 2.2), modally 2; bilateral posttemporals usually 3+3 (82%), occasionally 2+3 (14%), or 2+2 (4%).

Midbody scale rows 24–26 (mean 24.5), modally 24; paravertebrals 47–55 (mean 50.7), modally 50; subdigital lamellae usually weakly keeled (64%), occasionally smooth (36%), 15–18 below fourth finger (mean 16.3) modally 16, 18–22 below fourth toe (mean 19.7) modally 20; 12–14 supradigital lamellae above fourth finger (mean 13.0) modally 13, 15–18 above fourth toe (mean 16.1) modally 16; palmar and plantar scales acute, without calli and skin not visible between scales (Fig. 94); plantars 10–12 (mean 11.0), modally 11; palmars 8–11 (mean 9.9), modally 10.

Snout-vent length to 43.8 mm (mean 39.0 mm). *Percentages of snout-vent length*: body length 43.1–55.1% (mean 50.8%); tail length 126.0–141.5% (mean 133.8%); forelimb length 29.8–37.5% (mean 34.1%); hindlimb length 39.1–46.9% (mean 42.5%); forebody length 36.7–45.1% (mean 41.8%); head length 19.2–22.4% (mean 20.9%). *Percentages of head length*: head depth 34.8–44.3% (mean 39.2%); head width 57.8–69.3% (mean 62.4%); snout length 41.6–48.0% (mean 44.9%). Paravertebral scale width 3.2–4.9% (mean 3.9%) of snout-vent length; dorsolateral scale width 72.7–103.6% (mean 87.3%) of paravertebral scale width.

Lenticular scale organs 5–18 (mean 12.6), modally 13. Tooth counts not recorded. Hemipenis: length 8.0% (n = 1) of snout-vent length; width 70.0% (n = 1) of hemipenis length; trunk 52.3% (n = 1) of hemipenis length.

Details of holotype. Adult female (Fig. 95), NTM R22025. Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; anterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 24; paravertebrals 50; subdigital lamellae weakly keeled, 15 below fourth finger; 19 below fourth toe; supradigital lamellae 14 above fourth finger; 17 above fourth toe; palmars and plantars acute, skin not visible between scales; plantars 12; palmars 10. Snout-vent length 43.3 mm; body length 23.0 mm; tail not original; forelimb length 15.0 mm; hindlimb length 17.5 mm; forebody length 17.1 mm; head length 8.6 mm; head depth 3.6 mm; head width 5.1 mm; snout length 3.7 mm.

Colouration and pattern. Pale, greyish-brown *Cryptoblepharus*, with longitudinally aligned body pattern (Figs 96 and 97). Intensity of body pigmentation and patterning is

Fig. 94. Ventral surface of hind foot of *Cryptoblepharus ochrus* sp. nov. showing pale, acute plantar scales (NTM R22024, Coward Springs, SA). Scale: x20.

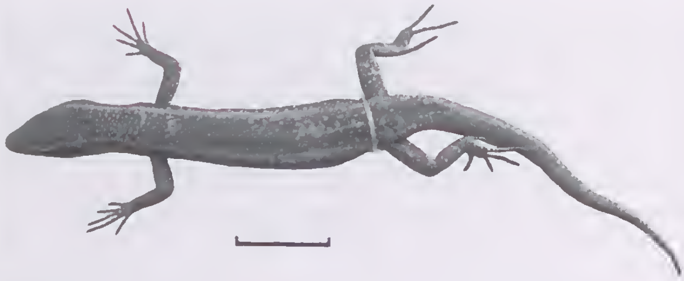

Fig. 95. Holotype of *Cryptoblepharus ochrus* sp. nov. (NTM R22025, Coward Springs, South Australia, 29°24'S 136°49'E, *ABTC* YO6). Scale bar = 10 mm.

Fig. 96. *Cryptoblepharus ochrus* sp. nov. preserved material, NTM R22026, Coward Springs, SA. Scale bar = 10 mm.

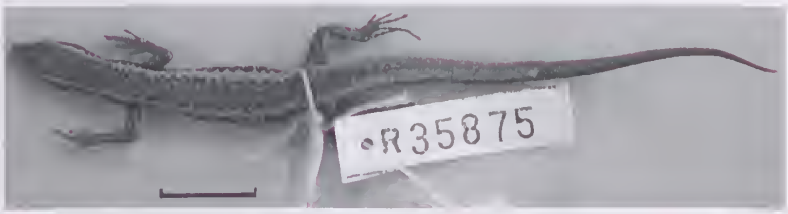

Fig. 97. *Cryptoblepharus ochrus* sp. nov. preserved material, SAM R35875, Finke River, SA). Scale bar = 10 mm.

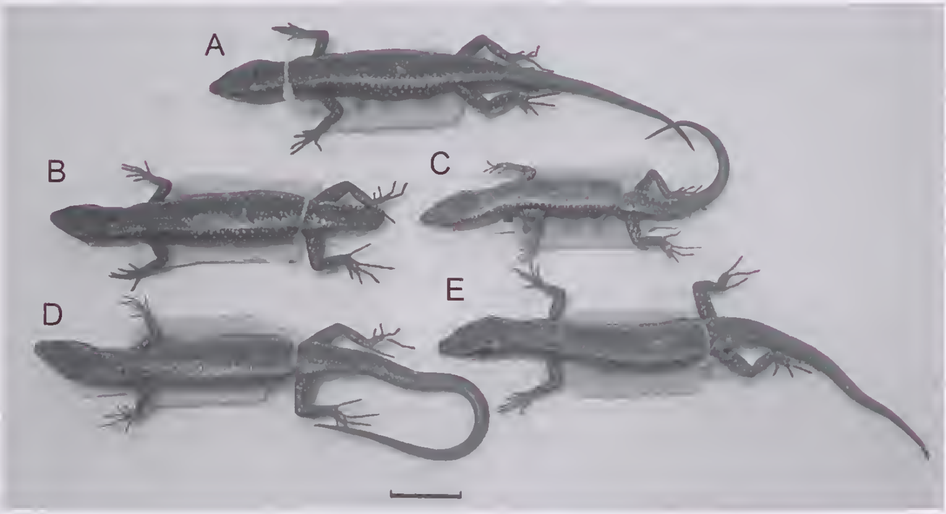

Fig. 98. *Cryptoblepharus ochrus* sp. nov., NTM preserved material from Coward Springs, South Australia. **A**, R22027; **B**, R22024; **C**, R22028; **D**, R22026; **E**, R22025 (holotype). Scale bar = 10 mm.

variable (Fig. 98), ranging from distinct to reduced. Most specimens conform to the following description.

Dorsal ground colour pale grey to brown, with broad, vertebral zone extending from above eye to hindlimb. Vertebral zone about four scales wide, grey-brown, speckled with dark and/or pale flecks and spots. The latter are most prominent on inner edges of laterodorsal scales, usually forming two obscure, broken, narrow black stripes from neck to tailbase. Obvious to obscure, pale grey laterodorsal stripes extend from above eye onto tail, about width of single laterodorsal scale, these taper anteriorly into narrow stripes extending to eye and posteriorly to form tail ground colour. Pale laterodorsal stripes usually uniform in colour with smooth edges. Head concolorous with vertebral zone, often patterned with dark margins to shields. Laterally, patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Pale lower temporal region is flecked with dark spots and streaks. Labials pale cream, patterned with occasional dark flecks.

Flanks patterned with grey-brown upper lateral zone, variable in width, extending from loreals onto tail. Flecked with dark streaks and pale flecks, upper lateral zone coalesces gradually into pale grey/pale grey-brown lower lateral zone. Lower lateral zone peppered with small pale and/or dark spots and streaks and coalesces into pale venter. Tail concolorous with body, patterned with broken continuations of dark vertebral and upper lateral zones. Limbs and toes concolorous with body, patterned with pale and dark speckling. Venter, including palmars and plantars, immaculate off-white.

Sex ratio and reproductive biology. Sex ratio favoured males (13:9), but was not significantly different from parity ($X^2 = 0.72$). Both sexes mature at approximately 34 mm snout-vent length. Adults average 39.0 mm snout-vent length and females grow larger than males (maximum SVL = 43.8 versus 42.2 mm). Breeding is year round, with reproductive animals collected in April (one male), May (one male), June (two males), August (one male, two females), September (one female), October (one male, one female), November (one male) and December (one male, two females).

Comparison with Australian congeners. Fixed allelic differences place *C. ochrus* sp. nov. in lineage 2 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTU carnA3, Horner and Adams 2007).

Morphologically distinguished from most lineage 1 members (except *C. australis*) by usually having five, rather than six, supraciliary scales and acute, instead of ovate, plantar scales. Distinguished from lineage 2 congeners *C. adamsi* sp. nov., *C. fuhni, C. gurrmul* sp. nov., *C. litoralis, C. pulcher, C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov. by acute plantars (versus rounded). Further distinguished from: *C. gurrmul* sp. nov., *C. l. horneri* and *C. l. litoralis* by fewer mid-body scale rows (modally 24 versus 26–28) and paravertebral scales (modally 50 versus 55–57); from *C. fuhni, C. gurrmul* sp. nov. and *C. zoticus* sp. nov. by more paravertebral scales (modally 50 versus 45–46) and deeper head (mean 39.2 versus 32.5–36.1 % of head length); from *C. virgatus* by more mid-body scale rows (modally 24 versus 22) and paravertebral scales (modally 50 versus 47); from *C. adamsi* sp. nov. and *C. pulcher* by pale plantar scales (versus darkly pigmented) and obscure pale laterodorsal stripes.

Cryptoblepharus ochrus sp. nov. is most similar to *C. australis, C. exochus* sp. nov., *C. mertensi* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. in having combinations of complex body patterns, acute plantar scales and being arboreal. However it differs from *C. australis* and *C. exochus* sp. nov. by having keeled, instead of smooth subdigital lamellae, more fourth toe supradigital scales (modally 16 versus 15) and shallower head (mean % of head length 39.2 instead of 42.3 and 42.8), further differs from *C. australis* by having fewer supraciliary scales (modally 5 versus 6) and from *C. exochus* sp. nov. by having more posterior temporal scales (modally 3 versus 2) and larger size (mean SVL 39.0 instead of 37.1 mm). Differs from *C. mertensi* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. by larger size (mean SVL 39.0 instead of 34.4 mm or less). Further differs from *C. mertensi* sp. nov., *C. pannosus* sp. nov. and *C. tytthos* sp. nov. by having more paravertebral scales (modally 50 versus 49 or less) and shallower head (mean % of head length 39.2 instead of 40.3 or more) and from *C. plagiocephalus* by having more fourth toe supradigital scales (modally 16 versus 15), posterior temporal scales (modally 3 versus 2) and (where present) narrow pale laterodorsal stripes instead of moderately broad, ragged edged stripes.

Additionally, *C. ochrus* sp. nov. is distinguished from Australian congeners by high number of lenticular scale organs (modally 13), all others except *C. cygnatus* sp. nov. (modally 11) have modal counts lower than eight.

Distribution. Northeastern South Australia (Fig. 99), extending from Wares Peak northwards to Finke River, west to Mintabie and east to Tilcha Bore.

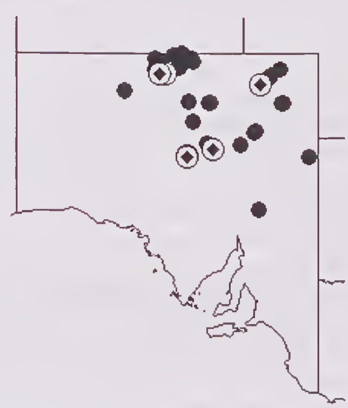

Fig. 99. Map of South Australia showing distribution of *Cryptoblepharus ochrus* sp. nov. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

Sympatry. Sympatric with *C. australis* (lineage 1) and *C. pannosus* sp. nov. (lineage 2) at 1.5 km northeast of Clifton Hills Outstation, South Australia.

Geographic variation. Geographic variation was investigated by dividing specimens into three disparate groups: *CHC*, an eastern group of two (2 ♂) samples from bioregion CHC ; *STPn*, a group of 10 (6 ♂, 4 ♀), from bioregion FIN and northern areas of STP; *STPs*, a group of 10 (5 ♂, 5 ♀), being samples from southern areas of bioregion STP.

Group pairs, were sexes were treated separately and combined, were subjected to tests of allometrically adjusted variables. No significant differences were detected between *CHC* and other groups (tested for males and combined sexes only). Groups *STPn* and *STPs* differed only in condition of the pale dorsolateral stripes, with *STPs* having a less conspicuous stripe on posterior half of body. These results indicate that, apart from less prominent pale dorsolateral stripes in southern populations, *C. ochrus* sp. nov. does not vary over its range.

Habits and habitats. A poorly known, arboreal taxon which, at Coward Springs, was observed on trunks of *Casuarina* sp. and man-made structures (pers. obs).

Etymology. From the Greek adjective *ochrus*, meaning pale; in reference to the pale pigmentation and obscure body pattern of samples from the type locality.

Cryptoblepharus pannosus sp. nov.

Ragged snake-eyed skink

(Plates 2.8–2.9; Figs 100–103; Table 9)

Cryptoblepharus carnabyi Storr, 1976. – Ingram and Covacevich 1981: 301; Wilson and Knowles 1988: 119; Covacevich and Couper 1991: 357; Ehmann 1992: 180; Cogger 2000: 404; Wilson and Swan 2003: 148 (not Storr, 1976: 60).

Type material examined. *Cryptoblepharus pannosus* Horner. HOLOTYPE: Adult male, NTM R23438 (Tissue sample No. *ABTC* CK5), town area, Roma, Queensland, Australia, 26°33'36"S 148°47'09"E. coll. P. and R. Horner, 20 January 1998. On Eucalyptus trunk, 0830 hours. PARATYPES (63 specimens): NORTHERN TERRITORY: NTM R13773-774, Lake Eames, 15°40'9"S 137°02'E, W. Houston, 18 July 1988, *ABTC* 103; NTM R14217, West Island, Sir Edward Pellew Group, 15°36'S 136°33'E, K. Johnson, 28 January 1988; NTM R14777, Calvert River mouth, Seven Emu Station, 16°20'S 137°43'E, K. Johnson, 4 June 1987; NTM R22937, Near mouth, McArthur River, 15°45'S,136°30'E, R. Chatto,10 October 1996, *ABTC* BC1; QUEENSLAND: NTM R18846-847, Leichhardt Falls, Leichhardt River, 18°13'20"S 139°52'40'E, P. and R. Horner, 15 December 1997, *ABTC* BV7; NTM R18850-851, Mine Ruins, Cumberland, 18°18'5"S 143°20'58"E, P. and R. Horner, 18 December 1997, *ABTC* BW2; NTM R18855, Council park, Georgetown, 18°17'27"S 143°32'57"E, P. and R. Horner, 18 December 1997, *ABTC* BW7; NTM R18857, Town Area, Mount Surprise, 18°08'56"S 144°19'01"E, P. and R. Horner, 18 December 1997, *ABTC* BW9; NTM R18887-888, R18890, R18892, Roadhouse, Hells Gate, 17°28'S 138°22'E, P. and R. Horner, 14 December 1997; NTM R18889, Leichhardt Falls, Leichhardt River, 18°13'20"S 139°52'40"E, P. and R. Horner, 15 December 1997; NTM R23439, town area, Roma, 26°33'36"S 148°47'09"E, P. and R. Horner, 20 January 1998, *ABTC* CK6; NTM R23444-445, town area, Augathella, 25°47'51"S 146°34'54"E, P. and R. Horner, 20 January 1998, *ABTC* CL2; NTM R23484, R23486-487, Doomadgee, 17°53'43"S 139°17'08"E, P. and R. Horner, 15 December 1997; NTM R25765, 12 Mile Creek (Karumba Road), Normanton, 17°31'30"S 141°09'20"E, P. Horner and S. Gregg, 14 May 2000, *ABTC* EH3; NTM R25769, Walkers Creek (Karumba Road), Normanton, 17°28'17"S 141°10'52"E, P. Horner and S. Gregg, 14 May 2000, *ABTC* EH7; NTM R25793, Chillagoe Rd (41 km E Karumba Rd), Normanton, 17°18'45"S 141°31'21"E, P. Horner and S. Gregg, 15 May 2000, *ABTC* EK4; NTM R25803, Smithburne River, Normanton, 17°11'31"S 141°43'35"E, P. Horner and S. Gregg, 15 May 2000, *ABTC* EL5; NTM R25829, Flinders River, Normanton, 17°52'33"S 140°46'49"E, P. Horner and S. Gregg, 16 May 2000, *ABTC* EO3; NTM R25843, Armstrong Creek, Normanton, 17°55'50"S 140°42'34"E, P. Horner and S. Gregg, 16 May 2000, *ABTC* EP8; NTM R25855, Wills Development Road, 60.6 km N of Gregory Downs, 18°08'37"S 139°15'27"E, P. Horner and S. Gregg, 17 May 2000, *ABTC* ER2; NTM R25873, Roadhouse, Hells Gate, 17°27'19"S 138°21'22"E, P. Horner and S. Gregg, 18 May 2000, *ABTC* ET1; SAM R5355, Mornington Island, 16°36'S 139°21'E, May 1960; SAM R34216, Westmoreland Station, 17°20'S 138°15'E, 2 June 1989; SAM R9854, Hann River / Kennedy Rd, 15°11'S 143°52'E, 15 June 1966; SAM R42876-877, 6 km E of Noonbah Station, 24°06'S 143°15'E, 16 October 1993; SAM R54425-426, Burke Development Rd, 13 km ENE of Karumba turnoff, 17°25'28"S 141°18'11"E, 15 May 2000; SAM R16563, Strathgordon Homestead, 14°41'S 142°10'E, 27 June 1968; ANWC R1607-608, Bolwarra station, SW of Chillagoe, 17°35'S 144°17'E, 13 June 1977; QM J37970-971, Porcupine Gorge, 28 km N of Hughenden, 20°03'S 144°25'E, 22 August 1980; QM J42796-799, Lynd River, Amber Station, 17°44'S 144°19'E, 22-24 August 1977; NEW SOUTH WALES: NTM R24810, town area, Dubbo, 32°15'S 148°37'E, September 1999, *ABTC* DV5; NTM R25701, State Forest, Moira, 35°57'S 144°51'E, J. Coventry, October 1999, *ABTC* DV7; ANWC R1477-478, Lake Cowal, 33°38'S 147°27'E, 27 August 1974; ANWC R912, 15 km W of Booligal, 33°54'S 144°37'E, 22 November 1975; ANWC R2773, 9 km S of Fairholme, Macquarie Marshes, 30°59'S 147°28'E,15 August 1979; ANWC R3908, Whoey Tank, SE of Mount Hope, Round Hill Nature Reserve, 32°58'S 146°10'E, 16 October 1982; ANWC R3909, Buddigower Nature Reserve, 18 km SW of West Wyalong, 34°02'S 147°06'E, 14 October 1982; ANWC R3025, Woorandara Station, 20 km W of Booligal, 33°53'S 144°39'E, 28 May 1973; SAM R14180, Darling River, 29 km N Wentworth, 33°50'S 142°01'E, 13 April 1974; SAM

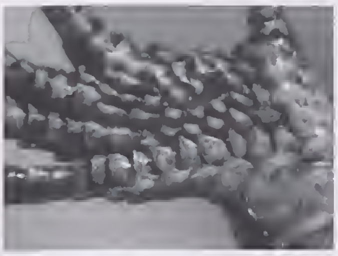

Fig. 100. Ventral surface of hind foot of *Cryptoblepharus pannosus* sp. nov. showing pale, acute plantar scales (NTM R22038, Sandy Creek, SA). Scale: x20.

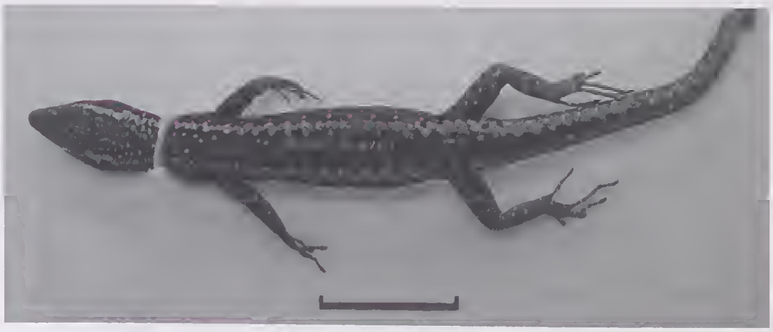

Fig. 101. Holotype of *Cryptoblepharus pannosus* sp. nov. (NTM R23438, town area, Roma, Queensland, Australia. 26°33'36"S 148°47'09"E, *ABTC* CK5). Scale bar = 10 mm.

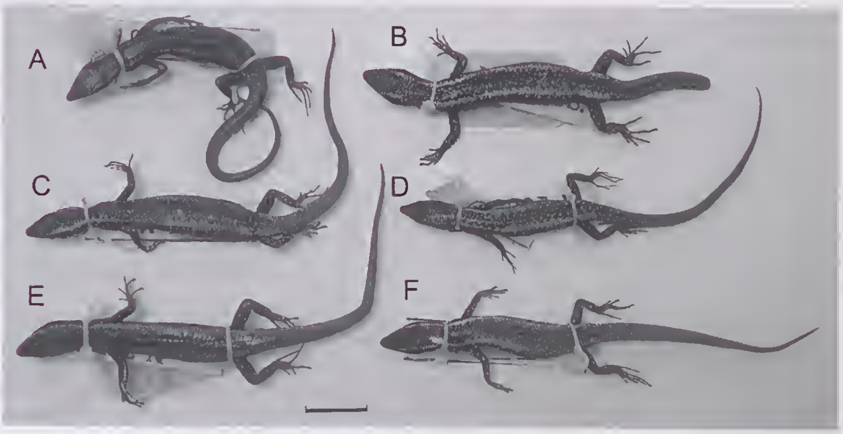

Fig. 102. *Cryptoblepharus pannosus* sp. nov. NTM preserved material. **A**, R22937, McArthur River, NT; **B**, R22038, Sandy Creek, SA; **C**, R18847, Leichhardt Falls, Qld; **D**, R25803, Smithburne River, Qld; **E**, R18846, Leichhardt Falls, Qld; **F**, R25873, Hells Gate, Qld. Scale bar = 10 mm.

R16526, 1 km N along Waugorah Rd, off Hay-Balranald Rd, 34°42'S 143°37'E, 27 December 1976; SOUTH AUSTRALIA: NTM R22038-039, Sandy Creek, 34°36'S 138°49'E, P. Horner, 26 December 1995, *ABTC* Y17; NTM R26246, Brookfield Conservation Park, 34°21'33"S 139°29'16"E, P. Horner, 2 December 2000; SAM R33540-541, Lancoona Homestead, 33°22'S 145°53'E, October 1986; VICTORIA: SAM R36612, 6 km E of Wemen, 34°45'S 142°41'E, *ABTC* L075;

Diagnosis. A medium sized (40–44 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of five supraciliary scales, 24 mid-body scale rows, 48 paravertebral scales, 10 plantar scales, 16 fourth finger subdigital lamellae and 19 fourth toe subdigital lamellae; mean values of 34.4 mm snout-vent length, head length 20.7% of snout-vent length, head depth 40.3% of head length, body length 50.6% of snout-vent length, forelimb length 33.8% of snout-vent length; strongly keeled subdigital lamellae; pale, acute plantar scales, and usually 3+3 posttemporal scales.

Description (64 specimens). Postnasals absent; prefrontals usually in broad contact (96%), occasionally in narrow contact (2%) or narrowly separated (2%); supraciliaries 5–6 (mean 5.1), modally 5; enlarged upper ciliaries 3–4 (mean 3.1), modally 3; loreals usually subequal (73%), occasionally anterior (22%) or posterior largest (5%); supralabials 7–8 (mean 7.0), modally 7; fifth supralabial usually subocular (98%), occasionally sixth (2%); infralabials 6; nuchals 2–5 (mean 2.2), modally 2; bilateral posttemporals usually 3+3 (58%), occasionally 1+2 (2%), 2+2 (20%), or 2+3 (20%).

Midbody scale rows 22–26 (mean 23.5), modally 24; paravertebrals 43–56 (mean 47.8), modally 48; subdigital lamellae strongly keeled, 13–18 below fourth finger (mean 15.8) modally 16, 16–22 below fourth toe (mean 19.4) modally 19; 11–14 supradigital lamellae above fourth finger (mean 12.7) modally 13, 14–17 above fourth toe (mean 15.2) modally 15; palmar and plantar scales acute, without calli and skin not visible between scales (Fig. 100); plantars 8–14 (mean 10.4), modally 10; palmars 7–12 (mean 9.1), modally 10.

Snout-vent length to 41.5 mm (mean 34.4 mm). *Percentages of snout-vent length*: body length 45.2–56.2% (mean 50.6%); tail length 114.5–148.2% (mean 133.4%); forelimb length 28.4–38.7% (mean 33.8%); hindlimb length

36.3–46.5% (mean 41.7%); forebody length 36.0–53.0% (mean 42.1%); head length 18.4–23.6% (mean 20.7%). *Percentages of head length*: head depth 33.4–49.9% (mean 40.3%); head width 54.2–73.3% (mean 61.9%); snout length 41.4–52.2% (mean 45.4%). Paravertebral scale width 3.4–5.2% (mean 4.1%) of snout-vent length; dorsolateral scale width 65.4–107.9% (mean 90.6%) of paravertebral scale width.

Lenticular scale organs 2–9 (mean 5.4), modally 6. Premaxillary teeth 5; maxillary teeth 16–19 (mean 17.8), modally 19; mandibular teeth 21–25 (mean 22.8), modally 23. Hemipenis: length 6.2–8.8% (mean 7.5%) of snout-vent length; width 76.4–104.1% (mean 90.9%) of hemipenis length; trunk 24.4–61.5% (mean 43.3%) of hemipenis length.

Details of holotype. Adult male (Fig. 101), NTM R23438. Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; anterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 24; paravertebrals 50; subdigital lamellae keeled, 15 below fourth finger; 18 below fourth toe; supradigital lamellae 13 above fourth finger; 14 above fourth toe; palmars and plantars acute, skin not visible between scales; plantars 10; palmars 9. Snout-vent length 33.8 mm; body length 16.6 mm; tail length 40.7 mm; forelimb length 11.2 mm; hindlimb length 15.0 mm; forebody length 15.2 mm; head length 7.0 mm; head depth 3.0 mm; head width 4.3 mm; snout length 3.1 mm.

Colouration and pattern. Brown, grey or blackish *Cryptoblepharus*, with longitudinally aligned, complex body pattern dominated by dark, broad vertebral zone and pale laterodorsal stripes (Plates 2.8 and 2.9). Intensity of body pigmentation and patterning is variable, ranging from pale to prominent (Fig. 102). Most specimens conform to the following description.

Dorsal ground colour brown, grey or blackish, with broad, dark vertebral zone extending from above eye to hindlimb. Vertebral zone 3–4 mid-dorsal scales wide, brown, grey or blackish, dotted with short irregular blackish streaks and spots. Latter most prominent on inner edges of dorsolateral scales and usually form two obscure, broken, narrow black stripes from neck to tailbase, where they merge. Pale grey or cream laterodorsal stripes extend from above eye onto tail, broadest on posterior half of body, about 1.5–2 laterodorsal scales wide, tapering anteriorly into prominent narrow stripes extending to eye and posteriorly to form tail ground colour. Edges of pale laterodorsal stripes ragged, interdigitating with dark vertebral and upper lateral zones. Laterodorsal stripes usually uniform, but may contain dark speckling. Head concolorous with vertebral zone, mottled with blackish flecks, specks and dark edges to shields. Laterally patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Pale lower temporal region flecked with dark spots and streaks. Labials pale, patterned with occasional dark flecks.

Flanks patterned with brown to dark grey upper lateral zone, variable in width, extending from loreals onto tail. Heavily flecked with dark streaks and pale flecks, upper lateral zone coalesces gradually into pale grey/pale grey-brown lower lateral zone. Lower lateral zone peppered with small pale and/or dark flecks and streaks and coalesces into pale venter. Tail concolorous with body, patterned with broken continuations of dark vertebral and upper lateral zones. Limbs and toes concolorous with body, patterned with pale and dark speckling. Venter immaculate off-white. Palmars and plantars often with darker skin visible around pale scales.

In some northern Gulf populations (GUC, GUP bioregions) body patterning is obscure, with much reduced dark pigmentation (Fig. 102 A, C, E). Far southern populations tend to have a greater amount of dark pigmentation (Fig. 102B).

Sex ratio and reproductive biology. Sex ratio favoured males (33:31), but was not significantly different from parity ($X^2 = 0.06$). Males mature at approximately 30.0 mm snout-vent length and females at 30.4 mm. Adults average 34.4 mm snout-vent length and females grow larger than males (maximum SVL = 41.5 versus 39.3 mm). Breeding is year round with reproductively active animals collected in all months except February and March. This finding also applies to southern populations (FLB, MDD, NSS and RIV bioregions), where reproductive animals were collected in May, July, August, October and December.

Comparison with Australian congeners. Fixed allelic differences place *C. pannosus* sp. nov. in lineage 2 of Australian *Cryptoblepharus* and also distinguish it from most congeners within that lineage (as OTU carnA5, Horner and Adams 2007). With no fixed allelic differences, *C. pannosus* sp. nov. is genetically similar to *C. adamsi* sp. nov. (as OTU virgA3, Horner and Adams 2007).

Morphologically distinguished from most lineage 1 members (except *C. australis*) by usually having five, rather than six, supraciliary scales and acute, instead of ovate, plantar scales. Distinguished from lineage 2 congeners *C. adamsi* sp. nov., *C. fuhni*, *C. gurrmul* sp. nov., *C. litoralis*, *C. pulcher*, *C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov. by acute plantars (versus rounded). Further distinguished from: *C. gurrmul* sp. nov., *C. l. horneri* and *C. l. litoralis* by fewer mid-body scale rows (modally 24 versus 26–28) and paravertebral scales (modally 48 versus 55–57); from *C. fuhni*, *C. gurrmul* sp. nov. and *C. zoticus* sp. nov. by more paravertebral scales (modally 48 versus 45–46) and deeper head (mean 40.3 versus 32.5–36.1 % of head length); from *C. virgatus* by more mid-body scale rows (modally 24 versus 22) and paravertebral scales (modally 48 versus 47); from *C. adamsi* sp. nov. and *C. pulcher* by pale plantar scales (versus darkly pigmented) and broad, ragged pale laterodorsal stripes.

Cryptoblepharus pannosus sp. nov. is most similar to *C. australis*, *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp.

nov. in having combinations of complex body patterns, acute plantar scales and being arboreal. However it differs from *C. australis* and *C. exochus* sp. nov. by having keeled instead of smooth subdigital lamellae, fewer paravertebral (modally 48 versus 52 and 51) and plantar scales (modally 10 versus 12) and smaller size (mean SVL 34.4 instead of 40.4 and 37.1 mm), further differs from *C. australis* by having fewer supraciliary scales (modally 5 versus 6). It differs from *C. ochrus* sp. nov. and *C. tytthos* sp. nov. by having broad, ragged laterodorsal stripes instead of obscure narrow stripes, fewer plantar scales (modally 10 versus 11) and size (mean SVL 34.4 instead of 39.0 and 31.1 mm), further differs from *C. ochrus* sp. nov. by having fewer paravertebral scales (modally 48 versus 50) and shorter hindlimbs (mean % of SVL 41.7 instead of 42.5) and from *C. tytthos* sp. nov. by having more fourth finger subdigital lamellae (modally 16 versus 15) and posterior temporal scales (modally 3 versus 2). It differs from *C. mertensi* sp. nov. by having more posterior temporal scales (modally 3 versus 2), longer forebody (mean % of SVL 42.1 instead of 40.6) and shallower head (mean % of head length 40.3 instead of 43.4) and from *C. plagiocephalus* by having more posterior temporal (modally 3 versus 2) and paravertebral scales (modally 50 versus 48), longer body (mean % of SVL 50.6 instead of 49.1) and shorter head (mean % of SVL 20.7 instead of 21.5).

Notwithstanding allozymic similarity (Horner and Adams 2007), comparison of 64 *C. pannosus* sp. nov. to 24 *C. adamsi* sp. nov. identified the following morphological differences: keeled versus smooth subdigital lamellae; acute versus ovate plantar scales; longer forelimbs (mean 12.5 versus 11.9 mm) and more fourth toe subdigital lamellae (modally 19 versus 18), palmar (modally 9 versus 8), plantar (modally 11 versus 9) and posterior temporal scales (modally 3 versus 2).

Distribution. Widely distributed through the eastern half of Australia, west of the Great Dividing Range (Fig. 103). Extending from Cape York Peninsula and Gulf regions of Queensland and the Northern Territory, through inland Queensland and New South Wales to far northern Victoria and eastern South Australia. The southern limit of distribution appears to follow the Murray River, though some records extend just past this. Records from northern Victoria are the most southerly for *Cryptoblepharus* in Australia.

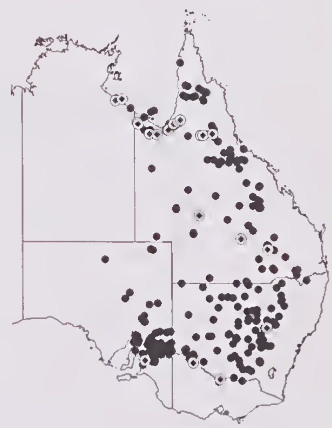

Fig. 103. Map of eastern Australia showing distribution of *Cryptoblepharus pannosus* sp. nov. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

Table 9. List of congeners sympatric with *Cryptoblepharus pannosus* sp. nov., giving areas of sympatry.

Congeners sympatric with *Cryptoblepharus pannosus* sp. nov.	**Area of sympatry**
C. adamsi sp. nov.	Qld: Hillgrove Station
C. australis	NSW: 15 km W of Booligal, Cuddie Springs, Brewarrina, Byerawering Stn, Lightning Ridge, Mootwingee National Park, Quambone, Sturt National Park, Thurloo Downs, Warraderry State Forest, Wilcannia, Yanco. Qld: 3 miles N of Bellata, Alton Downs, Augathella, Blackall, Emerald, Endfield Stn, Roma. SA: 11 km SW of Clifton Hills Outstation, Davernport Springs, Davies Ruins, east of Mount Bryan, Italowie Gap, Mutooroo Stn, Loch Ness Well (Gammon Ranges), Oraparinna Homestead
C. metallicus	Qld: 18 km N of Glen Garland Stn, 5 km S of Moranbah, Battery Stn, Brannigan Creek (nr Karumba), 13 km ENE of Karumba t/off (Burke Dev. Rd), Charters Towers, Doomadgee, Flinders River, Hells Gate, Karumba, Floraville Stn, Leichhardt Falls, Lynd River, Amber Station, Mount Surprise, Normanton, Oriners Outstation, Springfield railway crossing, Red Falls (west of Charters Towers), Shelfer crossing (Mitchell River), Strathgordon Homestead, Walkers Creek (Karumba Road)
C. ochrus sp. nov.	SA: nr Saint Mary's Peak (Wilpena)
C. p. pulcher	Qld: 8 km N of Wyberba, Ravenswood
Multiple sympatry	
C. l. litoralis + *C. metallicus*	Qld: Townsville
C. metallicus + *C. tytthos* sp. nov.	Qld: Mornington Island

Sympatry. *Cryptoblepharus pannosus* sp. nov. occurs in sympatry with *C. australis* and *C. metallicus* from lineage 1, and *C. adamsi* sp. nov., *C. l. litoralis*, *C. ochrus* sp. nov., *C. pulcher* and *C. tytthos* sp. nov. from lineage 2 (Table 9).

Geographic variation. Geographic variation was investigated by dividing specimens into four groups: *GUP*, a north-western group of 27 (13 ♂, 14 ♀) samples from bioregions GUC and GUP; *EIU*, a north-eastern group of 14 (8 ♂, 6 ♀) from bioregions CYP and EIU; *CHC*, a central eastern group of 7 (4 ♂, 3 ♀) from bioregions BBS, CHC, DRP and MGD, and *RIV*, a southern group of 16 (8 ♂, 8 ♀) from bioregions FLB, MDD, NSS and RIV.

Group pairs, where sexes were treated separately and combined, were subjected to tests of allometrically adjusted variables. Initial analysis failed to detect any significant difference between central and southern groups *CHC* and *RIV*, so these were combined to create a group (*RIV2*) of 23 (12 ♂, 11 ♀). Subsequent analyses showed that Group *GUP* was most divergent, differing from *EIU* and *RIV2* in head width (HW, mean 4.7 versus 4.9) and condition of pale stripes (narrow versus broad). Group *GUP* further differed from *EIU* in being larger (mean SVL 34.4 versus 32.5 mm) and having more paravertebrals (modally 48 versus 45), and from *RIV2* in having fewer mid-body scale rows (modally 22 versus 24) and more palmar and plantar scales (modally: PAL 10 versus 9; PLN 11 versus 9). Groups *EIU* and *RIV2* differ in snout-vent length (mean 32.5 versus 35.6 mm) and number of paravertebral scales (modally 45 versus 48).

These results indicate that geographic variation in *C. pannosus* sp. nov. principally consists of differences between north-western populations (group *GUP*) and eastern and southern populations. North-western specimens tend to be more obscurely patterned, with a narrower head and while not always significant between groups separated by sex, they also have generally fewer mid-body scale rows (modally 22 versus 24) and posttemporal scales (mean 2+2 versus 3+3). Variation between north-eastern and southern populations was limited to southern specimens having more paravertebrals and as in *C. buchananii*, being slightly larger and more darkly pigmented.

Habits and habitats. *Cryptoblepharus pannosus* sp. nov. inhabits a variety of environments. Typically arboreal, museum records note its use of woodland, shrubland, grassland, riparian, parkland and urban environments. Within these it has been associated with numerous tree and/or shrub species, including: *Acacia, Callitris, Casuarina, Erythrophleum, Eucalytpus, Melaleuca* spp. and *Mangifera indica*. Usually observed on living tree trunks, it has also been recorded from fallen logs, stumps and shrubs on a low rock outcrop. Equally at home on man made structures, records note its use of old stockyards, fence rails, council parks, mine ruins, concrete bridge supports and a rock platform supporting a sign post.

Etymology. From the Latin adjective *pannosus*, meaning ragged or tattered; in reference to the usually irregular borders of this taxon's pale dorsolateral stripes.

Cryptoblepharus plagiocephalus (Cocteau, 1836)

Péron's snake-eyed skink

(Plate 2.10; Figs 104–108)

Scincus plagiocephalus (part) Cocteau, 1836: plate (Shark Bay, Western Australia).

Ablepharus peroni (part) Duméril and Bibron, 1839: 813; Sternfeld 1918: 421.

Ablepharus boutonii Boulenger 1887: 346.

Ablepharus boutonii plagiocephalus (Cocteau, 1836). – Mertens 1931: 116; Worrell 1963: 34.

Cryptoblepharus plagiocephalus (Cocteau, 1836). – Cogger *et al.* 1983a: 142.

Cryptoblepharus carnabyi Storr 1976: 60. – Storr and Hanlon 1980: 431; Storr *et al.* 1981: 22; Cogger *et al.* 1983a: 141; Storr *et al.* 1983: 223; Storr and Harold 1985: 283; Wells and Wellington 1985: 27; Wilson and Knowles 1988: 119; Ehmann 1992: 180; Maryan 1996: 9; Stanger *et al.* 1998: 23; Storr *et al.* 1999: 22; Cogger 2000: 404; Wilson and Swan 2003: 148.

Type material examined. *Scincus plagiocephalus* Cocteau, 1836. LECTOTYPE: MNHP 7150, Baie des Chiens marins (Nouv.-Hollande), coll. Quoy et Gaimard. *Cryptoblepharus carnabyi* Storr, 1976 HOLOTYPE: WAM R21182, 11 km WSW of Youanmi, 28°37'S 118°43'E, Western Australia, coll. D. Serventy and G. Storr, 29 July 1963 (under bark of dead mulga at night).

Non-type material examined. See Appendix 4.

Diagnosis. A medium sized (40–44 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of five supraciliary scales, 24 midbody scale rows, 50 paravertebral scales and 9 palmar scales; mean values of 33.6 mm snout-vent length, body length 49.1% of snout-vent length, head length 21.5% of snout-vent length, head depth 39.5% of head length and forelimb length 33.9% of snout-vent length; pale, acute plantar scales; moderately keeled fourth toe subdigital lamellae, and wide pale dorsolateral stripes.

Description (28 specimens). Postnasals absent; prefrontals in broad contact (100%); supraciliaries 5–6 (mean 5.1), modally 5; enlarged upper ciliaries 3–4 (mean 3.2), modally 3; loreals usually subequal (65%), occasionally posterior loreal is largest (35%); supralabials 6–8 (mean 7.0), modally 7; fifth supralabial subocular (100%); infralabials 6–7 (mean 6.1), modally 6; nuchals 2–4 (mean 2.2), modally 2; bilateral posttemporals usually 2+2 (44%), occasionally 2+3 (28%), or 3+3 (28%).

Midbody scale rows 22–26 (mean 24.4), modally 24; paravertebrals 45–58 (mean 49.2), modally 50; subdigital lamellae moderately keeled, 14–18 below fourth finger (mean 15.5) modally 16, 16–21 below fourth toe (mean 18.8) modally 20; 11–14 supradigital lamellae above fourth finger (mean 12.9) modally 13, 13–17 above fourth toe (mean 15.1) modally 15; palmar and plantar scales acute, without calli and skin not visible between scales (Fig. 104);

Fig. 104. Ventral surface of hind foot of *Cryptoblepharus plagiocephalus* showing pale, acute plantar scales (NTM R22074, Carnarvon, WA). Scale: x20.

Fig. 105. Holotype of *Cryptoblepharus carnabyi* Storr, 1976 (WAM R21182, 11 km west south west of Youanmi, Western Australia). Insert shows plantar scale morphology.

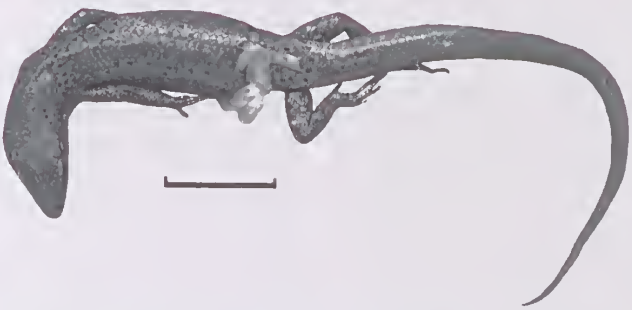

Fig. 106. *Cryptoblepharus plagiocephalus* preserved WAM specimen (R45828, Cape Inscription, Dirk Hartog Island, WA). Scale bar = 10 mm.

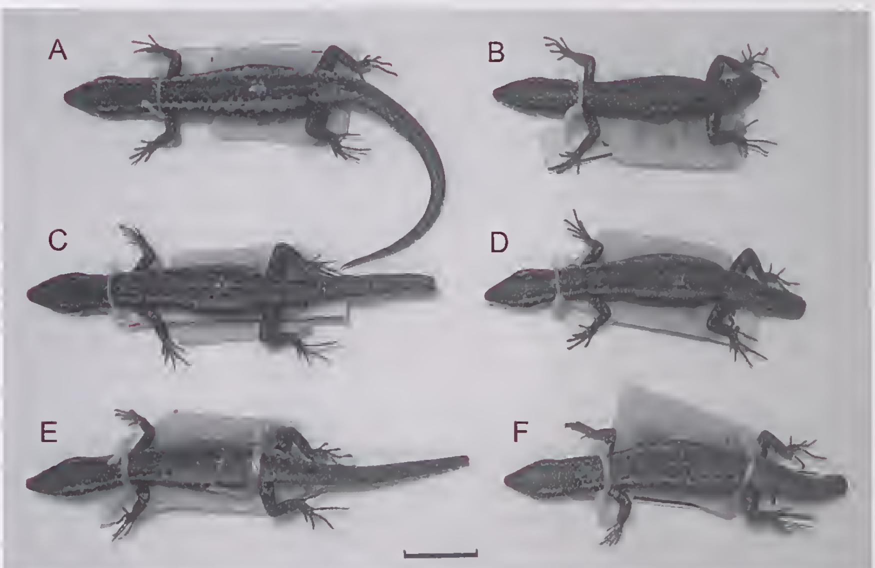

Fig. 107. *Cryptoblepharus plagiocephalus*, preserved NTM specimens from Western Australia. **A**, = R22075, Carnarvon; **B**, R22070, Denham; **C**, R22074, **D**, R22076, **E**, R22078; **F**, R22077, Carnarvon. Scale bar = 10 mm.

plantars 9–13 (mean 10.7), modally 10; palmars 8–12 (mean 9.6), modally 9.

Snout-vent length to 40.3 mm (mean 33.6 mm). *Percentages of snout-vent length*: body length 40.8–55.8% (mean 49.1%); tail length 127.8–151.5% (mean 140.9%); forelimb length 30.7–39.6% (mean 33.9%); hindlimb length 36.8–50.1% (mean 42.2%); forebody length 38.0–50.1% (mean 42.9%); head length 19.4–24.5% (mean 21.5%). *Percentages of head length*: head depth 30.2–53.0% (mean 39.5%); head width 53.9–68.3% (mean 61.8%); snout length 42.0–50.4% (mean 45.9%). Paravertebral scale width 3.2–4.8% (mean 3.9%) of snout-vent length; dorsolateral scale width 81.8–108.3% (mean 92.1%) of paravertebral scale width.

Lenticular scale organs 4–12 (mean 7.5), modally 5. Premaxillary teeth 5–6 (mean 5.5); maxillary teeth 17–18 (mean 17.5); mandibular teeth 20–22 (mean 21.0). Hemipenis: length 6.0–9.1% (mean 7.2%) of snout-vent length; width 73.0–120.7% (mean 98.9%) of hemipenis length; trunk 39.9–48.3% (mean 43.9%) of hemipenis length.

Details of primary types. *Scincus plagiocephalus* Cocteau, 1836. LECTOTYPE: MNHP 7150. Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; loreals subequal; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 24; paravertebrals 48; subdigital lamellae moderately keeled, 14 below fourth finger; 17 below fourth toe; supradigital lamellae 11 above fourth finger; 13 above fourth toe; palmars and plantars acute, skin not visible between scales; plantars 10; palmars 8. Snout-vent length 35 mm; body length 17 mm; tail not original; forelimb length 11 mm; hindlimb length 14 mm; forebody length 15 mm; head length 7.9 mm; head depth 3.2 mm; head width 5.3 mm; snout length 3.6 mm.

Cryptoblepharus carnabyi Storr, 1976. HOLOTYPE: WAM R21182 (Fig. 105). Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; loreals subequal; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 26; paravertebrals 48; subdigital lamellae moderately keeled, 18 below fourth finger; 21 below fourth toe; supradigital lamellae 13 above fourth finger; 16 above fourth toe; palmars and plantars acute, skin not visible between scales (Fig. 108); plantars 12; palmars 10. Snout-vent length 34.9 mm; body length 17.1 mm; tail not original; forelimb length 11.9 mm; hindlimb length 16.1 mm; forebody length 15.1 mm; head length 7.4 mm; head depth 3.0 mm; head width 4.7 mm; snout length 3.3 mm.

Colouration and pattern. A brownish-grey *Cryptoblepharus*, with longitudinally aligned, complex body pattern dominated by broad, dark vertebral zone and pale laterodorsal zones/stripes (Plate 2.10). Intensity of body pigmentation and patterning is variable, ranging from pale to prominent (Figs 106 and 107). Most specimens conform to the following description.

Dorsal ground colour brown-grey, with broad, dark vertebral zone extending from above eye to hindlimb. Vertebral zone about four scales wide, brown-grey, dotted with short longitudinal blackish streaks and spots. Latter most prominent on outer edges of dorsolateral scales and usually form two broken, narrow black stripes from neck to tailbase, where they merge. Pale grey-brown laterodorsal stripes extend from above eye onto tail, broadest on posterior half of body, about 1.5 width of laterodorsal scale, tapering anteriorly into prominent narrow stripes extending to eye and posteriorly to form tail ground colour. Edges of pale laterodorsal stripes smooth to ragged. Laterodorsal stripes usually uniform, but may contain dark speckling. Head concolorous with vertebral zone, mottled with blackish flecks and specks. Laterally patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Pale lower temporal region is flecked with dark spots and streaks. Labials pale cream, patterned with occasional dark flecks.

Flanks patterned with grey-brown upper lateral zone, variable in width, extending from loreals onto tail. Flecked with dark streaks and pale flecks, upper lateral zone coalesces gradually into pale grey/pale grey-brown lower lateral zone. Lower lateral zone peppered with small pale and/or dark spots and streaks and coalesces into pale venter. Tail concolorous with body, patterned with broken continuations of dark vertebral and upper lateral zones. Limbs and toes concolorous with body, patterned with pale and dark speckling. Venter, including palmars and plantars, immaculate off-white. Some Shark Bay populations have a reduced, speckled dorsal back pattern, with pale laterodorsal stripes absent or obscure (Fig. 106).

Sex ratio and reproductive biology. Sex ratio favoured males (15:13), but was not significantly different from parity ($X^2 = 0.14$). Both sexes mature at approximately 30 mm snout-vent length. Adults average 33.6 mm snout-vent length and females grow larger than males (maximum SVL = 40.3 versus 38.9 mm). Reproductive females were collected in September (2), December (1) and January (3), indicating seasonal breeding (summer), but small sample size limits analysis.

Comparison with Australian congeners. Fixed allelic differences place *C. plagiocephalus* in lineage 2 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTU carnA1, Horner and Adams 2007).

Morphologically distinguished from most lineage 1 members (except *C. australis*) by usually having five, rather than six, supraciliary scales and acute, instead of ovate, plantar scales. Distinguished from lineage 2 congeners *C. adamsi* sp. nov., *C. fuhni*, *C. gurrmul* sp. nov., *C. litoralis*, *C. pulcher*, *C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov. by acute plantars (versus rounded). Further distinguished from: *C. gurrmul* sp. nov., *C. l. horneri* and *C. l. litoralis* by fewer mid-body scale rows (modally 24 versus 26–28) and paravertebral scales (modally 50 versus 55–57); from *C. fuhni*, *C. gurrmul* sp. nov. and *C. zoticus* sp. nov. by more paravertebral scales (modally 50 versus

45–46) and deeper head (mean 39.5 versus 32.5–36.1% of head length); from *C. virgatus* by more mid-body scale rows (modally 24 versus 22) and paravertebral scales (modally 50 versus 47); from *C. adamsi* sp. nov. and *C. pulcher* by pale plantar scales (versus darkly pigmented) and broad, ragged pale laterodorsal stripes.

Cryptoblepharus plagiocephalus is most similar to *C. australis*, *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov. and *C. tytthos* sp. nov. in having combinations of complex body patterns, acute plantar scales and being arboreal. However it differs from both *C. australis* and *C. exochus* sp. nov. in having keeled instead of smooth subdigital lamellae and smaller size (mean SVL, 33.6 versus 40.4 and 37.1 mm), further differs from *C. australis* by having fewer supraciliary scales (modally 5 versus 6) and longer snout (mean % of head length: 45.9 versus 44.9) and from *C. exochus* sp. nov. by having fewer paravertebral (modally 50 versus 51) and palmar scales (modally 9 versus 10). Differs from *C. ochrus* sp. nov. and *C. tytthos* sp. nov. by having broad, ragged laterodorsal stripes instead of obscure narrow stripes and in size (mean SVL 33.6 instead of 39.0 and 31.3 mm), further differs from *C. ochrus* sp. nov. by having fewer fourth toe supradigital scales (modally 15 versus 16) and posterior temporal scales (modally 2 versus 3) and from *C. tytthos* sp. nov. by having shallower head (mean % of head length: 39.5 versus 40.6) and weakly, instead of strongly, keeled subdigital lamellae. Differs from *C. mertensi* sp. nov. by having longer forebody (mean % of SVL 40.6 instead of 42.9), shallower head (mean % of head length 39.5 instead of 43.4) and more paravertebral scales (modally 50 versus 49) and from *C. pannosus* sp. nov. by having fewer posterior temporal (modally 2 versus 3) and paravertebral scales (modally 48 versus 50), shorter body (mean % of SVL 49.1 instead of 50.6) and longer head (mean % of SVL 21.5 instead of 20.7).

Distribution. Mid and southern regions of Western Australia, extending from north of Port Hedland, south to about Geraldton and inland to about Kalgoolie (Fig. 108). Storr *et al.* (1983) record it (as *C. carnabyi*) from the Houtman Abrolhos island group, off Geraldton.

Sympatry. *Cryptoblepharus plagiocephalus* occurs in sympatry with *C. buchananii* from lineage 1 on Dirk Hartog Island, Shark Bay (Maryan 1996), Greenough, and in the Exmouth (Storr and Hanlon 1980) and Geraldton regions (Storr *et al.* 1983).

Geographic variation. Geographic variation was investigated by dividing specimens into three disparate groups: *CAR*, a mid-north Western Australia group of 10 (3 ♂, 7 ♀) samples from bioregions CAR, DL and PIL; *GS*, a Geraldton Sandplain group of 12 (7 ♂, 5 ♀), from bioregion GS; *MUR*, a mid-south Western Australia group of 6 (5 ♂, 1 ♀), from bioregions COO, MUR and YAL.

Group pairs, where sexes were treated separately and combined, were subjected to U-tests of allometrically adjusted variables. A significant difference was detected between males of group *GS* versus those of groups *CAR* and *MUR*. Differentiation was due to *GS* males having fewer palmar scales (modally 9 versus 10). This character lost significance when combined sexes were analysed. Analysis of sexes combined revealed significant differences in *GS* versus *CAR* and *MUR* (mean forelimb length 12.9 versus 11.9 and 12.4 % of SVL) and *CAR* versus *GS* and *MUR* (mean head length 7.6 versus 7.9 and 8.1 % of SVL).

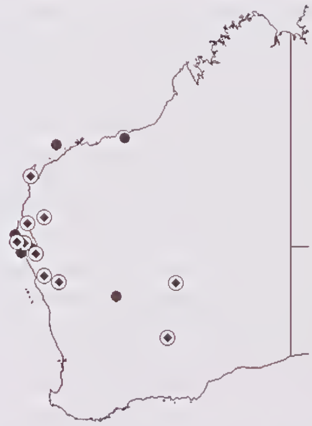

Fig. 108. Map of Western Australia showing distribution of *Cryptoblepharus plagiocephalus*. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

These results indicate that geographic variation in *C. plagiocephalus* is not highly significant, being limited to Geraldton Sandplain populations having slightly longer forelimbs and mid-northern populations having slightly shorter heads.

Habits and habitats. Normally arboreal, though museum records note its use of 'brick fences' at Carnarvon and 'building walls near beach' at Denham. Literature records note its abundance (as *C. carnabyi*) on coastal limestone, piles of driftwood and dead logs on beaches on Dirk Hartog Island (Maryan 1996). Wholly terrestrial on the Houtman Abrolhos Islands, where it shelters in limestone crevices and under reef debris (Storr *et al.* 1983). Recorded from a thicket at the foot of a cliff on North West Cape (Storr and Hanlon 1980), and noted as widespread on Barrow Island, where it was moderately common in habitats providing vertical surfaces such as mangroves, eucalypts, walls of buildings and sides of sink-holes (Storr and Harold 1985).

Taxonomic history. Some detail is required to unravel the confusing taxonomic history of *Cryptoblepharus plagiocephalus*.

Between 1801 and 1803, a French expedition, commanded by Post-Captain Nicolas Baudin and with François Péron (zoologist) and Charles Lesueur (natural history artist) aboard, collected animals at Geographe Bay, Rottnest Island, Swan River, Garden Island, Cottesloe and Shark Bay, Western Australia (Marchant 1982), as well as coastal South Australia and the Sydney area.

In 1836, J.T. Cocteau described 'Cryptoblepharus de Péron'. In his description, Cocteau stated that François

Péron first distinguished the species and gave the manuscript name *Scincus plagyocephalus*. By using Péron's manuscript name (cited as *plagyocephalus* in the text but, correctly, as *plagiocephalus* in the figure legend) as a latin binomen, Cocteau validated that name (Brygoo 1986). Duméril and Bibron (1839) applied the binomen *Ablepharus peronii* to "L'Abléphare de Péron" and are credited as authors of that name. Cocteau's (and Péron's) description of a skink from "Tasmania and Shark Bay" was reviewed by Mertens (1931), who determined that Tasmania was outside the taxon's distribution and was, therefore, an error. Mertens (1931) also placed Duméril and Bibron's *A. peronii* in the synonymy of *A. b. plagiocephalus*. As the same composite series of specimens were used in all three early descriptions, Mertens (1931) also placed parts of *A. peronii* in synonymy with *A. b. leschenault* and *A. b. poecilopleurus*.

Guibé (1954) lists two syntypes of *A. b. plagiocephalus*: MNHP 3088, "Terre van Diemen, Péron et Lesueur", and MNHP 7150, "Baie des Chiens marins (Nouv.-Hollande), Quoy et Gaimard". Both these specimens, lodged in the Muséum National d'Histoire Naturelle, were examined by Glenn Shea in August 1997 and scored against morphological criteria used in this project. Analysis of that data confirmed the types agreed most closely with OTU carnA1 from Western Australia. As OTU carnA1 does not occur on the south-west coast of Western Australia, coastal South Australia or New South Wales, Péron and Lesueur could only have collected their specimen at Shark Bay. Similarly, "Baie des Chiens marins" or "Bay of sea dogs" is an early French name for Shark Bay (Mertens 1931). Quoy and Gaimard were ships surgeons (and naturalists) on the 'Uranie', commanded by Louis de Freycinet, which surveyed Shark Bay in 1818. They went ashore on Dirk Hartog Island and Peron Peninsula, these being the only places they landed in Australia (Marchant 1982). On the return voyage to France the 'Uranie' was wrecked on the Falkland Islands and most of their scientific specimens were lost (Marchant 1982).

Mertens (1931), determined the taxon *A. b. punctatus* Sternfeld 1918 (herein synonymised with *C. buchananii*) to be identical with *A. b. plagiocephalus*. Storr (1961) supported this finding by restricting the type locality of *plagiocephalus* to Swan River, Western Australia. This inappropriate action was rectified by Cogger *et al.* (1983a), who designated MNHP 7150 as the lectotype of *C. plagiocephalus*, thus confirming the type locality as Shark Bay.

In describing the taxon '*C. carnabyi*', Storr (1976) differentiated his new species from *C. plagiocephalus* by "each subdigital lamella bearing a fine weak keel terminating in a mucron, palmar and plantar scales white and sharp pointed, and supraciliaries normally 5". These character states correspond to those found on the two *plagiocephalus* types. Thus Storr, by failing to examine the types of *plagiocephalus* prior to describing *carnabyi*, applied a new name to an existing taxon. By the Principle of Priority (International Commission on Zoological Nomenclature 1999), Storr's binomen must now be placed in the synonymy of *C. plagiocephalus*.

Cryptoblepharus pulcher (Sternfeld, 1918)
Elegant snake-eyed skink

(Plates 3.1–3.2; Figs 109–115; Table 10)

Ablepharus boutoni pulcher Sternfeld, 1918: 423 (Australia).

Ablepharus boutonii virgatus Garman, 1901. – Mertens 1931:112. - Mertens 1964: 104; Worrell 1963: 35.

Ablepharus boutonii clarus Storr, 1961: 176. Worrell 1963: 35.

Cryptoblepharus boutonii virgatus (Garman, 1901). – (Mertens, 1931); Cook 1973: 15.

Cryptoblepharus virgatus clarus (Storr, 1961). – Storr 1976: 55; Wilson and Knowles 1988: 120.

Cryptoblepharus clarus (Storr, 1961). – Wells and Wellington 1985: 27.

Cryptoblepharus virgatus virgatus (Garman, 1901). – Wilson and Knowles 1988: 120.

Cryptoblepharus virgatus (Garman, 1901). – Storr *et al.* 1981: 25; Cogger *et al.* 1983a: 142; Covacevich and Couper 1991: 357; Ehmann 1992: 183; Stanger *et al.* 1998: 23; Storr *et al.* 1999: 25; Cogger 2000: 406; Hutchinson and Edwards 2000: 103; Daly *et al.* 2001: 85; Greer and Jefferys 2001: 3; Wilson and Swan 2003: 150.

Cryptoblepharus suburbia Wells and Wellington, 1985: 27.

Cryptoblepharus virgatus suburbia Wells and Wellington, 1985. – Wells and Wellington 1989: 29.

Diagnosis. A medium sized (40–44 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of five supraciliary scales, 24 mid-body scale rows and 50 paravertebral scales; mean head depth

Fig. 109. Map of Australia showing distribution of *Cryptoblepharus pulcher*. Note disjunct ranges of (**A**) *C. p. clarus* (southern Western and South Australia) and (**B**) *C. p. pulcher* (eastern Australia). Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

of 39.3% of head length; plain, rounded, dark pigmented plantar scales, and narrow, pale dorsolateral stripes.

Description (79 specimens). Postnasals absent; prefrontals usually in broad contact (98%), occasionally in narrow contact (1%) or narrowly separated (1%); supraciliaries 5–6 (mean 5.0), modally 5; enlarged upper ciliaries 2–4 (mean 3.0), modally 3; loreals usually subequal (65%), occasionally anterior (19%) or posterior loreal (16%) largest; supralabials 6–8 (mean 7.0), modally 7; fifth supralabial usually subocular (96%), occasionally fourth (2%) or sixth (2%); infralabials 6; nuchals 2–6 (mean 2.5), modally 2; bilateral posttemporals usually 2+2 (86%), occasionally 2+3 (13%), or 3+3 (1%).

Midbody scale rows 22–26 (mean 23.8), modally 24; paravertebrals 42–55 (mean 48.7), modally 50; subdigital lamellae smooth, 12–17 below fourth finger (mean 14.8) modally 15, 16–22 below fourth toe (mean 18.5) modally 19; 11–14 supradigital lamellae above fourth finger (mean 12.4) modally 12, 14–18 above fourth toe (mean 15.8) modally 16; palmar and plantar scales rounded, without calli and skin visible between scales; plantars 7–12 (mean 9.3), modally 9; palmars 6–9 (mean 7.8), modally 8.

Snout-vent length to 41.7 mm (mean 35.6 mm). *Percentages of snout-vent length*: body length 44.5–56.9% (mean 51.2%); tail length 114.0–142.3% (mean 126.8%); forelimb length 28.8–36.6% (mean 32.2%); hindlimb length 35.6–47.0% (mean 40.5%); forebody length 36.7–46.5% (mean 41.2%); head length 17.8–22.6% (mean 20.0%). *Percentages of head length*: head depth 29.2–53.4% (mean 39.3%); head width 55.0–71.9% (mean 63.2%); snout length 41.9–49.7% (mean 45.0%). Paravertebral scale width 3.3–5.1% (mean 4.0%) of snout-vent length; dorsolateral scale width 71.4–107.4% (mean 91.0%) of paravertebral scale width.

Lenticular scale organs 1–12 (mean 4.0), modally 4. Premaxillary teeth 5–6 (mean 5.3), modally 5; maxillary teeth 19–20 (mean 19.3), modally 19; mandibular teeth 24. Hemipenis: length 5.6–9.2% (mean 7.3%) of snout-vent length; width 73.6–115.0% (mean 99.5%) of hemipenis length; trunk 31.9–51.9% (mean 39.4%) of hemipenis length.

Colouration and pattern. A brownish-black *Cryptoblepharus*, with longitudinally aligned, complex body pattern dominated by narrow, brown vertebral zone, black dorsolateral and prominent silvery laterodorsal stripes. Intensity of body patterning is variable, both individually and geographically, ranging from obscure to prominent. Most specimens conform to the following description.

Dorsal ground colour brown or brown-black, with narrow vertebral zone extending from above eye to hindlimb. Vertebral zone as wide as single paravertebral scale, pale to dark brown and mottled with blackish flecks. Distinct, black dorsolateral stripes extend from above eye onto tail-base, where they merge creating a blackish, ragged-edged, median, tapering stripe on anterior half of tail. Inner margin of dark dorsolateral stripes ragged, interdigitating with paler vertebral zone. Prominent, narrow, pale grey to silvery laterodorsal stripes extend from above eye onto tail. Pale laterodorsal stripes usually smooth edged and without patterning, about half to two-thirds width of dorsolateral scale. Head concolorous with vertebral zone or coppery brown, usually with dark mottling on scales. Laterally patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Pale lower temporal region is flecked with dark spots and streaks. Labials cream to brown, patterned with fine dark margins to scales.

Flanks patterned with black upper lateral zone, similar in width to dark dorsolateral stripes, extending from loreals onto tail and forming a smooth outer border to pale laterodorsal stripes. Usually flecked with pale specks and spots, upper lateral zone is about two lateral scales wide and coalesces gradually into grey-brown lower lateral zone. Lower lateral zone peppered with small pale and/or dark spots and streaks and coalesces into pale venter. Tail concolorous with body, patterned with continuations of blackish dorsolateral and pale laterodorsal stripes. Limbs and toes concolorous with body, patterned with pale and dark speckling. Venter immaculate off-white. Palmar and plantar surfaces dark grey to dark brown, subdigital lamellae often blackish.

Comparison with Australian congeners. Fixed allelic differences place *C. pulcher* in lineage 2 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTUs virgA1 and virgB, Horner and Adams 2007).

Morphologically distinguished from lineage 1 members (*C. australis, C. buchananii, C. cygnatus* sp. nov., *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus, C. metallicus, C. ruber* and *C. wulbu* sp. nov.) by usually having five, rather than six, supraciliary scales and simple striped body pattern on a blackish ground colour.

Distinguished from lineage 2 congeners: *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. by having dark rounded, instead of pale acute, plantar scales and simple striped body pattern on a blackish ground colour; from *C. litoralis* and *C. gurrmul* sp. nov. by fewer mid-body scale rows (modally 24 versus 26–28) and paravertebral scales (modally 50 versus 55–57); from *C. fuhni, C. ustulatus* sp. nov. and *C. zoticus* sp. nov. by more paravertebral scales (modally 50 versus 45–46) and deeper head (mean 40.2 versus 32.5–36.1 % of head length). *Cryptoblepharus pulcher* is most similar to *C. adamsi* sp. nov. and *C. virgatus* in having combinations of simple striped body pattern, flat ovate plantar scales and being arboreal. However it differs from both by having dark plain plantar scales rather than pale callused plantars. Further differs from *C. adamsi* sp. nov. by having narrow smooth edged pale laterodorsal stripes instead of moderately broad, ragged edged stripes) and fewer fourth finger supradigital scales (modally 12 instead of 13) and from *C. virgatus* by having 24 midbody scale rows, instead of 22, more paravertebral scales (modally 50 instead of 47) and narrower paravertebral scales (mean % of SVL 4.2 instead of 4.5). Additionally, *C. pulcher* has a low number of lenticular scale organs (modally 4), all others except *C. buchananii* and *C. wulbu* sp. nov. (modally 4 and 3) have modal counts of five or higher.

Distribution. Far eastern Australia and far southern coastal regions of Western and South Australia (Fig. 109).

Habits and habitats. *Cryptoblepharus pulcher* occurs in a variety of woodland and open forest habitats. Normally arboreal, museum records note its use of tree trunks, palms and grass-tree trunks. Often associated with parkland adjoining beaches, it is a common commensal with man where records note its use of fences, walls and posts. It has been recorded from under rocks at Yalwal, NSW and Dalyup River, WA.

Subspecies. *Cryptoblepharus pulcher* is a polytypic taxon comprised of two allopatric subspecies: *Cryptoblepharus pulcher clarus*; *Cryptoblepharus pulcher pulcher*.

Cryptoblepharus pulcher clarus (Storr, 1961)

Bright snake-eyed skink

(Plate 3.1; Figs 109A-111)

Type material examined. *Ablepharus boutoni clarus* Storr, 1961. PARATYPE: QM J30921 (formerly WAM R18225), 23 km east of Esperance, 33°50'S 122°05'E, Western Australia, G. Storr, 9 December 1959.

Non-type material examined. See Appendix 4.

Diagnosis. As given above for species. Very similar to conspecific *C. p. pulcher* but distinguished by having more midbody scale rows (mean 24.6 instead of 23.2), fourth finger (mean 15.1 instead of 14.6) and toe subdigital lamellae (mean 18.9 instead of 18.1), plantar scales (mean 9.8 instead of 8.9) and generally broader pale laterodorsal stripes. In addition, *C. p. clarus* has an allopatric distribution apparently restricted to far southern regions of Western and South Australia (Fig. 109A) and may be further distinguished by two sexually dimorphic characters, where male *C. p. clarus* are larger than those of *C. p. pulcher* (mean SVL 36.1 instead of 33.7 mm) and female *C. p. clarus* have more paravertebral scales than those of *C. p. pulcher* (mean 50.2 instead of 48.4).

Fig. 110. Ventral surface of hind foot of *Cryptoblepharus pulcher clarus* showing dark, ovate plantar scales (NTM R22041, Smoky Bay, SA). Scale: x20.

With no fixed allelic differences, *C. p. clarus* is genetically similar to *C. p. pulcher*.

Description (31 specimens). As described above for species, except for the following variation. Prefrontals usually in broad contact (97%), occasionally in narrow contact (3%); enlarged upper ciliaries 3; loreals usually subequal (65%) or

Fig. 111. *Cryptoblepharus pulcher clarus.* NTM preserved material. **A.** = R22047, Deralinya, WA; **B**, R22058, Dalyup River, WA; **C**, R22040, Smoky Bay, SA; **D**, R22050, Dalyup River, WA; **E** and **F**, R22043 and R22042, Cocklebiddy, WA. Scale bar = 10 mm.

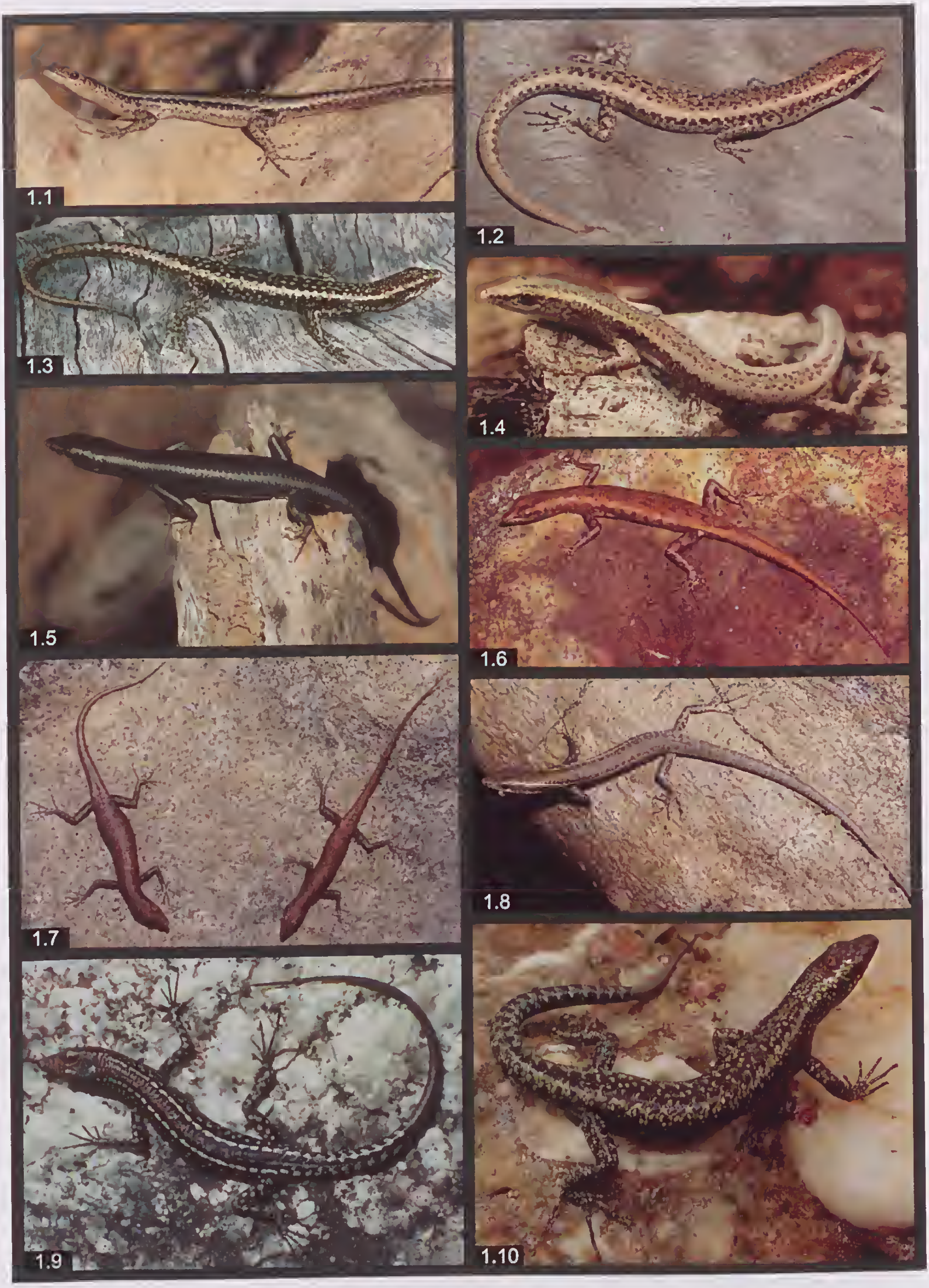

Plate 1: 1.1, *Cryptoblepharus adamsi* sp. nov., Bowen, Qld; **1.2**, *Cryptoblepharus australis*, Alice Springs, NT; **1.3**, *Cryptoblepharus buchananii*, Perth, WA, Photo G. Harold; **1.4**, *Cryptoblepharus cygnatus* sp. nov., Annaburroo, NT; **1.5**, *Cryptoblepharus cygnatus* sp. nov., melanistic specimen, NTM R16387, Darwin, NT; **1.6**, *Cryptoblepharus daedalus* sp. nov., NTM R25985, Jasper Gorge, NT; **1.7**, *Cryptoblepharus daedalus* sp. nov., Joe Creek, NT, Photo S. Swanson; **1.8**, *Cryptoblepharus exochus* sp. nov., NTM R24806, Mosquito Flat, Bradshaw Station, NT; **1.9**, *Cryptoblepharus fuhni*, Cape Melville, Qld, Photo S. Wilson; **1.10**, *Cryptoblepharus gurrmul* sp. nov., NTM R28475, North Goulburn Island, NT.

Plate 2: **2.1,** *Cryptoblepharus juno* sp. nov., NTM R16784, Dead Horse Spring, Lake Argyle, WA; **2.2,** *Cryptoblepharus litoralis horneri*, Truant Island, NT; **2.3,** Topotypic *Cryptoblepharus litoralis litoralis*, NTM R18895, Flying Fish Point, Qld; **2.4,** *Cryptoblepharus megastictus*, Mitchell Plateau, WA; **2.5,** *Cryptoblepharus mertensi* sp. nov., NTM R22644, Roper River, NT; **2.6.** *Cryptoblepharus metallicus*, Bowen, Qld; **2.7,** Topotypic *Cryptoblepharus metallicus*, NTM R28373, near Gregory's Tree, Timber Creek, NT; **2.8,** *Cryptoblepharus pannosus* sp. nov., NTM R26246, Brookfield, SA; **2.9,** *Cryptoblepharus pannosus* sp. nov., Westmar, Qld, Photo S. Swanson; **2.10,** *Cryptoblepharus plagiocephalus,* Zuytdorp Point, Shark Bay, WA, Photo G. Harold.

Plate 3: 3.1, Topotypic *Cryptoblepharus pulcher clarus*, NTM R22055, Dalyup River, WA; **3.2,** *Cryptoblepharus pulcher pulcher*, Trewantin, Qld; **3.3,** *Cryptoblepharus ruber*. NTM R27512, Mt Elizabeth Station, WA; **3.4,** *Cryptoblepharus ruber*. NTM R27511, Willare Bridge, Fitzroy River, WA; **3.5,** *Cryptoblepharus tytthus* sp. nov., NTM R27507, Willare Bridge, Fitzroy River, WA; **3.6,** *Cryptoblepharus ustulatus* sp. nov., Dales Gorge, WA, Photo G. Harold; **3.7,** *Cryptoblepharus ustulatus* sp. nov., Fortescue Falls, WA, Photo S. Swanson; **3.8,** *Cryptoblepharus virgatus*, Lions Den Hotel, Bloomfield Track. Qld; **3.9,** *Cryptoblepharus wulbu* sp. nov., NTM R26064, Mount Borradaile, NT; **3.10,** *Cryptoblepharus zoticus* sp. nov, NTM R26641, Kingfisher Camp, Nicholson River, Qld.

Plate 4: 4.1. *Cryptoblepharus baliensis baliensis,* deceased specimen, Bali Island, Indonesia, Photo K. Martin; **4.2,** Paratype of *Cryptoblepharus cursor larsonae* ssp. nov., NTM R21146, Samalona Island, off Ujung Pandang, south Sulawesi, Indonesia, Photo H. Larson; **4.3,** *Cryptoblepharus egeriae*, Christmas Island, Indian Ocean, Photo S. Donnellan; **4.4,** *Cryptoblepharus eximius*, Fiji, South Pacific Ocean, Photo S. Swanson; **4.5,** *Cyptoblepharus keiensis*, Cape Pattinson, Kai Islands, Indonesia, Photo S. Donnellan; **4.6,** *Cryptoblepharus novohebridicus*, Efate, Vanuatu. South Pacific Ocean; **4.7;** *Cryptoblepharus poecilopleurus paschalis*, Isla de Pascua (Easter Island), Chile, Photo A. Horner; **4.8,** *Cryptoblepharus poecilopleurus poecilopleurus*, Bora-Bora, French Polynesia, Photo I. Archibald; **4.9,** *Cryptoblepharus richardsi* sp. nov., Misima Island, Louisiade Archipelago, Papua New Guinea, Photo S. Richards; **4.10,** *Cryptoblepharus xenikor* sp. nov., Trans-Fly region, Papua New Guinea. Photo S. Richards.

posterior largest (32%), occasionally anterior (3%) largest; supralabials 6–7 (mean 6.9), modally 7; fifth supralabial usually subocular (97%), occasionally fourth (3%); nuchals 2–5 (mean 2.4), modally 2; bilateral posttemporals usually 2+2 (81%), occasionally 2+3 (16%), or 3+3 (3%).

Midbody scale rows 24–26 (mean 24.6), modally 24; paravertebrals 45–55 (mean 49.5), modally 50; subdigital lamellae smooth, 14–17 below fourth finger (mean 15.1) modally 15, 17–21 below fourth toe (mean 18.9) modally 19; 12–13 supradigital lamellae above fourth finger (mean 12.3) modally 12, 14–17 above fourth toe (mean 15.6) modally 16; palmar and plantar scales rounded, without calli and skin visible between scales (Fig. 110); plantars 8–12 (mean 9.8), modally 10; palmars 6–9 (mean 7.6), modally 8.

Snout-vent length to 40.6 mm (mean 36.7 mm). *Percentages of snout-vent length*: body length 47.2–56.9% (mean 50.9%); tail length 113.9–129.0% (mean 121.8%); forelimb length 29.3–36.3% (mean 32.3%); hindlimb length 36.1–45.0% (mean 40.5%); forebody length 36.6–46.4% (mean 40.9%); head length 18.8–22.6% (mean 20.3%). *Percentages of head length*: head depth 32.9–53.4% (mean 39.8%); head width 58.8–71.9% (mean 65.2%); snout length 42.1–48.4% (mean 45.1%). Paravertebral scale width 3.4–4.8% (mean 4.0%) of snout-vent length; dorsolateral scale width 71.4–100.8% (mean 88.2%) of paravertebral scale width.

Details of paratype. QM J30921. Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; loreals subequal; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 5. Midbody scale rows 24; paravertebrals 48; subdigital lamellae smooth, 16 below fourth finger; 19 below fourth toe; supradigital lamellae 12 above fourth finger; 14 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 10; palmars 7. Snout-vent length 39.3 mm; body length 21.2 mm; tail not original; forelimb length 11.8 mm; hindlimb length 16.1 mm; forebody length 15.7 mm; head length 7.6 mm; head depth 3.3 mm; head width 4.9 mm; snout length 3.5 mm.

Colouration and pattern. As described above for species (see Plate 3.1, Fig. 111). In many specimens the pale laterodorsal stripes are slightly broader with a more ragged outer margin than those of *C. p. pulcher*.

Sex ratio and reproductive biology. Sex ratio favoured females (19:12), but was not significantly different from parity ($X^2 = 0.20$). Of the samples examined ten were reproductively active (5 ♂, 5 ♀), nine of which were collected in December and one in January, indicating they may breed during summer months.

Distribution. Far south western Australia (Fig. 109A), occupying the coast and hinterlands of southern Western Australia and western South Australia. Ranges from Wardang Island and southern Yorke Peninsula in South Australia to about Ravensthorpe in Western Australia.

Sympatry. None recorded.

Geographic variation. Geographic variation was investigated by dividing specimens into two groups: *WA*, a Western Australian group of 25 (8 ♂, 17 ♀) samples from bioregions ESP, HAM and MAL; *SA*, a South Australian group of 6 (4 ♂, 4 ♀) from bioregion EYB.

ANOVA tests of all morphological characters failed to identify any significant differences between Western and South Australian populations of *C. p. clarus*.

Habits and habitats. As for species. Topotypic specimens at Dalyup River WA were abundant on dead timber and under rocks by a section of disused highway (pers. obs.). Inactive specimens have been taken from cracks within branches of standing dead timber at Smoky Bay, SA (pers. obs.).

Taxonomic history. Storr's (1961) description of *Ablepharus boutonii clarus* was based on the distinctive striped body pattern of southern Western Australia (Esperance) populations, in comparison to other Western Australian populations of *Cryptoblepharus* which, at the time, were all considered *C. plagiocephalus*. In his description, Storr noted the similarity of *clarus* to geographically distant *virgatus* and commented that a specimen from Hornsby, NSW (described in Loveridge 1934) probably belonged to a form intermediate between the two.

Cryptoblepharus pulcher pulcher (Sternfeld, 1918)

Elegant snake-eyed skink

(Plate 3.2; Figs 109, 112–115; Table 10)

Type material examined. *Ablepharus boutoni pulcher* Sternfeld, 1918. LECTOTYPE: SMF 15680, Neuholland, coll. von Pöehl, Hamburg, 1887. *Cryptoblepharus suburbia* Wells and Wellington, 1985. HOLOTYPE: AM R116951 (field no. 28471, in description), Sydney, New South Wales, coll. R. Wells.

Non-type material examined. See Appendix 4.

Diagnosis. As given above for species. Very similar to conspecific *C. p. clarus* but distinguished by having fewer midbody scale rows (mean 23.2 instead of 24.6), fourth finger (mean 14.6 instead of 15.1) and toe subdigital lamellae (mean 18.1 instead of 18.9), plantar scales (mean 8.9 instead of 9.8) and generally narrower pale laterodorsal stripes. In addition, *C. p. pulcher* has an allopatric distribution apparently restricted to eastern regions of Queensland and New South Wales (Fig. 109B) and may be further distinguished by two sexually dimorphic characters, where male *C. p. pulcher* are smaller than those of *C. p. clarus* (mean SVL 33.7 instead of 36.1 mm) and female *C. p. pulcher* have fewer paravertebral scales than those of *C. p. clarus* (mean 48.4 instead of 50.2).

With no fixed allelic differences, *C. p. pulcher* is genetically similar to *C. p. clarus*.

Description (48 specimens). As described above for species, except for the following variation. Prefrontals usually in broad contact (98%), occasionally in narrow contact (2%); enlarged upper ciliaries 2–4 (mean 3.0), modally 3; loreals usually subequal (65%) or anterior largest (29%),

Fig. 112. Ventral surface of hind foot of *Cryptoblepharus pulcher pulcher* showing dark, ovate plantar scales (NTM R18991, Gympie, Qld). Scale: x20

Fig. 113. Lectotype of *Ablepharus boutoni pulcher* Sternfeld, 1918. SMF 15680, Australia.

Fig. 114. *Cryptoblepharus pulcher pulcher*. NTM preserved material. **A**, **B** and **C**, R23746, R23691 and R23690, Sydney, NSW; **D**, R18951, Mackay, Qld; **E**, R18980, Tannum Sands, Qld; **F**, R23751, Yalwal, NSW. Scale bar = 10 mm.

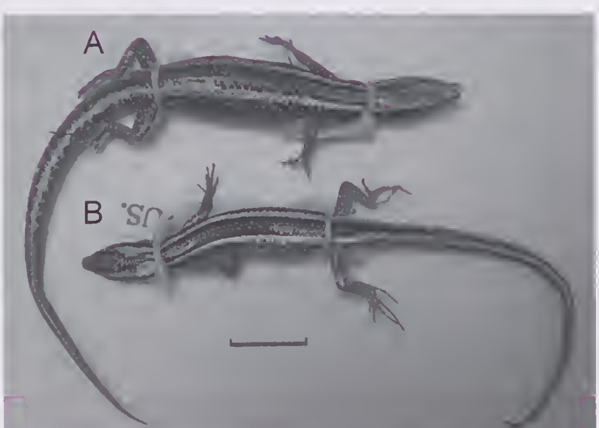

Fig. 115. Examples of genetic OTU virgA1x3, a hybrid of *C. pulcher pulcher* x *C. adamsi* sp. nov. (**A** = NTM R18931, Dingo Beach, Qld; **B** = NTM R18949, Airlie Beach, Qld). Scale bar = 10 mm.

occasionally posterior (6%) largest; supralabials 6–8 (mean 7.0), modally 7; fifth supralabial usually subocular (89%), occasionally sixth (7%) or fourth (4%); nuchals 2–6 (mean 2.4), modally 2; bilateral posttemporals usually 2+2 (90%), occasionally 2+3 (10%).

Midbody scale rows 22–26 (mean 23.2), modally 24; paravertebrals 42–53 (mean 48.2), modally 47; subdigital lamellae smooth, 12–16 below fourth finger (mean 14.6) modally 15, 16–22 below fourth toe (mean 18.2) modally 19; 11–14 supradigital lamellae above fourth finger (mean 12.4) modally 13, 14–18 above fourth toe (mean 15.8) modally 16; palmar and plantar scales rounded, without calli and skin visible between scales (Fig. 112); plantars 7–11 (mean 8.9), modally 8.9; palmars 6–9 (mean 8.0), modally 8.

Snout-vent length to 41.7 mm (mean 34.9 mm). *Percentages of snout-vent length*: body length 44.5–55.9% (mean 51.2%); tail length 114.4–142.3% (mean 128.9%); forelimb length 28.7–36.6% (mean 32.1%); hindlimb length 35.6–47.0% (mean 40.4%); forebody length 36.7–44.5% (mean 41.3%); head length 17.8–21.8% (mean 19.7%). *Percentages of head length*: head depth 29.2–45.1% (mean 38.9%); head width 55.0–70.5% (mean 61.9%); snout length 41.9–49.7% (mean 44.9%). Paravertebral scale width 3.2–5.1% (mean 4.0%) of snout-vent length; dorsolateral scale width 79.7–107.3% (mean 92.9%) of paravertebral scale width.

Details of primary types. *Ablepharus boutoni pulcher* Sternfeld, 1918. LECTOTYPE: SMF 15680 (Fig. 113). Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; loreals subequal; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 24; paravertebrals 46; subdigital lamellae smooth, 14 below fourth finger; 19 below fourth toe; supradigital lamellae 12 above fourth finger; 15 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 10; palmars 9. Snout-vent length 38.9 mm; body length 19.2 mm; tail not original; forelimb length 11.9 mm; hindlimb length 14.6 mm; forebody length 14.9 mm; head length 7.3 mm; head depth 3.3 mm; head width 4.6 mm; snout length 3.1 mm.

Cryptoblepharus suburbia Wells and Wellington, 1985. HOLOTYPE: AM R116951. Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; loreals subequal; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 4. Midbody scale rows 22; paravertebrals 47; subdigital lamellae smooth, 16 below fourth finger; 18 below fourth toe; supradigital lamellae 13 above fourth finger; 15 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 8; palmars 8. Snout-vent length 35.1 mm; body length 18.3 mm; tail length 46.5 mm; forelimb length 10.8 mm; hindlimb length 14.1 mm; forebody length 14.0 mm; head length 6.7 mm; head depth 2.7 mm; head width 4.6 mm; snout length 3.3 mm.

Colouration and pattern. As described above for species (see Plate 3.2 and Fig. 114). In many specimens the pale laterodorsal stripes are slightly narrower with a smoother outer margin than those of *C. p. clarus*.

Sex ratio and reproductive biology. Sex ratio favoured females (19:12), but was not significantly different from parity ($X^2 = 0.60$). Of the samples examined 47 were reproductively active (24 ♂, 23 ♀), 42 of which were collected in January, additional reproductives were collected in April (2 ♂) and September (2 ♂, 1 ♀).

Distribution. Far eastern Australia (Fig. 109B), ranging from about Ingham in far north-eastern Queensland to about Jervis Bay, on the south coast of New South Wales and inland as far as Rolleston and Alton Downs in Queensland, Kandos and Wombeyan Caves in New South Wales.

Sympatry. *Cryptoblepharus p. pulcher* occurs in sympatry with *C. metallicus* from lineage 1, *C. adamsi* sp. nov., *C. l. litoralis* and *C. pannosus* sp. nov. from lineage 2 (Table 10).

Geographic variation. Geographic variation was investigated by dividing specimens into three groups: *North*, a northern group of 8 (5 ♂, 3 ♀) samples from bioregions BBN and CMC; *Central*, a central group of 28 (14 ♂, 14 ♀) samples from bioregions BBS and SEQ; *South*, a southern group of 12 (5 ♂, 7 ♀) samples from bioregions NET and SB.

ANOVA tests of all morphological characters failed to identify any significant differences between northern populations and those from the central and southern groups. Significant differences were detected between males of the central and southern groups, but not females. Differentiation was due to southern males having longer limbs than those of the central group (mean % of SVL: FL 33.8 versus 32.4%; RL 44.2 versus 41.1%).

Table 10. List of congeners sympatric with *Cryptoblepharus pulcher pulcher*, giving areas of sympatry.

Congeners sympatric with *Cryptoblepharus pulcher pulcher*	Area of sympatry
C. adamsi sp. nov.	Qld: Mount Larcom
C. l. litoralis	Qld: Airlie Beach, Cape Hillsborough, Dingo Beach, Emu Park, Hayman Island, Hinchinbrook Island, North Keppel Island, Townsville
C. metallicus	Qld: Bluff Mtn nr Biggenden, Clairview, Dingo Beach, Magnetic Island, Moura, Powlathanga Stn, Theodore, Warrawee Stn, Rowes Bay
C. pannosus sp. nov.	Qld: Ravenswood, 8 km N of Wyberba

These results suggest that geographic variation in *C. p. pulcher* is limited to males of southern populations having longer limbs than those of populations from central parts of its range.

Hybrid zone. The taxon 'OTU virgA1x3' (Fig. 115) was determined by allozyme analysis as being of *C. pulcher pulcher* x *C. adamsi* sp. nov. hybrid origin (Horner and Adams 2007). *Cryptoblepharus pulcher pulcher* and *C. adamsi* sp. nov. were genetically distinguished from each other by three fixed allelic differences at loci *Acyc, Got-2* and *PepA-2*, with OTU virgA1x3 being intermediate between them at those loci (Horner and Adams 2007). OTU virgA1x3 was identified from eight individuals from mid-coastal Queensland, five from the Whitsunday region (NTM R18931-33, R18938, Dingo Beach; NTM R18949, Airlie Beach) and three (QM J48420–21, J48423) from Townsville. Genetically determined *C. p. pulcher* occur at Airlie Beach (NTM R18927-28) and *C. adamsi* sp. nov. at 5.4 kilometres west of Dingo Beach (NTM R18937-38). Thus, the hybrid zone falls within the distribution of both *C .p. pulcher* and *C. adamsi* sp. nov. Morphological analysis was limited by the small sample size of hybrids, however in an analysis of group pairs of both sexes combined, *C. p. pulcher* and *C. adamsi* sp. nov. were distinguished by six significant differences, while OTU virgA1x3 was distinguished from *C. p. pulcher* by number of posterior temporal scales (mean 2.4 versus 2.0), plantar pigmentation, condition of pale laterodorsal stripes and plantar scales, and from *C. adamsi* sp. nov. by only forebody length (mean 16.2 versus 15.3 mm) and plantar pigmentation.

Viability of the hybrids is unknown, though both sexes were represented in the allozyme identified sample. The female (NTM R18931) was gravid with two well-developed eggs (Fig. 115A). Pending further study, OTU virgA1x3 was recognised as arising from hybridisation between *C. p. pulcher* and *C. adamsi* sp. nov. Extent of the hybrid zone is unknown, but herein is assumed limited to the general region between the Whitsunday coast and Townsville, north-east Queensland. Morphologically, OTU virgA1x3 cannot be reliably recognised from either parent stock, though relatively smooth edged, pale dorsolateral stripes align it most closely with *C. p. pulcher*.

Habits and habitats. As for species. Greer (1989) records *C. p. pulcher* (as *C. virgatus*) utilising piracy when feeding, standing just outside columns of foraging ants and dashing in to snatch food morsels from burdened worker ants. Additionally, Greer and Jeffreys (2001) record *C. p. pulcher* (as *C. virgatus*) preying on swarming winged ants as they disperse from their home nest. In this situation only the alates were targeted, with worker ants being carefully avoided.

Reproductive behaviour was recorded by Stammer (1988), who noted use of a brick-wall, and its inner cavity, as a "nursery" and egg-laying area over four successive years. Observed in Cronulla, a suburb of Sydney, the maximum number of hatchlings sighted by Stammer (1988) in any one year was five, suggesting that more than one female had used the oviposition site. Juveniles were only observed within the summer months of November to March, with hatchings estimated to have taken place during each of these months.

Taxonomic history. Richard Sternfeld (1918) described *Ablepharus boutoni pulcher* from two Senckenberg Museum specimens (No. 6347, two examples) supplied by C. Poehl in 1887. Sternfeld gave the type locality as simply "Neuholland", and diagnosed the taxon by "..b) Schuppen in 22–24 Reihen. Oberseite schhön rotbraun, die Dorsolateralstreifen silberweiß, auf dem Halse zu einer dünnen Linie verschmälert, nach hinten zu allmählich wieder breiter werdend; die hellen Streifen mehr oder weniger scharf schwarz begrenzt. Schnauze außergewöhnlich kurz". (" Scales in 22–24 rows. Upper side beautifully bay, dorsolateral stripes silver, narrowing on the neck to a thin painted line, gradually becoming wide again on the back; the light stripes more or less keenly black edged. Snout exceptionally short"). Post description, the two syntypes have been allocated new SMF catalogue numbers and are now labelled SMF 15680 and 15681.

Mertens (1931) placed *A. b. pulcher* in the synonymy of *A. b. virgatus*, and in a later work (Mertens 1967) designated SMF 15680 as lectotype. Though the type locality of *A. b. pulcher* is simply 'Australia', the lectotype has narrow silvery dorsolateral stripes (Fig. 113) typical of eastern *C. pulcher* and most likely was collected from mid-coastal eastern Australia.

Wells and Wellington (1985), in their controversial classification of Australian amphibians and reptiles, did not mention *A. b. pulcher* but described a new taxon from the Sydney region, *Cryptoblepharus suburbia*. Diagnosis of this taxon was based on a description of the holotype and references to previous works and illustrations. *Cryptoblepharus suburbia* was placed in the synonymy of *C. virgatus* by Shea and Sadlier (1999), but herein is transferred to the synonymy of *C. pulcher pulcher*.

Cryptoblepharus ruber Börner and Schüttler, 1981

Tawny snake-eyed skink

(Plates 3.3–3.4; Figs 116–119; Table 11)

Ablepharus boutoni plagiocephalus (Cocteau, 1836). – Mertens 1964: 107.

Cryptoblepharus plagiocephalus (Cocteau, 1836). – Storr and Smith 1975: 86; Storr 1976: 56; Smith and Johnstone 1978: 43; Storr *et al.* 1999: 24; Smith and Johnstone 1981: 222; Cogger *et al.* 1983a: 142; Wilson and Knowles 1988: 120; Kendrick and Rolfe 1991: 351; Ehmann 1992: 182; Horner 1991: 18; Cogger 2000: 406; Bush *et al.* 1995: 112, Fig. page 112; Stanger *et al.* 1998: 23; Wilson and Swan 2003: 148.

Cryptoblepharus plagiocephalus ruber Börner and Schüttler, 1981: 4.

Cryptoblepharus ruber Börner and Schüttler, 1981. – Wells and Wellington 1985: 27.

Fig. 116. Ventral surface of hind foot of *Cryptoblepharus ruber*, showing callused, pale, ovate plantar scales (NTM R24775, Bradshaw Station, NT). Scale: x20.

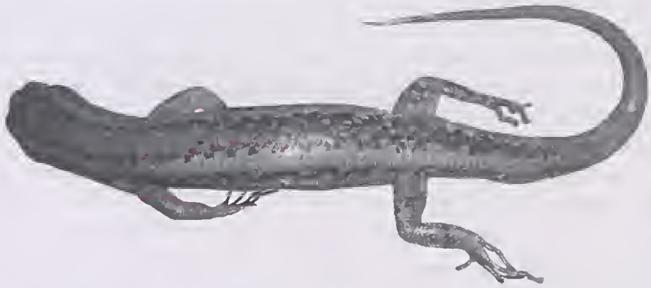

Fig. 117. Holotype of *Cryptoblepharus plagiocephalus ruber*, SMF 32823, Kalindi Grotto, Bachsten Creek, WA.

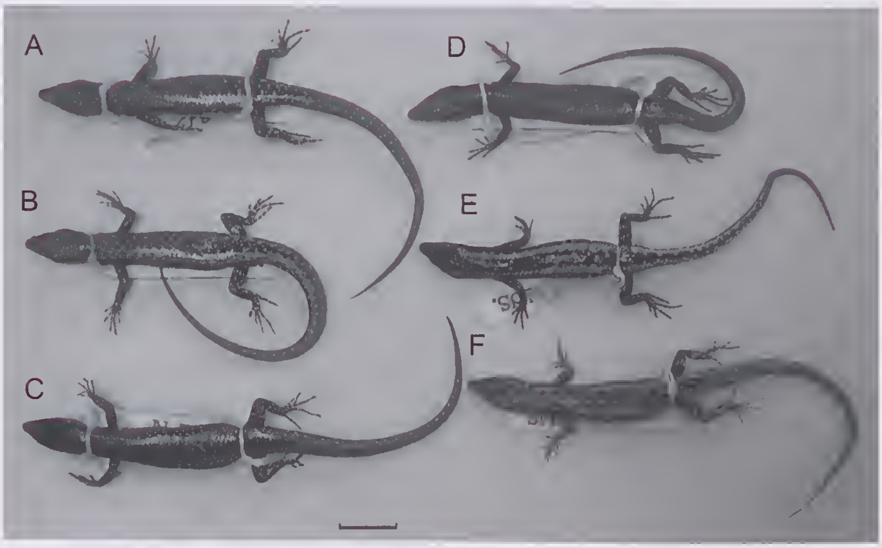

Fig. 118. *Cryptoblepharus ruber*: NTM preserved material. **A**, R23669, Brandy Bottle Creek, NT; **B**, R20841, Keep River, NT; **C**, R22352, Keep River, NT; **D**, R22083, Broome, WA; **E**, R22529, Mt. Elizabeth Station, WA; **F**, R22522, Mitchell Falls, WA. Scale bar = 10 mm.

Type material examined. *Cryptoblepharus plagiocephalus ruber* Börner and Schüttler, 1981. HOLOTYPE: SMF 32823, Kalindi Grotto, Bachsten Creek, north-west Australia, coll. A. Schulz, 10 August 1938.

Non-type material examined. See Appendix 4.

Diagnosis. A large (45–50 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of six supraciliary scales, 24 mid-body scale rows and 54 paravertebral scales; mean values of hindlimb length 40.9% of SVL, head depth 41.1% of head length, tail length 132.6% of SVL; smooth subdigital lamellae; rounded, usually callused plantar scales; greyish, longitudinally aligned body pattern and being arboreal.

Description (31 specimens). Postnasals absent; prefrontals usually in broad contact (97%), occasionally in narrow contact (3%); supraciliaries 6–7 (mean 6.0), modally 6; enlarged upper ciliaries 3; posterior loreal largest (84%), occasionally subequal (16%); supralabials 6–8 (mean 7.0), modally 7; fifth supralabial usually subocular (95%), occasionally fourth (3%) or sixth (2%); infralabials 6; nuchals usually 2 (91%), occasionally 3 (3%) or 4 (6%); bilateral posttemporals usually 3+3 (91%), occasionally 2+3 (6%), or 2+2 (3%).

Midbody scale rows 23–26 (mean 24.5), modally 24; paravertebrals 45–56 (mean 52.3), modally 54; subdigital lamellae smooth, 14–18 below fourth finger (mean 15.7) modally 16, 17–21 below fourth toe (mean 18.8), modally 18; 12–16 supradigital lamellae above fourth finger (mean 13.1) modally 13, 14–19 above fourth toe (mean 15.7), modally 15; palmar and plantar scales rounded, usually capped with shiny, dark brown calli (Fig. 116), skin usually visible between scales; plantars 8–11 (mean 9.2), modally 9; palmars 6–9 (mean 7.8), modally 8.

Snout-vent length to 47.2 mm (mean 40.9 mm). *Percentages of snout-vent length*: body length 39.8–58.3% (mean 51.4%); tail length 114.4–168.3% (mean 132.6%); forelimb length 27.1–39.8% (mean 33.5%); hindlimb length 34.0–44.8% (mean 40.9%); forebody length 36.4–47.2% (mean 42.1%); head length 18.7–22.9% (mean 20.8%).

Percentages of head length: head depth 34.0–49.3% (mean 41.1%); head width 55.3–68.4% (mean 61.5%); snout length 41.1–48.0% (mean 44.7%). Paravertebral scale width 3.1–4.6% (mean 4.0%) of snout-vent length; dorsolateral scale width 78.5–105.5% (mean 90.7%) of paravertebral scale width.

Lenticular scale organs 4–15 (mean 8.6), modally 9. Premaxillary teeth 5; maxillary teeth 21–22; mandibular teeth 25. Hemipenis: length 5.6–8.1% (mean 6.9%) of snout-vent length; width 67.3–96.4% (mean 79.9%) of hemipenis length; trunk 39.1–56.6% (mean 50.9%) of hemipenis length.

Details of holotype. SMF 32823 (Fig. 117). Postnasals absent; prefrontals in broad contact; supraciliaries 6; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 26; paravertebrals 51; subdigital lamellae smooth, 15 below fourth finger; 18 below fourth toe; supradigital lamellae 13 above fourth finger; 16 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 9; palmars 8. Snout-vent length 40.4 mm; body length 21.2 mm; tail not original; forelimb length 13.8 mm; hindlimb length 18.2 mm; forebody length 17.6 mm; head length 8.9 mm; head depth 4.1 mm; head width 5.8 mm; snout length 4.0 mm.

Colouration and pattern. Greyish or brownish, with longitudinally aligned, complex body pattern dominated by broad, dark vertebral zone and pale laterodorsal zones/stripes (Plates 3.3 and 3.4). Intensity of body pigmentation and patterning is variable, both individually and geographically, ranging from pale and obscure to dark and prominent (Plates 3.3 and 3.4, Fig. 118A–F). Most specimens conform to the following description.

Dorsal ground colour grey or grey-brown, with broad, dark vertebral zone extending from above eye to hindlimb. Vertebral zone as wide as paired paravertebral scales, dark grey to dark brown, peppered with pale spots and/or specks and dotted with short longitudinal black streaks and spots. The latter are often prominent on outer edges of paravertebral scales, forming two narrow, broken black stripes from neck to tailbase, where they merge creating a blackish median, tapering stripe on anterior third of tail. Pale grey to pale brown laterodorsal zones extend from above eye onto tail, broadest on posterior half of body, about half width of dark vertebral zone, tapering anteriorly into prominent narrow stripes to eye, and posteriorly to form tail ground colour. Edges of pale laterodorsal zones usually ragged, interdigitating with broken dark paravertebral stripes and dark upper lateral zone. Laterodorsal zones usually uniform, but may have fine pale and/or dark speckling. Head concolorous with vertebral zone or coppery brown, with fine dark margins to scales. Laterally patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Pale lower temporal region is flecked with dark spots and streaks. Labials pale cream.

Laterally, a dark upper zone, variable in width, extends from loreals onto tail, forming a ragged border to pale dorsolateral zone. Flecked with pale specks and short streaks, upper lateral zone may be represented by narrow broken black stripe but usually is about two lateral scales wide and coalesces gradually into pale grey/pale grey-brown lower lateral zone. Lower lateral zone is peppered with small pale and/or dark spots and streaks and coalesces into pale venter. Tail concolorous with body, patterned with broken continuations of blackish vertebral and upper lateral zones. Limbs and toes concolorous with body, patterned with pale and dark speckling. Ventral surface immaculate off-white. Palmar and plantar scales off-white, most capped with dark brown calli.

Sex ratio and reproductive biology. Sex ratio favoured males (17:14), but was not significantly different from parity ($X^2 = 0.28$). Males mature at about 36 mm snout-vent length and females at 38 mm. Adults average 40.9 mm snout-vent length and females are larger than males (maximum SVL = 47.2 versus 45.4 mm). Samples were mostly non-reproductive, though collection of a gravid female (NTM R22518, Jacks Hole WA) in July indicates breeding may take place during the monsoonal dry season.

Comparison with Australian congeners. Fixed allelic differences place *C. ruber* in lineage 1 of Australian *Cryptoblepharus* and also distinguish it from most congeners within that lineage (as OTUs plagA1, plagA2 and plagA3, Horner and Adams 2007). With no fixed allelic differences, *C. ruber* is genetically similar to *C. megastictus* (as OTUs plagA2 and megaA4, Horner and Adams 2007).

Morphologically distinguished from lineage 2 members *C. adamsi* sp. nov., *C. fuhni*, *C. gurrmul* sp. nov., *C. litoralis*, *C. pulcher*, *C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov. by usually having six, rather than five, supraciliary scales and complex body pattern on a grey or brown ground colour and from *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. by usually having six, rather than five, supraciliary scales and ovate, instead of acute, plantar scales.

Distinguished from lineage 1 congeners *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus* and *C. wulbu* sp. nov. by ground colour and body pattern characteristics (greyish, longitudinally aligned pattern versus reddish, randomly speckled or blotched pattern), by being arboreal rather saxicoline and by fewer mid-body scale rows (modally 24 versus 26), deeper head (mean 41.1 versus 32.5–36.0 % of SVL), and shorter hindlimbs (mean 40.9 versus 44.6–47.3 % of SVL.

Cryptoblepharus ruber is most similar to *C. buchananii*, *C. cygnatus* sp. nov. and *C. metallicus* in having combinations of complex body patterns, flat ovate plantar scales, usually six supraciliary scales and being arboreal. However, it differs from *C. cygnatus* sp. nov. in having smooth instead of callused subdigital lamellae, callused instead of smooth plantar scales, more paravertebral scales (modally: 54 versus

Table 11. List of congeners sympatric with *Cryptoblepharus ruber*, giving areas of sympatry.

Congeners sympatric with *Cryptoblepharus ruber*	Area of sympatry
C. exochus sp. nov.	NT :Spirit Hills
C. juno sp. nov.	WA: Lake Argyle, Old Argyle Downs
C. megastictus	WA: Mitchell Plateau
C. metallicus	WA: Kununurra
C. tytthos sp. nov.	WA: Broome, Coulomb Point, Derby, Old Cherabun, Willare bridge
Multiple sympatry	
C. exochus sp. nov. + *C. metallicus* + *C. juno* sp. nov.	NT: Bradshaw Stn
C. mertensi sp. nov. + *C. metallicus*	NT: Roper River

49) and fewer plantar scales (modally: 9 versus 11). Differs from *C. buchananii* in having more fourth finger subdigital lamellae (modally: 16 versus 14), fewer palmar scales (modally: 9 versus 10) and a shorter, wider head (mean HL 20.8 instead of 21.2% of SVL; mean HW 61.5 instead of 59.8% of head length). Differs from *C. metallicus* in having more paravertebral (modally 54 versus 48) and posterior temporal scales (modally: 3 versus 2), shorter tail (mean % of SVL 132.6 instead of 144.2) and larger size (mean SVL 40.9 instead of 38.6 mm).

Notwithstanding allozymic similarity (Horner and Adams 2007), comparison of 31 *C. ruber* to nine *C. megastictus* identified the following morphological differences: midbody scale rows (modally 24 versus 26), paravertebral scales (modally 54 versus 45), snout-vent length (mean 41 versus 35 mm), head depth (mean 41 versus 32 % of head length) and condition of plantar scales (callused instead of plain). They also differ in ground colour and body pattern characteristics.

Distribution. North-western and mid-northern Australia, from the Roper River region, western Gulf of Carpentaria, through mid-northern Northern Territory to northern parts of Western Australia (Fig. 119).

Sympatry. *Cryptoblepharus ruber* occurs in sympatry with *C. juno* sp. nov., *C. megastictus* and *C. metallicus* from lineage 1, *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. tytthos* sp. nov. from lineage 2 (Table 11).

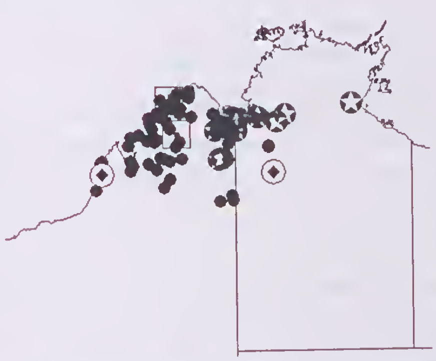

Fig. 119. Map of north-western Australia showing distribution of *Cryptoblepharus ruber*. Circled diamonds indicate collection localities of genetically identified OTU plagA1, open squares indicate OTU plagA2, circled stars indicate OTU plagA3 (Horner and Adams 2007).

Geographic variation. Geographic variation was investigated by dividing specimens into four disparate groups: *DL*, a western group of four (2 ♂, 2 ♀) samples from bioregion DL; *NK*, a north-western group of five (3 ♂, 2 ♀), composed of samples from bioregion NK; *OVP*, a central group of five (4 ♂, 1 ♀), composed of samples from bioregions CK, GUC and OVP; *VB*, a north-eastern group of 17 (8 ♂, 9 ♀), composed of samples from bioregion VB.

Group pairs, where sexes were treated separately and combined, were analysed by tests of all variables. When specimens were combined significant differences were detected only in head width between *DL* and *NK*, *OVP* and *VB*, and body length between *NK* and *OVP* and *VB*. These differences were not significant when sexes were analysed separately. These results indicate that geographic variation in the morphology of *C. ruber* was not significant.

Though morphologically homogeneous, *C. ruber* shows considerable genetic diversity. As detailed in Horner and Adams (2007), analysis of allozyme data separated the taxon into three distinct OTUs (plagA1, plagA2 and plagA3) each distinguished by two fixed allelic differences. Unable to be morphologically, ecologically or geographically differentiated for species diagnoses, descriptions and keys these OTUs were merged, although it is recognised that the resulting species, *C. ruber*, represents a complex of morphologically indeterminate taxa.

Habits and habitats. *Cryptoblepharus ruber*'s geographic range encompasses a variety of habitats. Typically arboreal, museum records note its occurrence in open woodland, grassland with scattered trees, riparian, parkland and urban habitats. Within these it has been associated with numerous tree and/or shrub species, including *Excoecaria parvifolia*, *Melaleuca* sp., *Lophostemon* sp. *Eucalyptus rudis* and *Casuarina* sp. In urban environments it has been observed in parkland, on fences and on palm trunks. Smith and Johnstone (1981) note the use of sandstone and laterite, as well as tree trunks.

Taxonomic history. Börner and Schüttler (1981) described *Cryptoblepharus plagiocephalus ruber* from a single specimen (SMF 32823) collected at Kalindi Grotto, Bachsten Creek, northwest Australia. They distinguished the taxon from "*C. plagiocephalus*" (= *C. metallicus*) solely on colour and pattern, citing coppery head and neck, broad vertebral zone and tan, sharply delineated, 'supraciliary'

(= laterodorsal?) stripes. Cogger *et al*. (1983a) placed *C. plagiocephalus ruber* in the synonymy of *C. plagiocephalus*. Wells and Wellington (1985), without comment or justification, elevated the taxon to species status, naming it *C. ruber*.

Cryptoblepharus tytthos sp. nov.

Pygmy snake-eyed skink

(Plate 3.5; Figs 120–123)

Cryptoblepharus carnabyi Storr 1976: 60.

Type material examined. *Cryptoblepharus tytthos* Horner. HOLOTYPE: Adult female, NTM R25994 (Tissue sample No. ABTC EV5), Coulomb Point, 70 km north of Broome, Western Australia, 17°23'07"S 122°09'42"E. coll. P. and D. Horner, 28 June 2000. Lophostemon forest, dense shrubland on sandy soil, on tree trunk. PARATYPES (33 specimens): WESTERN AUSTRALIA: WAM R46117, 24 km SSW of Christmas Creek, L. Smith et al., 19°05'S 125°48'E, 17 April 1974; WAM R51233, Old Cherrabun, 18°29'S 125°19'E, 16 July 1975; WAM R58497, Martins Well, 16°34'S 122°51'E, 26 April 1977; WAM R75829, Anna Plains, 19°15'S 121°29'E, M. Bamford, 28 August 1981; NTM R7099, Broome,17°58'S 122°19'E, G. Gow, et al., 11 June 1979; WAM R114244, 9 km NE of Broome, 17°54S 122°16E, ABTC R114244; QM J30936-937, Coulomb Point, 17°21'S 122°09'E, H. Butler, July 1971 (also paratypes of C. carnabyi Storr, 1976); WAM R114246, Coulomb Point Nature Reserve, 17°18'S 122°18E, ABTC R114246; WAM R40263, Coulomb Point, 17°22'S 122°09'E, H. Butler, July 1971; WAM R58468, 7 km NNE of Coulomb Point, 17°19'S 122°12'E, 14 April 1977; WAM R73894, Coulomb Point, 17°21'S 122°09'E. J. Rolfe, 17 June 1981; NTM R25995-997, Coulomb Point, 17°23'07"S 122°09'42"E, P. Horner, 28 June 2000, ABTC EV6- EV8; WAM R114224, Cape Leveque, 16°23'S 122°55'E, ABTC R114224; WAM R19914, Derby, 17°18'S 123°37'E, W. Dawson, 22 May 1963; WAM R22331, Derby, 17°18'S 123°37'E, G. Beamish, 2 May 1964; WAM R23004, Derby, 17°18'S 123°37'E, G. Storr et al., 1 September 1964; WAM R23006, 8 km S of Derby, 17°23'S 123°39'E, G. Storr et al., 1 September 1964; SAM R53908, Willare Bridge, 71 km SW of Derby, 17°43'S 123°38'E, ABTC R53908; SAM R53888-889, 16 km N of Windjana Gorge, 17°21'S 124°51'E, ABTC R53888-889; NTM R7268, 79 km SE of Fitzroy Crossing, 18°48'S 125°53'E, G. Gow, et al., 21 June 1979; NTM R7269-270, 50 km SE Fitzroy Crossing, 18°38'S 125°47'E G. Gow, et al., 21 June 1979; NTM R22086-088, 38 km SE of Fitzroy Crossing, 18°27'05"S 125°45'16"E, P. Horner, 24 January 1996, ABTC Y56-Y57; QUEENSLAND: SAM R14760 A-D, Mornington Island, Qld, 16°33'S 139°24'E, P. Aitken and N. Tindale, May 1963.

Diagnosis. A small (<40 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of five supraciliary scales, 24 mid-body scale rows, 48 paravertebral scales, 11 plantar scales, 15 fourth finger subdigital lamellae and 18 fourth toe subdigital lamellae; mean values of 31.3 mm snout-vent length, head depth 40.6% of head length, forelimb length 32.2% of snout-vent length, 15.5 maxillary and 17.5 mandibular teeth; strongly keeled fourth toe subdigital lamellae; pale, acute plantar scales, and narrow, obscure, pale dorsolateral stripes.

Description (34 specimens). Postnasals absent; prefrontals usually in broad contact (96%), occasionally narrowly separated (4%); supraciliaries 5–6 (mean 5.0), modally 5; enlarged upper ciliaries 3–4 (mean 3.0), modally 3; loreals usually subequal (73%), occasionally anterior (21%) or posterior (6%) loreal largest; supralabials 7–8 (mean 7.0), modally 7; fifth supralabial usually subocular (99%), occasionally sixth (1%); infralabials 6; nuchals 2–5 (mean 2.2), modally 2; bilateral posttemporals usually 2+2 (61%), occasionally 2+3 (31%), or 3+3 (8%).

Midbody scale rows 22–26 (mean 23.9), modally 24; paravertebrals 43–53 (mean 48.6), modally 48; subdigital lamellae strongly keeled, 13–18 below fourth finger (mean 15.1) modally 15, 16–21 below fourth toe (mean 18.6) modally 18; 11–14 supradigital lamellae above fourth finger (mean 12.8) modally 13, 13–18 above fourth toe (mean 14.9) modally 15; palmar and plantar scales acute, without calli and skin not visible between scales (Fig. 120); plantars 9–14 (mean 11.1), modally 11; palmars 7–12 (mean 9.8), modally 9.

Snout-vent length to 38.6 mm (mean 31.3 mm). *Percentages of snout-vent length*: body length 44.6–57.0% (mean 50.9%); tail length 122.6–147.0% (mean 133.8%); forelimb length 27.0–39.7% (mean 32.2%); hindlimb length 33.9–48.8% (mean 41.4%); forebody length 38.5–49.0% (mean 42.3%); head length 19.1–23.6% (mean 21.3%). *Percentages of head length*: head depth 34.3–48.5% (mean 40.6%); head width 55.8–70.3% (mean 61.6%); snout length 43.3–49.5% (mean 46.0%). Paravertebral scale width 3.3–4.7% (mean 4.0%) of snout-vent length; dorsolateral scale width 76.5–104.2% (mean 88.4%) of paravertebral scale width.

Lenticular scale organs 4–13 (mean 7.1), modally 6. Premaxillary teeth 5–6 (mean 5.5); maxillary teeth 15–16 (mean 15.5); mandibular teeth 17–18 (mean 17.5). Hemipenis proportions not measured.

Details of holotype. Adult female (Fig. 121), NTM R25994. Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; loreals subequal; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 24; paravertebrals 47; subdigital lamellae keeled, 15 below fourth finger; 17 below fourth toe; supradigital lamellae 11 above fourth finger; 14 above fourth toe; palmars and plantars acute, skin not visible between scales; plantars 10; palmars 9. Snout-vent length 32.9 mm; body length 17.8 mm; tail not original; forelimb length 10.2 mm; hindlimb length 13.3 mm; forebody length 12.6 mm; head length 6.2 mm; head depth 2.4 mm; head width 4.1 mm; snout length 3.1 mm.

Fig. 120. Ventral surface of hind foot of *Cryptoblepharus tytthos* sp. nov., showing pale, acute plantar scales (NTM R22086, 38 km east of Fitzroy Crossing, WA). Scale: x20.

Fig. 121. Holotype of *Cryptoblepharus tytthos* sp. nov. (NTM R25994, Coulomb Point, Western Australia, 17°23'07"S 122°09'42"E, *ABTC* EV5). Scale bar = 10 mm.

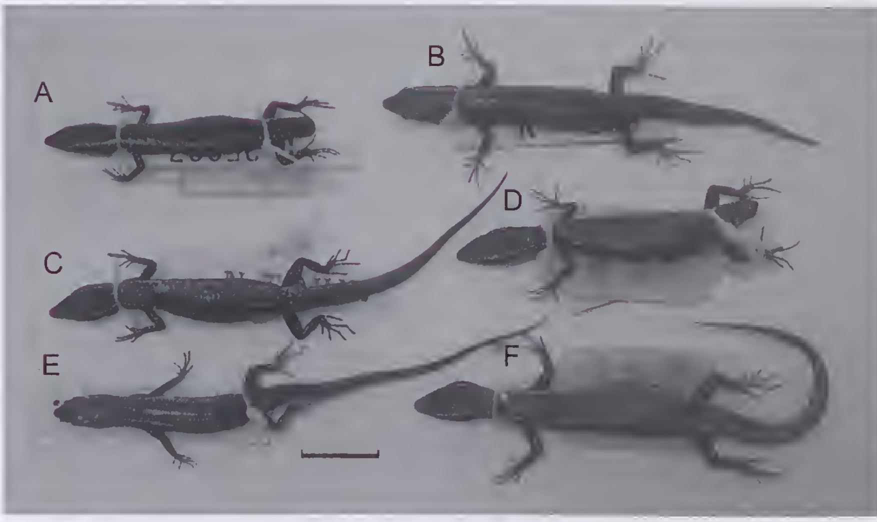

Fig. 122. *Cryptoblepharus tytthos* sp. nov., NTM preserved material from Western Australia. **A**, R25997, Coulomb Point; **B**, R7268, 79 km east of Fitzroy Crossing; **C**, R25994 (holotype), Coulomb Point; **D**, R22087, 38 km east of Fitzroy Crossing; **E**, R7099, Broome; **F**, R22086, 38 km east of Fitzroy Crossing. Scale bar = 10 mm.

Colouration and pattern. A brownish-grey *Cryptoblepharus*, with longitudinally aligned, reduced body pattern (Plate 3.5). Intensity of body pigmentation and patterning is variable, ranging from pale to prominent (Fig. 122A–F). Most specimens conform to the following description.

Dorsal ground colour brown-grey, with broad, vertebral zone extending from above eye to hindlimb. Vertebral zone about four scales wide, brown-grey, peppered with dark and/or pale flecks and spots. The latter occasionally form two broken, narrow black stripes from neck to tailbase. Obvious to obscure, pale grey laterodorsal stripes extend from above eye onto tail, most prominent on anterior half of body, about width of single laterodorsal scale, these taper anteriorly into narrow stripes extending to eye and are often absent on posterior half of body. Edges of pale laterodorsal stripes usually smooth. Laterodorsal stripes usually uniform, but may contain dark speckling. Head concolorous with vertebral zone, often patterned with dark margins to shields. Laterally patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Pale lower temporal region is flecked with dark spots and streaks. Labials pale cream, patterned with occasional dark flecks.

Flanks patterned with grey-brown upper lateral zone, variable in width, extending from loreals onto tail. Flecked with dark streaks and pale flecks, upper lateral zone coalesces gradually into pale grey/pale grey-brown lower lateral zone. Lower lateral zone peppered with small pale and/or dark spots and streaks and coalesces into pale venter. Tail concolorous with body, patterned with broken continuations of dark upper lateral zones. Limbs and toes concolorous with body, patterned with pale and dark speckling. Venter, including palmars and plantars, immaculate off-white.

Sex ratio and reproductive biology. Sex ratio favoured females (19:15), but was not significantly different from parity ($X^2 = 0.47$). Both sexes mature at approximately 26 mm snout-vent length. Adults average 31.3 mm snout-vent length and females are larger than males (maximum SVL = 38.6 versus 34.2 mm). Breeding is year round, with reproductive animals collected in January (two females), May (two males) and June (three females).

Comparison with Australian congeners. Fixed allelic differences place *C. tytthos* sp. nov. in lineage 2 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTUs carnA2 and carnA4, Horner and Adams 2007).

Morphologically distinguished from most lineage 1 members (except *C. australis*) by usually having five, rather than six, supraciliary scales and acute, instead of ovate, plantar scales. Distinguished from lineage 2 congeners *C. adamsi* sp. nov., *C. fuhni*, *C. gurrmul* sp. nov., *C. litoralis*, *C. pulcher*, *C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov. by acute plantars (versus rounded). Further distinguished from: *C. gurrmul* sp. nov., *C. l. horneri* and *C. l. litoralis* by fewer mid-body scale rows (modally 24 versus 26–28) and paravertebral scales (modally 48 versus 55–57); from *C. fuhni*, *C. gurrmul* sp. nov. and *C. zoticus* sp. nov. by more paravertebral scales (modally 48 versus 45–46) and deeper head (mean 40.6 versus 32.5–36.1 % of head length); from *C. virgatus* by more mid-body scale rows (modally 24 versus 22) and paravertebral scales (modally 48 versus 47); from *C. adamsi* sp. nov. and *C. pulcher* by pale plantar scales (versus darkly pigmented) and broad, ragged pale laterodorsal stripes.

Cryptoblepharus tytthos sp. nov. is most similar to *C. australis*, *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov. and *C. plagiocephalus* in having combinations of complex body patterns, acute plantar scales and being arboreal. However it differs from both *C. australis* and *C. exochus* sp. nov. in having keeled instead of smooth subdigital lamellae and smaller size (mean SVL, 31.3 versus 40.4 and 37.1 mm), further differs from *C. australis* by having fewer supraciliary (modally 5 versus 6), paravertebral (modally 48 versus 52) and plantar scales (modally 11 versus 12) and from *C. exochus* sp. nov. by having fewer paravertebral scales (modally 48 versus 51) and subdigital lamellae (modally FTL 15 versus 16; HTL 18 versus 20). It differs from *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov. and *C. plagiocephalus* by being smaller (mean SVL, 31.3 instead of 33.6 mm or more) and having shorter forelimbs (mean % of SVL 32.2 instead of 33.8 or more). Further differs from *C. mertensi* sp. nov. by having shallower head (mean % of head length 40.6 instead of 43.4), fewer fourth finger subdigital lamellae (modally 15 versus 16) and more plantar scales (modally 11 versus 10), from *C. ochrus* sp. nov. by having fewer paravertebral scales (modally 48 versus 50) and deeper head (mean % of head length 40.3 instead of 39.2), from *C. pannosus* sp. nov. by having fewer fourth finger subdigital lamellae (modally 15 versus 16) and posterior temporal scales (modally 2 versus 3) and from *C. plagiocephalus* by having obscure narrow laterodorsal stripes instead of broad, ragged stripes, deeper head (mean % of head length: 40.6 versus 39.5) and strongly, instead of weakly, keeled subdigital lamellae.

Distribution. Far north-western Australia, ranging coastally from Anna Plains, near the northern end of Eighty Mile Beach, north to Cape Leveque and inland to Christmas Creek, south-east of Fitzroy Crossing (Fig. 123). A disjunct population apparently occurs on Mornington Island, southern Gulf of Carpentaria, Queensland, although some doubt exists over the origin of these specimens (SAM R14760 A-D, Mark Hutchinson pers. comm.).

Sympatry. *Cryptoblepharus tytthos* sp. nov. occurs in sympatry with *C. buchananii* and *C. metallicus* from lineage 1, and *C. pannosus* sp. nov. from lineage 2. Sympatric with *C. buchananii* at Broome, Coulomb Point, Derby, and the Willare Bridge 71 km south-west of Derby in Western Australia. Sympatry with more than one congener occurs on Mornington Island in the Gulf of Carpentaria (*C. metallicus* and *C. pannosus* sp. nov.).

Geographic variation. Geographic variation was investigated by dividing specimens into three disparate groups: *DL*, a west coastal group of 22 (9 ♂, 13 ♀); *GUP*, a Queensland group of 4 (3 ♂, 1 ♀), and *OVP*, a western inland group of 8 (3 ♂, 5 ♀).

Group pairs, where sexes were treated separately and combined, were subjected to U-tests of allometrically adjusted variables. Initial analysis failed to detect any significant difference between groups *GUP* and *OVP*, so these were combined to create a group (*OVP2*) of 12 (6 ♂, 6 ♀). Comparison of separate sexes from *DL* and *OVP2* revealed some variation in body proportions, though this was inconsistent across sexes, and significance was lost when sexes were combined and tested.

These results indicate that *C. tytthos* sp. nov. does not vary significantly over its range.

Though morphologically homogeneous, *C. tytthos* sp. nov. shows considerable genetic diversity. As detailed in Horner and Adams (2007), analysis of allozyme data separated the taxon into two discrete OTUs (carnA2 and carnA4) distinguished by four fixed allelic differences. Unable to be morphologically, ecologically or geographically differentiated for species diagnoses, descriptions and keys these OTUs were merged. It is noted, however, that the resulting composite species, *C. tytthos* sp. nov., represents a complex of morphologically indeterminate taxa.

Habits and habitats. An arboreal species recorded from low open woodland and shrubland. At Coulomb Point *C. tyt-*

Fig. 123. Map of northern Australia showing distribution of *Cryptoblepharus tytthos* sp. nov. Circled diamonds indicate collection localities of genetically identified OTU carnA2, stars indicate OTU carnA4 (Horner and Adams 2007).

thos sp. nov. was abundant on trunks of a dense *Lophostemon* forest, on sandy soil (pers. obs.). Museum records note its use of man-made structures, such as 'old rubbish', windmill bores, bridge supports, old stockyard posts and railings.

Etymology. From the Greek adjective *tytthos*, meaning little or small; in reference to this taxon being the smallest known species of *Cryptoblepharus*. Introduced as a noun in apposition.

Cryptoblepharus ustulatus sp. nov.

Russet snake-eyed skink

(Plates 3.6–3.7; Figs 124–127)

Type material examined. *Cryptoblepharus ustulatus* Horner. HOLOTYPE: Adult female, WAM R125492 (Tissue sample No. ABTC R125492), 30 km east of Newman, Western Australia, 23°19'S 120°02'E. 16 August 1995. PARATYPES (30 specimens): WESTERN AUSTRALIA: NTM R22079-082, Fortesque Falls, 22°28'37"S 118°32'57"E, 21 January 1996, P. Horner, *ABTC* Y49-52; SAM R29335-339, Python Pool, 21°20'S 117°14'E, 21 September 1985, B. Miller and S. Sarre, *ABTC* R29336-339; SAM R29340, Dales Gorge, 22°30'S 118°36'E, B. Miller and S. Sarre, 22 September 1985, *ABTC* R29340; WAM R14296, Dolphin Island, 20°29'S 116°51'E, G. Storr, 5 June 1962; WAM R20023, Big Hill Pool, Mount Herbert, 21°20'S 117°14'E, Hamersley Expedition, 25 July 1958; WAM R37485, Hancock Gorge, 25 km south of Wittenoom, 22°21'S 118°16'E, Hale School Expedition, 20 July 1970; WAM R51622-623, 10 km northeast of Mount Newman, 23°17'S 119°45'E, H. Butler, 3 December 1975; WAM R52705, Marandoo Minesite, Mount Bruce, 22°38'S 118°09'E, H. Butler, 21 April 1976; WAM R73935, Weeli Wolli Spring, 22°55'S 119°13'E, L. Smith and R. Johnstone, 6 November 1981; WAM R74893, Weano Gorge, Hamersley Range National Park, 22°25'S 118°15'E, L. Smith and R. Johnstone, 23 November 1981; WAM R84265, Burrup Peninsula, 20°36'S 116°48'E, H. Butler, 18 August 1983; WAM R90709, Cadjeput Rock Hole, 21°32'08"S 119°08'09"E, J. Dell and R. How, *ABTC* R90709; WAM R100645, Woodstock, 21°31'35"S 119°08'57"E, *ABTC* R100645; WAM R102400, Barlee Range Nature Reserve, 23°04'S 115°47'E, 14 June 1994; WAM R104222-223, Woodstock, 21°31'35"S 119°08'57"E, *ABTC* R104222-223; WAM R104234, Woodstock, 21°33'S 119°07'E; WAM R108595, 12 km south-west of Pannawonica, 21°47'S 116°15'E, *ABTC* R108595; WAM R113268, junction of Jimmawurrada Creek and Robe River, 21°44'S 116°15'E, G. Connell, 14 December 1991; WAM R121998, Weeli Wolli Spring, 22°55'S 119°13'E, *ABTC* R121998; WAM R125492-493, 30 km east of Newman, 23°19'S 120°02'E, *ABTC* R125492-493; WAM R132576, Burrup Peninsula, 20°40'14"S 116°45'22"E, *ABTC* R132576.

Diagnosis. A medium sized (40–44 mm SVL), long-legged, very shallow-headed, saxicoline *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of five supraciliary scales, 22 mid-body scale rows, 46 paravertebral scales, 18 smooth fourth toe subdigital lamellae, 9 palmar and 11 plantar scales; mean values of 35.2 mm snout-vent length, hindlimb length 44.3% of snout-vent length and head depth of 34.7% of head length; rounded, plain plantar scales; obscure, pale dorsolateral stripes, and reddish, longitudinally aligned body pattern.

Description (31 specimens). Postnasals absent; prefrontals in broad contact (100%); supraciliaries 5–6 (mean 5.0), modally 5; enlarged upper ciliaries 3–4 (mean 3.0), modally 3; loreals usually subequal (77%), occasionally anterior (13%) or posterior (10%) largest; supralabials 7–8 (mean 7.1), modally 7; fifth supralabial usually subocular (93%), occasionally sixth (7%); infralabials 6; nuchals 2–5 (mean 2.3), modally 2; bilateral posttemporals 2+3 (39%), 3+3 (32%), or 2+2 (29%).

Midbody scale rows 21–26 (mean 23.0), modally 22; paravertebrals 42–50 (mean 46.5), modally 46; subdigital lamellae smooth, 13–16 below fourth finger (mean 14.6) modally 15, 15–21 below fourth toe (mean 18.0) modally 18; 11–14 supradigital lamellae above fourth finger (mean 12.4) modally 12, 13–18 above fourth toe (mean 15.1) modally 15; palmar and plantar scales rounded, without calli and skin not visible between scales (Fig. 124); plantars 9–12 (mean 10.7), modally 11; palmars 8–11 (mean 9.3), modally 9.

Snout-vent length to 41.6 mm (mean 35.2 mm). *Percentages of snout-vent length*: body length 44.6–56.1% (mean 50.0%); tail length 136.5–161.9% (mean 144.4%); forelimb length 31.0–38.9% (mean 34.7%); hindlimb length 38.5–50.0% (mean 44.3%); forebody length 37.9–46.5% (mean 42.2%); head length 19.3–23.5% (mean 20.9%). *Percentages of head length*: head depth 26.0–43.0% (mean 34.7%); head width 54.1–67.6% (mean 59.2%); snout length 40.6–48.5% (mean 44.1%). Paravertebral scale width 3.2–4.8% (mean 4.0%) of snout-vent length; dorsolateral scale width 76.8–104.5% (mean 89.1%) of paravertebral scale width.

Lenticular scale organs 3–12 (mean 5.8), modally 6. Tooth counts and hemipenis proportions not measured.

Details of holotype. Adult female (Fig. 125), WAM R125492. Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 24; paravertebrals 46; subdigital lamellae smooth, 16 below fourth finger; 20 below fourth toe; supradigital lamellae 13 above fourth finger; 15 above fourth toe; palmars and plantars rounded, skin not visible between scales; plantars 11; palmars 10. Snout-vent length 36.4 mm; body length 18.4 mm; tail length 51.2 mm; forelimb length 12.7 mm; hindlimb length 15.2 mm; forebody length 15.3 mm; head length 7.3 mm; head depth 3.1 mm; head width 4.4 mm; snout length 3.2 mm.

Colouration and pattern. A reddish *Cryptoblepharus*, with reduced, longitudinally aligned body pattern (Plates 3.6 and 3.7). Intensity of body pigmentation and patterning is variable (Fig. 126A–F), but most specimens conform to the following description.

Fig. 124. Ventral surface of hind foot of *Cryptoblepharus ustulatus* sp. nov., showing pale, ovate plantar scales (NTM R22079, Fortescue Falls, WA). Scale: x20.

Fig. 125. Holotype of *Cryptoblepharus ustulatus* sp. nov. (WAM R125492, 30 km east of Newman, Western Australia, 23°19'S 120°02'E, *ABTC* R125492). Scale bar = 10 mm.

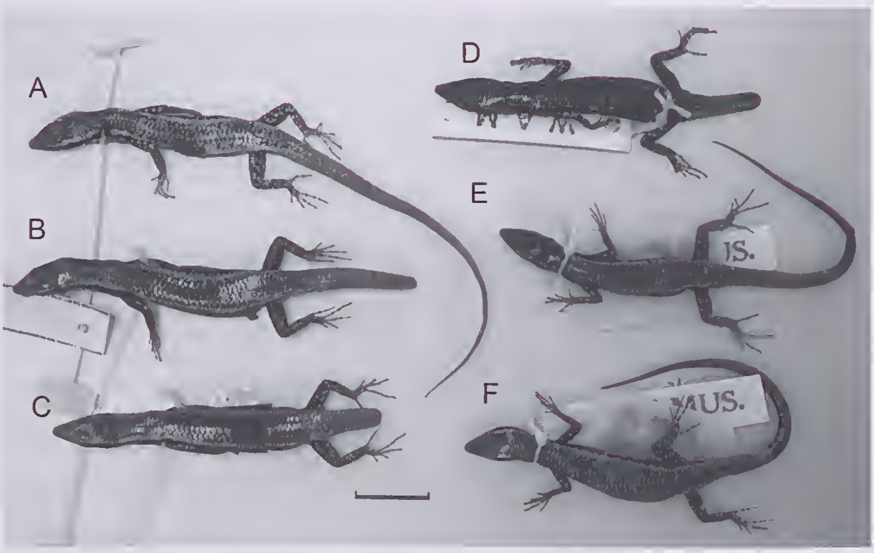

Fig. 126. *Cryptoblepharus ustulatus* sp. nov., preserved material from Western Australia. **A–C**, WAM R100645, R104222, R104223, Woodstock; **D**, WAM R132576, Burrup Peninsula; **E–F**, NTM R22080, R22082, Fortescue Falls. Scale bar = 10 mm.

Dorsal ground colour pale russet to brick-red (greyish in spirit), with broad, vertebral zone extending from above eye to hindlimb. Vertebral zone about four scales wide, russet, often immaculate but may have a longitudinal series of blackish flecks on dorsolateral scales forming two obscure, discontinuous, narrow black stripes from neck to tailbase. Obscure, pale laterodorsal stripes extend from above eye to tailbase, about width of single laterodorsal scale, these taper anteriorly into narrow stripes. Pale laterodorsal stripes usually uniform in colour with uneven edges. Head concolorous with vertebral zone, often patterned with dark margins to shields. Laterally patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Lower temporal region patterned with large pale spots and streaks. Labials pale, patterned with occasional dark flecks.

Flanks patterned with distinct blackish upper lateral zone, 1–2 lateral scales in width, extending from loreals onto tail. Splotched with pale blotches, spots and flecks, upper lateral zone distinct from pale lower lateral zone. Lower lateral zone peppered with small pale and/or dark spots and streaks and coalesces into pale venter. Tail concolorous with body, patterned with broken continuations of dark upper lateral zones. Limbs and toes concolorous with body, patterned with pale and dark speckling. Venter, including palmars and plantars, immaculate off-white.

Sex ratio and reproductive biology. Sex ratio favoured females (21:10), and was significantly different from parity ($X^2 = 3.90$). Both sexes mature at approximately 32 mm snout-vent length. Adults average 35.2 mm snout-vent length and females grow larger than males (maximum SVL = 41.6 versus 39.0 mm). Breeding is indeterminate with only four reproductive animals in the sample. These consisted of a male collected in July, and three females collected in November, December and January. The latter records suggest that they may breed during summer months.

Comparison with Australian congeners. Fixed allelic differences place *C. ustulatus* sp. nov. in lineage 2 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTU megaB, Horner and Adams 2007).

Morphologically distinguished from lineage 1 members (*C. australis, C. buchananii, C. cygnatus* sp. nov., *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus, C. metallicus, C. ruber* and *C. wulbu* sp. nov.) by usually having five, rather than six, supraciliary scales and (except for *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus* and *C. wulbu* sp. nov.) reduced body pattern on reddish ground colour.

Distinguished from most lineage 2 congeners (except *C. zoticus* sp. nov.) by having reddish ground colour rather than brown, grey or blackish. Further Distinguished from congeners: *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. by rounded plantar scales (versus acute), fewer paravertebral scales (modally 46 versus 48–51), and shallower head (mean 34.7 versus 39.2–43.3 % of head length); from *C. litoralis* and *C. gurrmul* sp. nov. by fewer midbody scale rows (modally 22 versus 26–28) and paravertebral scales (modally 46 versus 55–57); from *C. fuhni* by smooth, less numerous fourth toe subdigital lamellae (versus callused; modally 18 versus 21), shorter hindlimbs (mean 44.3 versus 52.8 % of SVL) and by being smaller (mean SVL, 35.2 versus 41.6 mm); from *C. adamsi* sp. nov. and *C. pulcher* by fewer paravertebral scales (modally 45 versus 50), more plantar scales (modally 10 versus 9), longer limbs (FL, mean 35.0 versus 32.2 % of SVL; RL, mean 42.2 versus 40.9 and 40.5 % of SVL), and shallower head (mean 32.5 versus 40.2 and 39.3 % of head length); from *C. virgatus* by having more posterior temporal scales (modally 3 versus 2), shallower head (mean 34.7 versus 38.2 % of head length) and longer hindlimbs (mean 44.3 versus 41.0 % of SVL).

Cryptoblepharus ustulatus sp. nov. is most similar to *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus, C. wulbu* sp. nov. and *C. zoticus* sp. nov. in having combinations of reddish ground colour and saxicoline habits. However, it differs from *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus* and *C. wulbu* sp. nov. by having fewer supraciliary scales (modally 5 versus 6) and further differs from *C. daedalos* sp. nov. and *C. juno* sp. nov. by having fewer plantar (modally 11 versus 15 and 12) and paravertebral scales (modally 46 versus 48 and 49) and shorter hindlimbs (mean 44.3 versus 46.8 and 46.5% of SVL). Further differs from *C. megastictus* and *C. wulbu* sp. nov. by having fewer midbody scale rows (modally 22 versus 26) and subdigital lamellae (modally FTL 15 versus 16 and 17; HTL 18 versus 19 and 22). Differs from *C. zoticus* sp. nov. by having fewer midbody scale rows (modally 22 versus 24) and fourth finger subdigital lamellae (modally 15 versus 16) and more palmar (modally 9 versus 8) and plantar scales (modally 11 versus 10).

Distribution. The Pilbara region of Western Australia. Ranges from Dolphin Island and Burrup Peninsula on the coast, south-west to Barlee Range Nature Reserve and inland to 30 km east of Mount Newman (Fig. 127).

Sympatry. Sympatric with *C. buchananii* at Weeli Wooli Spring and on the Burrup Peninsula.

Geographic variation. Geographic variation was investigated by dividing specimens into two disparate groups: *GAS*, a southern group of 5 (1 ♂, 4 ♀), from bioregion Gascoyne, and *PIL*, a northern group of 26 (9 ♂, 17 ♀), from bioregion Pilbara.

Small sample size of group *GAS* prevented analysis of separate sexes, so combined sexes were subjected to U-tests of all variables. Results revealed geographic variation in *C. ustulatus* sp. nov. was limited to a minor difference in head depth, with southern populations having a deeper head (mean 3.1 versus 2.7 mm).

Habits and habitats. A saxicoline species which, at Fortescue Falls, was found on rocks and rockfaces. Vegetation at this site consisted of sedges and small *Melaleuca* sp. Numerous specimens were observed, some of which actively foraged close to the flowing waters of the falls.

Etymology. From the Latin adjective *ustulatus*, meaning russet-backed; in reference to the broad, russet coloured vertebral zone, characteristic of this taxon.

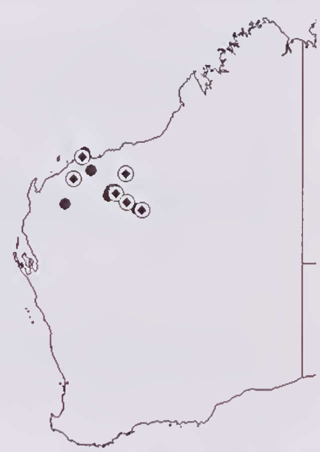

Fig. 127. Map of Western Australia showing distribution of *Cryptoblepharus ustulatus* sp. nov. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

Cryptoblepharus virgatus (Garman, 1901)

Striped snake-eyed skink

(Plate 3.8; Figs 128–131; Table 12)

Ablepharus virgatus Garman, 1901: 10 (Cooktown, Queensland).

Ablepharus boutonii virgatus Garman, 1901. – Mertens 1931: 112; Loveridge 1934: 375; Mertens 1964: 108; Worrell 1963: 35.

Cryptoblepharus virgatus virgatus (Garman, 1901). – Wilson and Knowles 1988: 120; Wilson and Swan 2003: 150.

Cryptoblepharus virgatus (Garman, 1901). – Storr 1976: 55; Storr *et al*. 1981: 25; Cogger *et al*. 1983a: 142; Wells and Wellington 1985: 28; Swanson 1987: 38; Covacevich and Couper 1991: 357; Ehmann 1992: 183; Stanger *et al*. 1998: 23; Storr *et al*. 1999: 25; Cogger 2000: 406.

Type material examined. *Ablepharus virgatus* Garman, 1901. HOLOTYPE: MCZ 6485, Cooktown, Queensland, coll. E.A.C. Olive.

Non-type material examined. See Appendix 4.

Diagnosis. A small (<40 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of five supraciliary scales, 22 mid-body scale rows, 47 paravertebral scales, and eight plantar scales; mean values of hindlimb length 41.0% of snout-vent length, and head depth of 38.2% of head length; plain, rounded, pale plantar scales; smooth subdigital lamellae; continuous, smooth-edged, narrow pale dorsolateral stripes; greyish ground colour, and arboreality.

Description (31 specimens). Postnasals absent; prefrontals usually in broad contact (97%), occasionally in narrow contact (3%); supraciliaries 5–6 (mean 5.2), modally 5; enlarged upper ciliaries 3; posterior loreal usually largest (58%), occasionally subequal (32%) or anterior largest (10%); supralabials 6–7 (mean 7.0), modally 7; fifth supralabial usually subocular (97%), occasionally fourth (3%); infralabials 6; nuchals 2–6 (mean 2.4), modally 2; bilateral

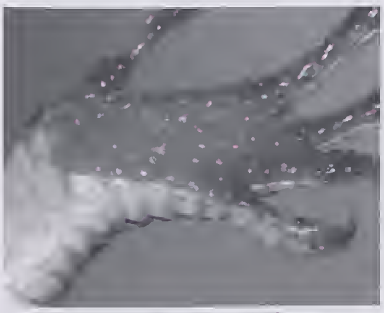

Fig. 128. Ventral surface of hind foot of *Cryptoblepharus virgatus,* showing pale, ovate plantar scales (NTM R18874, Cooktown, Qld). Scale: x20.

Fig. 129. Holotype of *Ablepharus virgatus* Garman, 1901. MCZ 6485, Cooktown, Queensland, Australia.

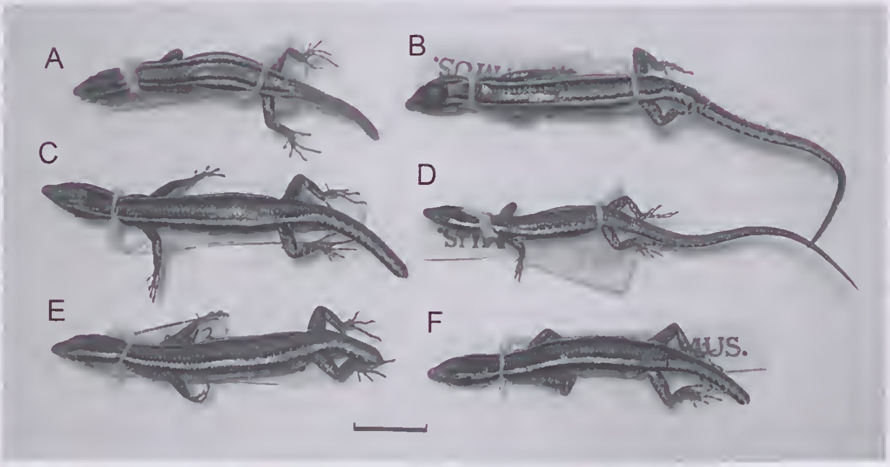

Fig. 130. *Cryptoblepharus virgatus, preserved* material from Queensland. **A**, R18881, Lions Den Hotel; **B**, R18873, Cooktown; **C**, R18868, Cooktown; **D**, R18899, Flying Fish Point; **E**, R18872, Cooktown; **F**, R18869, Cooktown. Scale bar = 10 mm.

posttemporals usually 2+2 (88%), occasionally 2+3 (8%), or 3+3 (4%).

Midbody scale rows 20–24 (mean 21.8), modally 22; paravertebrals 43–52 (mean 47.3), modally 47; subdigital lamellae smooth, 14–17 below fourth finger (mean 15.7) modally 16, 16–22 below fourth toe (mean 19.6) modally 19; 11–14 supradigital lamellae above fourth finger (mean 12.4) modally 12, 14–18 above fourth toe (mean 15.6) modally 15; palmar and plantar scales rounded, occasionally capped with dark brown calli, and skin visible between scales (Fig. 128); plantars 8–12 (mean 9.5), modally 10; palmars 7–11 (mean 8.4), modally 8.

Snout-vent length to 39.7 mm (mean 34.8 mm). *Percentages of snout-vent length*: body length 45.8–55.4% (mean 50.4%); tail length 113.9–137.0% (mean 128.6%); forelimb length 28.6–38.3% (mean 33.1%); hindlimb length 32.3–45.8% (mean 41.0%); forebody length 32.3–45.8% (mean 42.8%); head length 18.8–22.3% (mean 20.7%). *Percentages of head length*: head depth 32.0–44.9% (mean 38.2%); head width 50.9–65.4% (mean 57.6%); snout length 42.0–51.0% (mean 44.9%). Paravertebral scale width 3.7–5.7% (mean 4.5%) of snout-vent length; dorsolateral scale width 64.3–103.4% (mean 80.9%) of paravertebral scale width.

Lenticular scale organs 4–16 (mean 7.5), modally 7. Premaxillary teeth 5–6 (mean 5.3), modally 5; maxillary teeth 19–20 (mean 19.5), modally 19; mandibular teeth 23–24 (mean 23.5), modally 23. Hemipenis: length 5.9–9.1% (mean 7.9%) of snout-vent length; width 87.7–111.5% (mean 100.2%) of hemipenis length; trunk 31.7–64.3% (mean 48.3%) of hemipenis length.

Details of holotype. MCZ 6485 (Fig. 129). Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; anterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 20; paravertebrals 47; subdigital lamellae smooth, 14 below fourth finger; 17 below fourth toe; supradigital lamellae 12 above fourth finger; 15 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 8; palmars 7. Snout-vent length 39.7 mm; body length 26.0 mm; tail not original; forelimb length 11.4 mm; hindlimb length 12.8 mm; forebody length 15.6 mm; head length 7.5 mm; head depth 3.3 mm; head width 4.4 mm; snout length 3.4 mm.

Colouration and pattern. A greyish *Cryptoblepharus*, with longitudinally aligned, simple body pattern dominated by broad, grey vertebral zone, and prominent dark dorsolateral and pale laterodorsal stripes (Plate 3.8). Intensity of body patterning is variable, ranging from obscure to prominent (Fig. 130A–F). Most specimens conform to the following description.

Dorsal ground colour grey to grey-brown, with broad vertebral zone extending from above eye to hindlimb. Vertebral zone unpatterned, as wide as paired paravertebral scales and grey to grey-brown in colour. Distinct, black dorsolateral stripes extend from above eye onto tailbase, where they merge creating a blackish, ragged, median, tapering stripe on anterior half of tail. Inner margin of dark dorsolateral stripes slightly ragged. Prominent, narrow, creamish to white laterodorsal stripes extend from above eye onto tail. Pale laterodorsal stripes smooth edged and without patterning, about as wide as laterodorsal scale. Head concolorous with vertebral zone or coppery brown, usually with vague dark mottling on scales. Laterally patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Vague, broken, pale stripe extends from supralabials to forelimb. Labials creamish, patterned with fine dark margins to scales.

Flanks patterned with blackish-grey upper lateral zone, similar in width to dark dorsolateral stripes, extending from loreals onto tail and forming a smooth outer border to pale laterodorsal stripes. Usually immaculate, but occasionally flecked with pale specks and spots, upper lateral zone is about two lateral scales wide and coalesces gradually into greyish lower lateral zone. Lower lateral zone maybe peppered with small pale and/or dark spots and coalesces into pale venter. Tail concolorous with body, patterned with continuations of blackish dorsolateral stripes, pale laterodorsal stripes and dark upper lateral zone. Limbs and toes concolorous with body, patterned with pale and dark speckling. Venter immaculate off-white. Palmar and plantar surfaces light grey to pale brown, subdigital lamellae often dark brown.

Sex ratio and reproductive biology. Sex ratio favoured males (18:13), but was not significantly different from parity ($X^2 = 0.80$). Males mature at approximately 32 mm snout-vent length and females at 33 mm. Adults average 34.8 mm snout-vent length and males are slightly larger than females (maximum SVL = 39.7 versus 39.3 mm). Breeding probably occurs at most times of the year, with reproductive males collected in August (1), November (1), December (9) and January (1), and females in August (2) and December (5). Clerke (1989), in a study of a Townsville population, determined that males mature at 30 mm snout-vent length and females at 30.4 mm. In his study Clerke (1989) also determined that males were reproductive from April onwards and females were sexually active in August, September and October, and concluded that reproduction was cyclic in this population.

Comparison with Australian congeners. Fixed allelic differences place *C. virgatus* in lineage 2 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTU virgA2, Horner and Adams 2007).

Morphologically distinguished from lineage 1 members (*C. australis, C. buchananii, C. cygnatus* sp. nov., *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus, C. metallicus, C. ruber* and *C. wulbu* sp. nov.) by usually having five, rather than six, supraciliary scales and simple striped body pattern on a blackish ground colour.

Distinguished from lineage 2 congeners: *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. by hav-

Table 12. List of congeners sympatric with *Cryptoblepharus virgatus*, giving areas of sympatry.

Congeners sympatric with *Cryptoblepharus virgatus*	Area of sympatry
C. adamsi sp. nov.	Qld: Cairns, Mareeba
C. fuhni	Qld: Melville Range
C. l. litoralis	Qld: Cooktown, Dauar Island, Flying Fish Point, Hammond Island, King Island, Lizard Island, Moa Island, Murray Island, Purtaboi Island, Somerset, Stoney Point, Temple Bay, Thursday Island, Tip of Cape York, Warraber Island, Yam Island
C. metallicus	Qld: Coen, Horn Island, Townsville
Mulitple sympatry	
C. l. litoralis + *C. metallicus*	Qld: Horn Island

ing rounded, instead of acute, plantar scales and simple striped body pattern on a blackish ground colour; from *C. litoralis* and *C. gurrmul* sp. nov. by fewer mid-body scale rows (modally 24 versus 26–28) and paravertebral scales (modally 50 versus 55–57); from *C. fuhni*, *C. ustulatus* sp. nov. and *C. zoticus* sp. nov. by more paravertebral scales (modally 50 versus 45–46) and deeper head (mean 40.2 versus 32.5–36.1 % of head length). *Cryptoblepharus virgatus* is most similar to *C. adamsi* sp. nov. and *C. pulcher* in having combinations of simple striped body pattern, flat ovate plantar scales and being arboreal. However it differs from both by having fewer mid-body scale rows (modally 22 versus 24) and paravertebral scales (modally 47 versus 50). Further differs from *C. adamsi* sp. nov. in having narrow smooth edged pale laterodorsal stripes instead of moderately broad ragged edged stripes and wider paravertebral scales (mean % of SVL 4.5 instead of 4.2) and from *C. pulcher* by having pale callused plantar scales rather than dark plain plantars and wider paravertebral scales (mean % of SVL 4.5 instead of 4.2).

Distribution. Far north-eastern Queensland, ranging from islands of Torres Strait, through northern and eastern Cape York Peninsula and coastally south to about Townsville (Fig. 131).

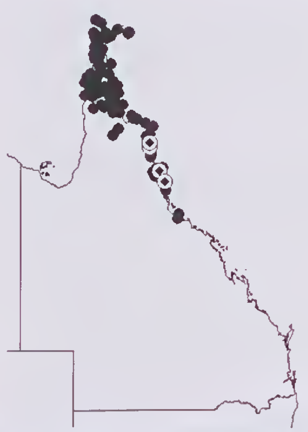

Fig. 131. Map of Queensland showing distribution of *Cryptoblepharus virgatus*. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

Sympatry. *Cryptoblepharus virgatus* occurs in sympatry with *C. metallicus* from lineage 1, *C. adamsi* sp. nov., *C. fuhni* and *C. l. litoralis* from lineage 2 (Table 12).

Geographic variation. Geographic variation was investigated by dividing specimens into two disparate groups: *CY*, a Cape York group of 23 (13 ♂, 10 ♀) samples from bioregion Cape York Peninsula (CYP), north of Cape Tribulation, and *NE*, a north-east group of 8 (5 ♂, 3 ♀), samples from bioregions CYP, south of Cape Tribulation and Wet Tropics (WT). Group pairs, where sexes were treated separately and combined, were subjected to U-tests of allometrically adjusted variables. Results revealed significant differences which were inconsistent between sexes and both sexes combined. Analysis of both sexes combined showed that group *CY* differed slightly from *NE* in head width (mean 4.4 versus 4.7 mm), fourth finger supradigital scales (modally 12 versus 13), number of plantar scales (modally 10 versus 11), and mid-body scale rows (mean 21.5 versus 22.6). Note that mid-body scale row modal values were the same (22) for both groups.

These results indicate that geographic variation in *C. virgatus* is clinal, with head width and numbers of fourth finger supradigital scales, plantar scales and mid-body scale rows slightly increasing from north to south.

Habits and habitats. An arboreal species which, in urban environments, is often observed on man-made structures. Museum records note its use of tree trunks, fence railings, posts and common association with beach vegetation. Covacevich and Ingram (1978) recorded a specimen from a tree growing amongst black boulders of the Melville Range.

Taxonomic history. Named by Samuel W. Garman, of the Museum of Comparative Zoology, Harvard University in 1901, *Ablepharus virgatus* has a relatively uneventful taxonomic history. Described from a single specimen collected at Cooktown, Queensland, by E.A.C. Olive (probably in the 1890's), the taxon was treated as a subspecies of *A. boutonii* by Mertens (1931), and a subspecies of *Cryptoblepharus* by most subsequent authors. Cogger *et al.* (1983a) treated the taxon as a full species.

Cryptoblepharus wulbu sp. nov.
Spangled snake-eyed skink
(Plate 3.9; Figs 132–137)

Type material examined. *Cryptoblepharus wulbu* Horner. HOLOTYPE: Adult female (gravid), NTM R26062 (Tissue sample No. ABTC FE8), Mount Borradaile, Arnhem Land, Northern Territory, Australia, 12°03'07"S 132°53'17"E, collected by P. Horner and J. Lea, 3 October 2000. From boulder on sandstone rock platform, 1045 hours. PARATYPES (10 specimens): NORTHERN TERRITORY: NTM R26056-057, same data as holotype, except 2 Oct 2000, ABTC FE2-FE3; NTM R26061, R26063-066, R26072-074, same data as holotype, except ABTC FE7, FE9, FF1-FF3.

Diagnosis. A small (<40 mm SVL), very long-legged, very shallow-headed, saxicoline *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of six supraciliary scales, 26 mid-body scale rows, 39 paravertebral scales, 22 fourth toe subdigital lamellae, and three lenticular scale organs; mean values of hindlimb length 47.3% of snout-vent length and head depth 34.9% of head length; reddish, blotched body pattern and saxicoline habits.

Description (11 specimens). Postnasals absent; prefrontals in broad contact (100%); supraciliaries 5–6 (mean 5.9), modally 6; enlarged upper ciliaries 3–4 (mean 3.2), modally 3; posterior loreal usually largest (82%), occasionally subequal (9%) or anterior largest (9%); supralabials 6–7 (mean 6.9), modally 7; fifth supralabial subocular (100%); infralabials 6, modally 6; nuchals 2–4 (mean 2.6), modally 2; bilateral posttemporals usually 3+3 (55%), occasionally 2+2 (27%), or 2+3 (18%).

Midbody scale rows 24–26 (mean 25.4), modally 26; paravertebrals 37–44 (mean 40.6), modally 39; subdigital lamellae smooth, 15–18 below fourth finger (mean 16.8) modally 17, 18–22 below fourth toe (mean 20.4), modally 22; 12–14 supradigital lamellae above fourth finger (mean 12.9) modally 13, 14–18 above fourth toe (mean 16.4), modally 17; palmar and plantar scales rounded (Fig. 132), without calli and skin visible between scales; plantars

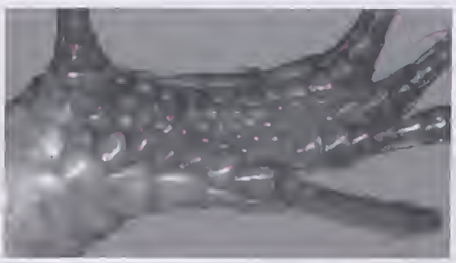

Fig. 132. Ventral surface of hind foot of *Cryptoblepharus wulbu* sp. nov., showing pale, ovate plantar scales (NTM R26063, Mount Borradaile, NT). Scale: x20.

Fig. 133. Holotype of *Cryptoblepharus wulbu* sp. nov., NTM R26062, Mount Borradaile, Northern Territory, Australia, 12°03'07"S 132°53'17"E.

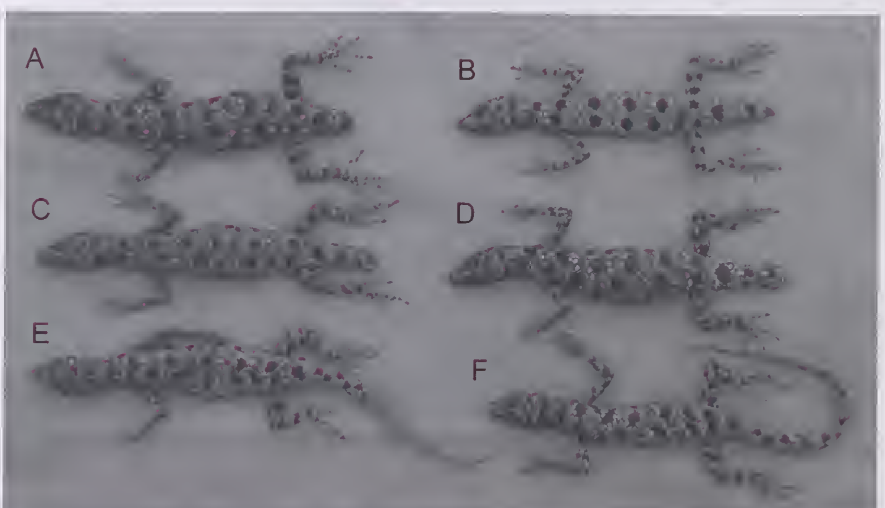

Fig. 134. *Cryptoblepharus wulbu* sp. nov., Mount Borradaile, Northern Territory. NTM specimens prior to preservation. **A**, R26056; **B**, R26061; **C**, R26057; **D**, R26062 (holotype); **E**, R26072; **F**, R26063.

12–14 (mean 13.3), modally 13; palmars 8–11 (mean 8.9), modally 8.

Snout-vent length to 39.0 mm (mean 35.8 mm). *Percentages of snout-vent length*: body length 47.7–53.8% (mean 50.1%); tail length 134.5% (n = 1); forelimb length 35.1–41.2% (mean 38.4%); hindlimb length 43.3–51.1% (mean 47.3%); forebody length 40.7–45.8% (mean 42.9%); head length 19.0–20.8% (mean 19.9%). *Percentages of head length*: head depth 31.3–38.2% (mean 34.9%); head width 61.1–70.4% (mean 65.4%); snout length 40.7–48.4% (mean 44.6%). Paravertebral scale width 3.8–4.6% (mean 4.3%) of snout-vent length; dorsolateral scale width 88.2–103.1% (mean 94.1%) of paravertebral scale width.

Lenticular scale organs 2–12 (mean 4.8), modally 3. Tooth counts not recorded. Hemipenis: length 8.4–9.6% (mean 9.0%) of snout-vent length; width 70.5–95.4% (mean 85.2%) of hemipenis length; trunk 35.2–61.8% (mean 48.0%) of hemipenis length.

Details of holotype. Adult female (Fig. 133), NTM R26062. Postnasals absent; prefrontals in broad contact; supraciliaries 5 (left) and 6 (right); enlarged upper ciliaries 3; posterior loreal largest; supralabials 7 (left) and 6 (right); fifth supralabial subocular (left), fourth (right); infralabials 6; nuchals 2. Midbody scale rows 26; paravertebrals 42; subdigital lamellae smooth, 18 below fourth finger; 22 below fourth toe; supradigital lamellae 13 above fourth finger; 17 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 14; palmars 9. Snout-vent length 37.3 mm; body length 18.8 mm; tail missing; forelimb length 13.7 mm; hindlimb length 16.2 mm; forebody length 15.5 mm; head length 7.1 mm; head depth 2.4 mm; head width 4.8 mm; snout length 3.3 mm.

Colouration and pattern. A reddish mauve *Cryptoblepharus*, with a body pattern dominated by random, large rounded dark blotches (Plate 3.9 and Fig. 134A–F).

Dorsal ground colour reddish mauve, patterned with rounded to irregular, large-blackish blotches, with scattered whitish spots randomly interspersed among the dark blotches. Head concolorous with body, but with occasional dark streaks, rather than blotches. Labials pale cream. Tail concolorous with body, but with blotches reduced in size. Limbs concolorous with body, patterned with dark streaks, blotches and spots. Venter immaculate off-white. Subdigital lamellae and palmar and plantar surfaces off-white, patterned with occasional dark flecks. As with other *Cryptoblepharus* taxa, 'softer' colours (reds, blues, yellows, etc) in the body pattern rapidly fade in preservative.

Sex ratio and reproductive biology. Sex ratio favoured females (6:5), but was not significantly different from parity ($X^2 = 0.09$). Males mature at approximately 33 mm snout-vent length and females at 34 mm. Adults average 35.8 mm snout-vent length and females are larger than males (maximum SVL = 39.0 versus 36.3 mm). Reproductively active individuals of both sexes were present in the population during October.

Comparison with Australian congeners. Fixed allelic differences place *C. wulbu* sp. nov. in lineage 1 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTU megaA3, Horner and Adams 2007).

Morphologically distinguished from lineage 2 members (*C. adamsi* sp. nov., *C. exochus* sp. nov., *C. fuhni*, *C. gurrmul* sp. nov., *C. litoralis*, *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus*, *C. pulcher*, *C. tytthos* sp. nov., *C. ustulatus* sp. nov., *C. virgatus* and *C. zoticus* sp. nov.) by usually having six, rather than five, supraciliary scales and (except for *C. ustulatus* sp. nov. and *C. zoticus* sp. nov.) blotched body pattern on reddish ground colour.

Distinguished from lineage 1 congeners: *C. australis*, *C. buchananii*, *C. cygnatus* sp. nov., *C. metallicus* and *C. ruber* by ground colour and body pattern characteristics (blotched body pattern on reddish ground colour versus longitudinally aligned body pattern on greyish ground colour) and by being saxicoline rather than arboreal. Further distinguished from *C. australis*, *C. buchananii*, *C. cygnatus* sp. nov., *C. metallicus* and *C. ruber* by more mid-body scale rows (modally 26 versus 24), fewer paravertebral scales (modally 39 versus 48–54), shallower head (mean 34.9 versus 41.1–43.3 % of head length) and longer hindlimbs (mean 47.3 versus 40.9–42.0 % of SVL).

Cryptoblepharus wulbu sp. nov. is most similar to *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus*, *C. ustulatus* sp. nov. and *C. zoticus* sp. nov. in having combinations of reddish ground colour and saxicoline habits. However, it differs from all these by having fewer paravertebral scales (modally 39 versus 45 or more). Further differs from *C. ustulatus* sp. nov. and *C. zoticus* sp. nov. by having more supraciliary scales (modally 6 versus 5), plantar scales (modally 13 versus 11 and 10) and midbody scale rows (modally 26 versus 22 and 24). Further differs from *C. megastictus* by having more plantar scales (modally 13

Fig. 135. Map of the Northern Territory showing distribution of *Cryptoblepharus wulbu* sp. nov. Circled diamond indicates genetically identified sample site (Horner and Adams 2007).

Fig. 136. Type locality of *Cryptoblepharus wulbu* sp. nov., outlier of Mount Borradaile, Northern Territory, Australia.

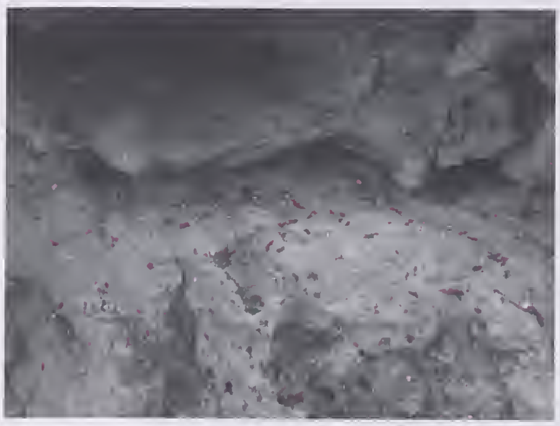

Fig. 137. Section of sandstone crevice on outlier of Mount Borradaile (Fig. 136), showing numerous scats of *Cryptoblepharus wulbu* sp. nov.

versus 10), longer limbs (mean % of SVL: FL 38.4 versus 36.8%; RL 47.3 versus 44.6%) and shorter head (mean 19.9 versus 21.9% of SVL). Further differs from *C. daedalos* sp. nov. by having fewer palmar scales (modally 8 versus 10) and shorter, wider head (mean HL 19.9 versus 21.6% of SVL; HW 65.4 versus 58.5% of head length) and from *C. juno* sp. nov. by having more plantar scales (modally 13 versus 12) and fourth finger subdigital lamellae (modally 17 versus 16) and a shorter, wider head (mean HL 19.9 versus 21.3% of SVL; HW 65.4 versus 58.2% of head length). Additionally, *C. wulbu* sp. nov. has the lowest number of lenticular scale organs (modally 3 versus 4–13) of any Australian *Cryptoblepharus*.

Distribution. Limited to the Mount Borradaile massif and its outliers, in north-western Arnhem Land, Northern Territory (Fig. 135).

Sympatry. At Mount Borradaile, *C. wulbu* sp. nov. is micro-sympatric with *C. cygnatus* sp. nov., a co-member of lineage 1.

Geographic variation. Taxon is known from a single locality.

Habits and habitats. A saxicoline species that inhabits rock faces, boulders, crevices and sandstone sheets (Fig. 136). Though limited in distribution *C. wulbu* sp. nov. is locally abundant, as exemplified in Fig. 137 which shows accumulated *C. wulbu* sp. nov. scats along a sandstone crevice. During October (sole collecting record) activity was most pronounced in late afternoon to dusk, when numerous individuals were observed in one small area. Gut contents of two specimens contained remains of orthopteran insects and a salticid spider.

Etymology. From the Amurdak Aboriginal language, *Wulbu* being a clan name for people from Mount Borradaile, the type locality. Used as a noun in apposition.

Cryptoblepharus zoticus sp. nov.

Agile snake-eyed skink

(Plate 3.10; Figs 138–141)

Cryptoblepharus megastictus Storr, 1976. – Wilson and Knowles 1988: 119; Covacevich and Couper 1991: 357; Horner 1991: 17; Ehmann 1992: 182; Cogger 2000: 405; Wilson and Swan 2003: 148.

Type material examined. *Cryptoblepharus zoticus* Horner. HOLOTYPE: Adult male, NTM R25845 (Tissue sample No. *ABTC* EQ1), 10 km south-east of Hells Gate Roadhouse, Queensland, Australia, 17°31'42"S 138°23'45"E. coll. P. Horner and S. Gregg, 18 May 2000. On small outlier of sandstone rock outcrop, 1400 hours. PARATYPES (16 specimens): NORTHERN TERRITORY: NTM R22438, R22587, Limmen Gate National Park, 15°46'30"S 135°19'31"E, T. Griffiths, 12 May 1996; NTM R31849, Sculthorpe Pound, 15°55'S 135°18'E, P. King, 28 August 1985; ANWC R987, junction of Glyde River and Amelia Creek, 16°36'S 136°11'E, 28 October 1975; ANWC R988, Amelia Springs, Mcarthur River, 16°36'S 136°11'E, 7 November 1975; AM R53644, 10 km east of Mcarthur River camp, Glyde River, 16°26'S 136°10'E, 10 February 1976; AM R60390-393, Borroloola, 16°04'S 136°18'E, 6 January 1977. QUEENSLAND: NTM R21451-452, Musselbrook Reserve, Ridgepole Waterhole, 18°40'18"S 138°20'48"E, P. Horner, 12 April 1995; NTM R26641-643, Kingfisher Camp, Bowthorn Station, 17°52'29"S 138°16'58"E, P. and R. Horner, 27 June 2001; SAM R34252, M89, Lawn Hill National park, 18°45'S 138°30'E, S. Donnellan *et al.*, 00 August 1989.

Diagnosis. A small (<40 mm SVL), short-legged, very shallow-headed, saxicoline *Cryptoblepharus*, distinguished from Australian congeners by combination of modal values of five supraciliary scales, 24 mid-body scale rows, 45 paravertebral scales, 19 smooth fourth toe subdigital lamellae, 8 palmar and 10 plantar scales; mean values of 33.4 mm snout-vent length, forelimb length 35.0% of snout-vent length; hindlimb length 42.2% of snout-vent length and head depth of 32.5% of head length; rounded, plain plantar scales, and reddish, irregularly speckled body pattern.

Description (17 specimens). Postnasals absent; prefrontals usually in broad contact (88%), occasionally in narrow contact (6%) or narrowly separated (6%); supraciliaries 5–6 (mean 5.1), modally 5; enlarged upper ciliaries 3; loreals usually subequal (50%) or anterior is largest (47%), occasionally posterior is largest (3%); supralabials 7; fifth

Fig. 138. Ventral surface of hind foot of *Cryptoblepharus zoticus* sp. nov., showing pale, ovate plantar scales (NTM R25845, Hells Gate, Qld). Scale: x20.

Fig. 139. Holotype of *Cryptoblepharus zoticus* sp. nov., NTM R25845, 10 km southeast of Hells Gate Roadhouse, Qld, 17°31'42"S 138°23'45"E, *ABTC* EQ1.

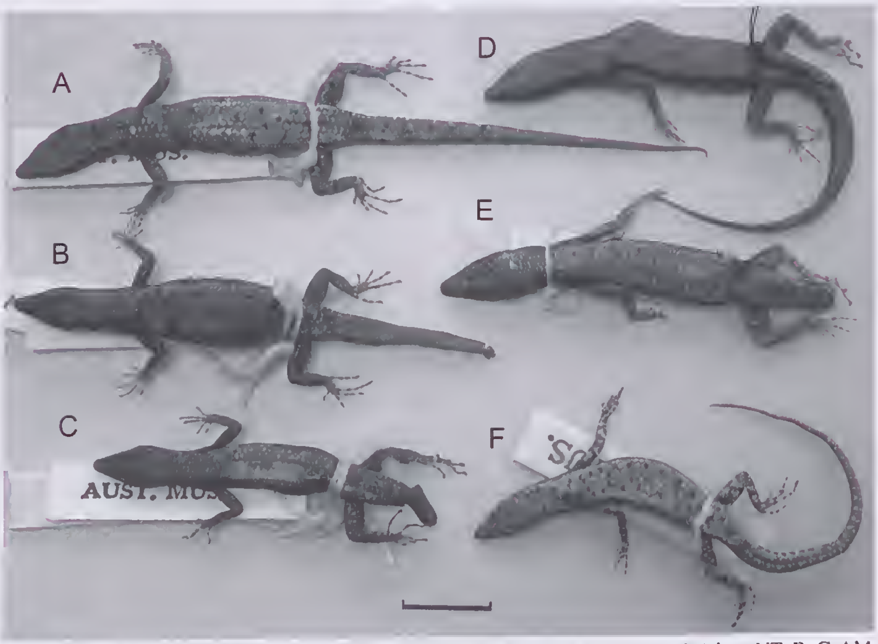

Fig. 140. *Cryptoblepharus zoticus* sp. nov. Preserved material. **A**, AM R53644, Glyde River, NT; **B–C**, AM R60390-391, Borroloola, NT; **D**, NTM R31849, Sculthorpe Pound, NT; **E**, NTM R22587, Limmen Gate, NT; **F**, NTM R26641, Kingfisher Camp, Nicholson River, Qld. Scale bar = 10 mm.

supralabial suboeular (100%); infralabials 6; nuehals 2–6 (mean 2.7), modally 2; bilateral posttemporals usually 3+3 (50%), oeeasionally 2+3 (31%), or 2+2 (19%).

Midbody seale rows 24–28 (mean 24.8), modally 24; paravertebrals 43–51 (mean 45.9), modally 45; subdigital lamellae smooth, 14–18 below fourth finger (mean 16.0) modally 16, 16–21 below fourth toe (mean 18.4) modally 19; 12–14 supradigital lamellae above fourth finger (mean 13.1) modally 13, 14–16 above fourth toe (mean 15.1) modally 15; palmar and plantar seales rounded, without ealli and skin not visible between seales (Fig. 138); plantars 7–13 (mean 9.8), modally 10; palmars 7–9 (mean 7.9), modally 8.

Snout-vent length to 38.7 mm (mean 33.4 mm). *Percentages of snout-vent length*: body length 43.9–52.0% (mean 48.6%); tail length 108.0–146.0% (mean 127.1%); forelimb length 29.6–39.0% (mean 35.0%); hindlimb length 38.4–46.0% (mean 42.2%); forebody length 38.7–46.3% (mean 42.8%); head length 19.8–22.8% (mean 21.1%). *Percentages of head length*: head depth 28.6–36.0% (mean 32.5%); head width 56.3–63.8% (mean 60.5%); snout length 41.5–50.1% (mean 45.6%). Paravertebral seale width 3.6–4.9% (mean 4.2%) of snout-vent length; dorsolateral seale width 75.2–110.9% (mean 91.1%) of paravertebral seale width.

Lentieular seale organs 3–12 (mean 6.0), modally 6. Tooth eounts and hemipenis proportions not measured.

Details of holotype. Adult male (Fig. 139), NTM R25845. Postnasals absent; prefrontals in broad eontact; supraeiliaries 5; enlarged upper eiliaries 3; loreals subequal; supralabials 7; fifth supralabial suboeular; infralabials 6;

nuchals 2. Midbody scale rows 26; paravertebrals 45; subdigital lamellae smooth, 15 below fourth finger; 17 below fourth toe; supradigital lamellae 13 above fourth finger; 15 above fourth toe; palmars and plantars rounded, skin not visible between scales; plantars 9; palmars 8. Snout-vent length 30.3 mm; body length 14.7 mm; tail length 44.2 mm; forelimb length 11.8 mm; hindlimb length 13.9 mm; forebody length 13.2 mm; head length 6.7 mm; head depth 2.0 mm; head width 4.0 mm; snout length 3.0 mm.

Colouration and pattern. A reddish *Cryptoblepharus*, with a body pattern dominated by random, speckling of dark spots, flecks and/or blotches (Plate 3.10). Intensity of body pigmentation and patterning is variable, ranging from pale and obscure to dark and prominent (Fig. 140A–F). Most specimens conform to the following description.

Dorsal ground colour russet to reddish, patterned with random, irregular brown-black spots, flecks, specks and/or blotches. Head concolorous with body, but with fewer dark markings. Labials pale cream. Tail concolorous with body, but with reduced speckling. Limbs concolorous with body, patterned with dark streaks and spots. Venter immaculate off-white. Subdigital lamellae, palmar and plantar surfaces off-white, patterned with occasional dark flecks.

Sex ratio and reproductive biology. Sex ratio favoured females (10:7), but was not significantly different from parity ($X^2 = 0.53$). Males mature at approximately 32.0 mm snout-vent length and females at 32.6 mm. Adults average 33.4 mm snout-vent length and males may be larger than females (maximum SVL = 38.6 versus 38.0 mm). Breeding appears to take place in the summer months, with seven reproductive animals being collected between October (one female), November (one female), January (two males, two females) and February (one female).

Comparison with Australian congeners. Fixed allelic differences place *C. zoticus* sp. nov. in lineage 2 of Australian *Cryptoblepharus* and also distinguish it from congeners within that lineage (as OTU megaA5, Horner and Adams 2007).

Morphologically distinguished from lineage 1 members (*C. australis, C. buchananii, C. cygnatus* sp. nov., *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus, C. metallicus, C. ruber* and *C. wulbu* sp. nov.) by usually having five, rather than six, supraciliary scales and (except for *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus* and *C. wulbu* sp. nov.) speckled or blotched body pattern on reddish ground colour.

Distinguished from most lineage 2 congeners (except *C. ustulatus* sp. nov.) by having reddish ground colour rather than brown, grey or blackish. Further Distinguished from congeners: *C. exochus* sp. nov., *C. mertensi* sp. nov., *C. ochrus* sp. nov., *C. pannosus* sp. nov., *C. plagiocephalus* and *C. tytthos* sp. nov. by rounded plantar scales (versus acute), fewer paravertebral scales (modally 45 versus 48–51), and shallower head (mean 32.5 versus 39.2–43.3 % of head length); from *C. litoralis* and *C. gurrmul* sp. nov. by fewer midbody scale rows (modally 24 versus 26–28) and paravertebral scales (modally 45 versus 55–57); from *C. fuhni* by smooth, less numerous fourth toe subdigital lamellae (versus callused; modally 19 versus 21), shorter hindlimbs (mean 42.2 versus 52.8 % of SVL) and by being smaller (mean SVL, 33.4 versus 41.6 mm); from *C. adamsi* sp. nov. and *C. pulcher* by fewer paravertebral scales (modally 45 versus 50), more plantar scales (modally 10 versus 9), longer limbs (FL, mean 35.0 versus 32.2 % of SVL; RL, mean 42.2 versus 40.5 and 40.9 % of SVL), and shallower head (mean 32.5 versus 39.3 and 40.2 % of head length); from *C. virgatus* by having more midbody scale rows (modally 24 versus 22), more posterior temporal scales (modally 3 versus 2) and shallower head (mean 32.5 versus 38.2 % of head length).

Cryptoblepharus zoticus sp. nov. is most similar to *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus*, *C. ustulatus* sp. nov. and *C. wulbu* sp. nov. in having combinations of reddish ground colour and saxicoline habits. However, it differs from *C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus* and *C. wulbu* sp. nov. by having fewer supraciliary scales (modally 5 versus 6) and further differs from *C. daedalos* sp. nov. and *C. juno* sp. nov. by having fewer plantar (modally 10 versus 15 and 12) and paravertebral scales (modally 45 versus 48 and 49) and shorter hindlimbs (mean 42.2 versus 46.8 and 46.5% of SVL). Further differs from *C. megastictus* by having fewer midbody scale rows (modally 24 versus 26), shorter head (mean 21.1 versus 21.9% of SVL) and speckled instead of blotched body pattern. Further differs from *C. wulbu* sp. nov. by having more paravertebral scales (modally 45 versus 39), fewer plantar scales (modally 10 versus 13) and longer head (mean 21.1 versus 19.9% of SVL). Differs from *C. ustulatus* sp. nov. by having more midbody scale rows (modally 24 versus 22) and fourth finger subdigital lamellae (modally 16 versus 15) and fewer palmar (modally 8 versus 9) and plantar scales (modally 10 versus 11).

Distribution. Rocky ranges of the southern gulf region of northern Australia (Fig. 141), ranging from Limmen Gate National Park in north-eastern Northern Territory, southeast to Mary Kathleen, near Mount Isa, Queensland.

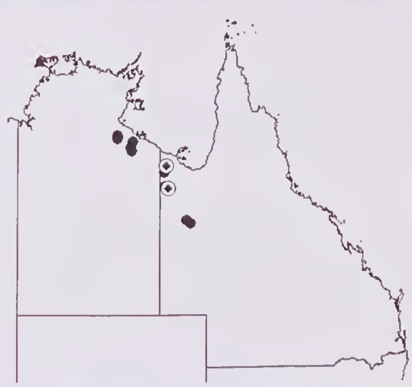

Fig. 141. Map of north-eastern Australia showing distribution of *Cryptoblepharus zoticus* sp. nov. Circled diamonds indicate genetically identified sample sites (Horner and Adams 2007).

Sympatry. *Cryptoblepharus zoticus* sp. nov. occurs in sympatry with *C. australis* and *C. metallicus* from lineage 1. Sympatric with: *C. australis* at Mary Kathleen, Queensland, and with *C. metallicus* at Century Project site, Lawn Hill Station, Queensland and 10 km south-east of Hells Gate Roadhouse, Queensland.

Geographic variation. Geographic variation was investigated by dividing specimens into two disparate groups: *GUC*, a western group of 10 (4 ♂, 6 ♀) samples from bioregions GFU and GUC; *GUP*, a group of 7 (3 ♂, 4 ♀) samples from bioregions GUP and MII.

Group pairs, were sexes were treated separately and combined, were subjected to U-tests of allometrically adjusted variables. Differences detected between males and females were inconsistent, but results for combined sexes indicate that western populations have more fourth toe subdigital lamellae (mean 19.0 versus 17.4) and plantar scales (mean 10.5 versus 8.7), while eastern populations have longer limbs (mean FL 13.6 versus 12.4 mm; RL 16.1 versus 15.1 mm).

Habits and habitats. A saxicoline species, recorded from exposed faces of sandstone ridges, boulders and outliers of low sandstone outcrops.

Etymology. From the Greek adjective *zoticus*, meaning lively; in reference to the perkiness of this taxon.

SOUTH-WEST INDIAN OCEAN REGION TAXA

Thirteen taxa are recognised from the region encompassing eastern Africa, islands of the Mozambique Channel, southern Seychelles, Madagascar and Mauritius (Fig. 142). Comprised of ten monotypic and one polytypic species, the generic content for the region is: *C. africanus*; *C. ahli*; *C. aldabrae*; *C. ater*; *C. bitaeniatus*; *C. boutoni*; *C. caudatus*; *C. cognatus*; *C. gloriosus gloriosus*; *C. gloriosus mayottensis*; *C. gloriosus mohelicus*; *C. quinquetaeniatus* and *C. voeltzkowi*.

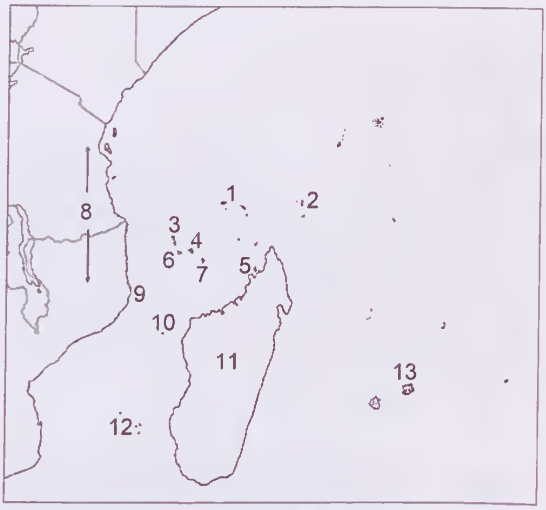

Fig. 142. Map of the south-west Indian Ocean region indicating general distributions of: 1, *Cryptoblepharus aldabrae* (Aldabra and Farquhar Island groups); 2, *C. g. gloriosus* (Ile Glorieuses); 3, *C. ater* (Grande Comore, Comoro Islands); 4, *C. gloriosus mayottensis* (Mayotte Island, Comoro Islands); 5, *C. cognatus* (Nosy Bé Island); 6, *C. quinquetaeniatus* (Nzwane, Comoro Islands); 7, *C. gloriosus mohelicus* (Mwali Island, Comoro Islands); 8, *C. africanus* (coastal east Africa between Muqdisho, Somalia and Black Rock, South Africa); 9, *C. ahli* (Ilha de Moçambique); 10, *C. caudatus* (Ile Juan de Nova); 11, *C. voeltzkowi* (Madagascar); 12, *C. bitaeniatus* (Europa Island); 13, *C. boutonii* (Mascarene Islands)

Key to Southwest Indian Ocean *Cryptoblepharus* taxa

1 a. Midbody scale rows 26 or less; body pattern simple or complex, but not composed of alternating, subequal, dark and pale stripes 2
b. Midbody scale rows 28; simple body pattern of alternating, subequal, dark and pale stripes .... *C. bitaeniatus*

2 a. Mode of 24 or less midbody scale rows 4
b. Mode of 26 midbody scale rows 3

3 a. Size medium (mean SVL: 37.0 mm); paravertebral scales usually 49; limbs relatively long (mean: forelimb 35.9% hindlimb 45.0% of SVL); head relatively small (mean: depth 45.0% width 61.6% of head length) .... *C. boutoni*
b. Size relatively large (mean SVL: 43.9 mm); paravertebral scales usually 55; limbs relatively short (mean: forelimb 30.9% hindlimb 39.4% of SVL); head relatively large (mean: depth 50.5% width 68.4% of head length) .... *C. caudatus*

4 a. Mode of 22 midbody scale rows 9
b. Mode of 24 midbody scale rows 5

5 a. Body pattern simple or complex, but not solely composed of small, irregular, pale spots, flecks and dots on dark background 6
b. Reduced body pattern of small, irregular, pale spots, flecks and dots on dark background .... *C. ater*

6 a. Size medium (mean SVL: <40 mm); paravertebral scales usually 52 or less; forelimbs relatively long (mean >33.5% of SVL); head relatively long (mean 20.5% of SVL) 7
b. Size large (mean SVL: 47.7 mm); paravertebral scales usually 56; forelimbs relatively short (mean 32.7% of SVL); head relatively short (mean 18.8% of SVL).. .... *C. ahli*

7 a. Paravertebral scales usually 50 or more; limbs relatively long (mean forelimb: >35% hindlimb: >44% of SVL); head relatively small (mean depth: <49% width: <64% of head length) 8
b. Paravertebral scales usually 47; limbs relatively short (mean forelimb: 33.7% hindlimb: 42.5% of SVL); head relatively large (mean depth: 49.4% width: 65.6% of head length) .... *C. aldabrae*

8 a. Size relatively small (mean SVL 36.5 mm); paravertebral scales usually 52; fourth toe subdigital lamellae usually 18; pale laterodorsal stripe smooth edged ... . *C. gloriosus mayottensis*

b. Size relatively large (mean SVL 39.9 mm); paravertebral scales usually 50; fourth toe subdigital lamellae usually 21; pale laterodorsal stripe ragged edged..... .... *C. voeltzkowi*

9 a. Body pattern simple or complex, but not solely composed of 5–7 very, narrow pale stripes on dark background.. 10

b. Simple body pattern of 5–7 very, narrow pale stripes on dark background ....*C. quinquetaeniatus*

10 a. Size medium (mean SVL <42 mm); hindlimbs relatively short (mean <43% of SVL); head relatively small (mean depth <44.5% width <61% of head length)... 11

b. Size relatively large (mean SVL 43.9 mm); hindlimbs relatively long (mean 44.2% of SVL); head relatively large (mean depth 46.9% width 63% of head length) .... *C. africanus*

11 a. Nuchal scales usually in two pairs; fourth finger subdigital lamellae usually 16; palmar scales usually 11 or more; plantar scales usually 11 or more........... 12

b. Nuchal scales usually a single pair; fourth finger subdigital lamellae usually 14; palmar scales usually 9; plantar scales usually 10 ....*C. cognatus*

12 a. Paravertebral scales usually 47; plantar scales usually 11; forelimbs relatively long (mean 35.4% of SVL); forebody relatively long (mean 42.7% of SVL)....... .... *C. gloriosus mohelicus*

b. Paravertebral scales usually 51; plantar scales usually 13; forelimbs relatively short (mean 30.1% of SVL); forebody relatively short (mean 39.2% of SVL .... *C. gloriosus gloriosus*

Cryptoblepharus africanus (Sternfeld, 1918)

(Fig. 143)

Type material examined. *Ablepharus boutoni africanus* Sternfeld, 1918. LECTOTYPE: SMF 15550, Manda Island, Coastal Province, Kenya, Africa. A. Voeltzkow, 1905. PARALECTOTYPES: SMF 15551-56, Tazi Cliffs, Manda Bay, Coastal Province, Kenya, Africa. A. Voeltzkow, 1905.

Non-type material examined. See Appendix 4.

Description (10 specimens). A large (45–50 mm SVL), long-legged, deep-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 4–6 (mean 5.2), modally 5; enlarged upper ciliaries 3–4 (mean 3.0), modally 3; posterior loreal usually largest; supralabials 6–8 (mean 7.2), modally 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.4), modally 6; nuchals 2–4 (mean 3.1), modally 4.

Midbody scale rows 21–24 (mean 22.2), modally 22; paravertebrals 48–54 (mean 50.2), modally 50; subdigital lamellae smooth, 14–16 below fourth finger (mean 15.7) modally 16, 18–22 below fourth toe (mean 20.3) modally 20; 13–14 supradigital lamellae above fourth finger (mean 13.3)

Fig. 143. Lectotype of *Ablepharus boutoni africanus* Sternfeld, 1918. SMF 15550, Manda Island, Coastal Province, Kenya, Africa.

modally 13, 16–19 above fourth toe (mean 17.5) modally 18; palmar and plantar scales rounded; plantars 9–11 (mean 10.5), modally 11; palmars 8–11 (mean 9.8), modally 10.

Snout-vent length to 47.6 mm (mean 43.9 mm); *Percentages of snout-vent length*: body length 48.4–59.6% (mean 54.0%); tail length 147.0–156.1% (mean 152.4%); forelimb length 31.7–37.3% (mean 34.7%); hindlimb length 40.2–47.2% (mean 44.2%); forebody length 38.5–43.0% (mean 40.1%); head length 18.4–20.8% (mean 19.3%). *Percentages of head length*: head depth 41.9–52.3% (mean 46.9%); head width 59.4–67.4% (mean 63.0%); snout length 42.6–47.9% (mean 44.5%). Paravertebral scale width 4.0–4.7% (mean 4.3%) of snout-vent length; dorsolateral scale width 74.1–84.0% (mean 78.8%) of paravertebral scale width.

A dark *Cryptoblepharus* with a complex body pattern of longitudinally aligned stripes, spots and specks. Dorsally, a broad, dark brown vertebral zone is bordered by ragged, narrow, black dorsolateral stripes and prominent broad, pale, smooth-edged laterodorsal stipes (Fig. 143).

Distribution. Rocky foreshores of the African east coast, from Muqdisho in Somalia, south to Black Rock, Tongaland coast, South Africa (Haacke 1977). Records from Luuq in Somalia and Mazoe in Zimbabwe (Mertens 1931) indicate *C. africanus* also occurs inland from the coast.

Remarks. A littoral species (Brygoo 1986; Canaris 1973; Canaris and Murphy 1965) that inhabits rocky outcrops and headlands. Forages in the intertidal zone (Haacke 1977) and beach strand line (Canaris and Murphy 1965). Röll (2001) determined *C. africanus* to be a visually guided predator that hunts insects on the shore and other small invertebrates in intertidal pools. Canaris (1973) recorded stomach contents of 82 specimens as comprising 70% marine crustaceans and 27% insect remains.

Cryptoblepharus ahli Mertens, 1928

(Fig. 144)

Type material examined. *Cryptoblepharus boutonii ahli* Mertens, 1928. HOLOTYPE: ZMB 33124, Mozambique Island, Nampula Province, Mozambique, Africa. W. Peters, 18 December 1848. PARATYPES: ZMB 1353 (1353A), ZMB 57156 (1353C), ZMB 57157 (1353), ZMB 57158 (1353D), ZMB 57159 (1353B), SMF 22187, Mo-

Fig. 144. Paratype of *Cryptoblepharus boutonii ahli* Mertens, 1928. ZMB 1353A, Ilha de Moçambique (Mozambique Island), Mozambique, Africa.

zambique Island, Nampula Province, Mozambique, Africa. W. Peters, 1842-1848.

Description (7 specimens). A very large (>50 mm SVL), short-legged, deep-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–6 (mean 5.1), modally 5; 3 enlarged upper ciliaries; loreals usually subequal in size; supralabials 7–8 (mean 7.1), modally 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.9), modally 7; nuchals 2–3 (mean 2.1), modally 2.

Midbody scale rows 24; paravertebrals 50–56 (mean 53.4), modally 56; subdigital lamellae smooth, 15–18 below fourth finger (mean 16.1) modally 15, 19–22 below fourth toe (mean 20.3) modally 20; 13–15 supradigital lamellae above fourth finger (mean 13.6) modally 13, 16–17 above fourth toe (mean 16.7) modally 17; palmar and plantar scales rounded; plantars 11–14 (mean 12.6), modally 12; palmars 10–13 (mean 11.6), modally 11.

Snout-vent length to 50.7 mm (mean 47.7 mm). *Percentages of snout-vent length*: body length 53.2–57.3% (mean 55.0%); tail length 159.9%; forelimb length 30.4–36.8% (mean 32.7%); hindlimb length 39.3–47.1% (mean 42.5%); forebody length 36.6–42.1% (mean 39.6%); head length 18.0–19.8% (mean 18.8%). *Percentages of head length*: head depth 40.2–50.6% (mean 46.1%); head width 56.7–66.6% (mean 63.5%); snout length 42.1–46.7% (mean 44.9%). Paravertebral scale width 3.2–3.7% (mean 3.4%) of snout-vent length; dorsolateral scale width 86.0–100.8% (mean 94.8%) of paravertebral scale width.

A brown-grey *Cryptoblepharus* with a complex body pattern of longitudinally aligned stripes, spots and specks. On the dorsum, a broad, brown vertebral zone is bordered by ragged, narrow, black dorsolateral stripes and prominent, broad, pale grey, smooth-edged laterodorsal stipes (Fig. 144).

Distribution. Ilha de Moçambique, Mozambique, Africa.

Remarks. Habits unknown. Mertens (1928) distinguished the taxon from, geographically neighbouring, *C. africanus* by size and colouration. Brygoo (1986) determined that the *C. ahli* values for these two variables fell within the range recorded for *C. africanus* and treated the name as a synonym of *C. b. africanus*. This study indicates significant morphological differences exist between the two taxa (snout-vent length 43.9 versus 47.7 mm, $p = 0.035^{*}$; mid-body scale rows 22 versus 24, $p = 0.002^{***}$; paravertebral scales 50 versus 56, $p = 0.012^{**}$; number of plantar scales 11 versus 12, $p = 0.001^{***}$) and supports recognition of *C. ahli*.

Cryptoblepharus aldabrae (Sternfeld, 1918)

(Fig. 145)

Type material examined. *Ablepharus boutoni aldabrae* Sternfeld, 1918. LECTOTYPE: SMF 15586, Aldabra, A. Voeltzkow, 1897. PARALECTOTYPES: SMF 15587-91, ZMB 16637, Aldabra, A. Voeltzkow, 1897.

Non-type material examined. See Appendix 4.

Description (7 specimens). A large (45–50 mm SVL), short-legged, very deep-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5; enlarged upper ciliaries 3–4 (mean 3.1), modally 3; posterior loreal usually largest; supralabials 6–7 (mean 6.8), modally 7; fifth supralabial usually subocular; infralabials 5–7 (mean 6.5), modally 7; nuchals 2–5 (mean 2.9), modally 3.

Midbody scale rows 22–24 (mean 23.4), modally 24; paravertebrals 46–56 (mean 49.7), modally 47; subdigital lamellae smooth, 14–16 below fourth finger (mean 15.0) modally 15, 18–21 below fourth toe (mean 19.5) modally 20; 12–13 supradigital lamellae above fourth finger (mean 12.6) modally 13, 14–18 above fourth toe (mean 15.7) modally 16; palmar and plantar scales rounded; plantars 12–17 (mean 13.3), modally 12; palmars 10–14 (mean 12.1), modally 13.

Snout-vent length to 45.6 mm (mean 36.9 mm). *Percentages of snout-vent length*: body length 50.6–58.3% (mean 54.5%); tail length 140.3–145.5% (mean 142.9%); forelimb length 31.1–35.6% (mean 33.7%); hindlimb length 39.5–45.5% (mean 42.5%); forebody length 36.5–44.0% (mean 41.4%); head length 18.1–21.8% (mean 20.5%). *Percentages of head length*: head depth 43.4–52.5% (mean 49.4%); head width 63.5–69.4% (mean 65.6%); snout length 43.1–48.8% (mean 45.0%). Paravertebral scale width 3.4–4.7% (mean 3.9%) of snout-vent length; dorsolateral scale width 82.0–96.7% (mean 87.1%) of paravertebral scale width.

A grey-brown *Cryptoblepharus* with a complex body pattern of longitudinally aligned stripes, spots and specks.

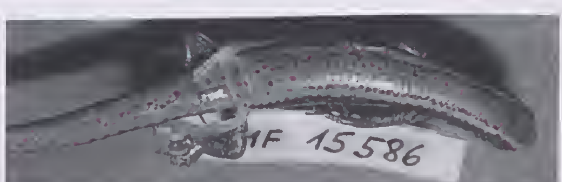

Fig. 145. Lectotype of *Ablepharus boutoni aldabrae* Sternfeld, 1918. SMF 15586, Aldabra Atoll, Seychelles, Africa.

Dorsally, a broad, brown vertebral zone is bordered by ragged, narrow, discontinuous, black dorsolateral stripes and narrow, pale grey, smooth-edged laterodorsal stipes that are most prominent anteriorly (Fig. 145).

Distribution. Aldabra and Farquhar island groups, Seychelles, Africa. Recorded from South and West Islands of the Aldabra Atoll, Assumption, Astove, Picard, Menai and Cosmoledo Atoll, and Saint Pierre Island of the Farquhar group (Brygoo 1986).

Remarks. Honegger (1966) noted this taxon preferred coral islands to granite islands and was as frequently seen in close proximity to the surf zone as in houses and huts. In the littoral zone it sheltered under drift wood or among dead coral sticks, while in buildings wall cracks were favoured. An interesting observation by Honegger (1966) is that reproduction is by soft-shelled eggs, he located over 70 (4 x 6 mm) eggs under one clump of broken coral.

Cryptoblepharus ater (Boettger, 1913)
(Fig. 146)

Type material examined. *Ablepharus boutoni atra* (sic) Boettger, 1913. LECTOTYPE: SMF 15571, Grande Comore, Comoro Islands, Africa. A. Voeltzkow, 1905. PARALECTOTYPES: ZMB 5552, 5552A, 19035, 19453C, 19453G, SMF 15573-575, BMNH 1946.8.15.84, Grande Comore, Comoro Islands, Africa. A. Voeltzkow, 1905.

Description (10 specimens). A large (45–50 mm SVL), short-legged, deep-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5; enlarged upper ciliaries 3; anterior loreal usually largest; supralabials 7–8 (mean 7.2), modally 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.6), modally 7; nuchals 2–4 (mean 2.4), modally 2.

Midbody scale rows 24–26 (mean 24.2), modally 24; paravertebrals 47–56 (mean 51.8), modally 50; subdigital lamellae smooth, 14–18 below fourth finger (mean 16.1) modally 16, 19–21 below fourth toe (mean 20.2) modally 21; 12–15 supradigital lamellae above fourth finger (mean 13.5) modally 13, 16–18 above fourth toe (mean 16.8) modally 17; palmar and plantar scales rounded; plantars 9–13 (mean 11.3), modally 12; palmars 9–12 (mean 10.3), modally 10.

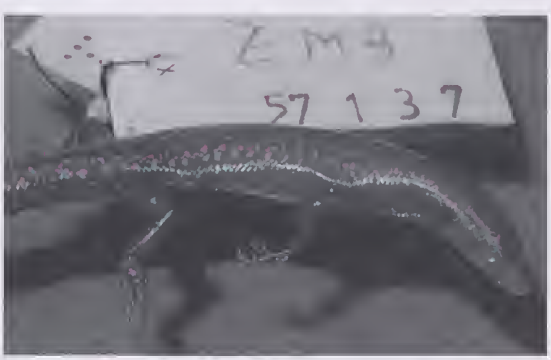

Fig. 146. Paralectotype of *Ablepharus boutonii atra* Boettger, 1913. ZMB 57137, Grande Comore, Comoro Islands, Africa.

Snout-vent length to 48.2 mm (mean 43.9 mm). *Percentages of snout-vent length*: body length 48.9–58.1% (mean 53.0%); tail length indeterminate; forelimb length 30.3–36.7% (mean 34.3%); hindlimb length 40.4–45.4% (mean 43.3%); forebody length 37.0–43.9% (mean 40.9%); head length 19.5–21.8% (mean 20.6%). *Percentages of head length*: head depth 41.3–50.2% (mean 45.4%); head width 55.8–64.9% (mean 62.2%); snout length 43.1–49.3% (mean 45.0%). Paravertebral scale width 4.3–4.7% (mean 4.5%) of snout-vent length; dorsolateral scale width 72.9–86.5% (mean 79.3%) of paravertebral scale width.

A blackish *Cryptoblepharus* with a reduced body pattern of small, pale streaks, spots and dots. These are usually most prominent laterodorsally, indicating an obscure, broken laterodorsal stripe (Fig. 146). As indicated in Fig. 146, the type series are russet to glossy brown in ground colour which is probably an artefact of preservation, as Boettger (1913) described the taxon as "Schwarz glänzend, fast einfarbig, … Körperseiten und Gliedmaßen wenig deutlich weißlich punktiert" ("Black shiny, almost monochrome, … Body sides and limbs with small distinct whitish dots"). Both Mertens (1931, 1964) and Brygoo (1986) refer to this taxon as a melanotic form.

Distribution. Endemic to the island of Grande Comore, Comoro Islands, Africa (Brygoo 1986).

Remarks. Boettger (1913) based his original description on 50 specimens, taken from the coast of Grande Comore.

Cryptoblepharus bitaeniatus (Boettger, 1913)
(Fig. 147)

Type material examined. *Ablepharus boutoni bitaeniata* (sic) Boettger, 1913. LECTOTYPE: SMF 15601, Europa Island, Reunion, Africa. A. Voeltzkow, 1905. PARALECTOTYPES: ZMB 19209, 19209A-C, 19520, 19520A-B, 25611, 25611A, Europa Island, Reunion, Africa. A. Voeltzkow, 1905.

Description (10 specimens). A medium sized (40–44 mm SVL), short-legged, deep-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5; enlarged upper ciliaries 3; posterior loreal usually largest; supralabials 7–8 (mean 7.2), modally 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.6), modally 7; nuchals 2–5 (mean 3.7), modally 4.

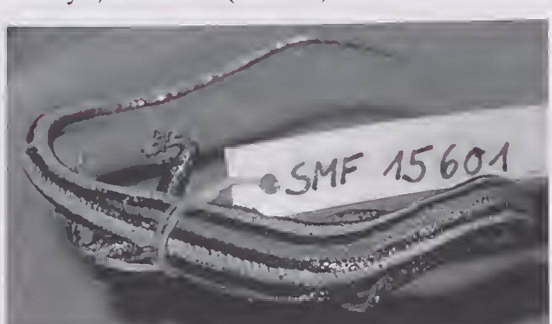

Fig. 147. Lectotype of *Ablepharus boutoni bitaeniata* Boettger, 1913. SMF 15601, Europa Island, Reunion, Africa.

Midbody scale rows 28–30 (mean 28.2), modally 28; paravertebrals 53–60 (mean 55.8), modally 53; subdigital lamellae smooth, 13–16 below fourth finger (mean 15.0) modally 16, 19–21 below fourth toe (mean 19.8) modally 19; 13–14 supradigital lamellae above fourth finger (mean 13.4) modally 13, 15–18 above fourth toe (mean 16.9) modally 17; palmar and plantar scales rounded; plantars 12–13 (mean 12.2), modally 12; palmars 9–11 (mean 10.1), modally 10.

Snout-vent length to 42.4 mm (mean 40.3 mm). *Percentages of snout-vent length*: body length 47.8–54.4% (mean 50.3%); tail length 127.3–127.4% (mean 127.4%); forelimb length 29.5–35.1% (mean 32.3%); hindlimb length 37.3–44.5% (mean 41.7%); forebody length 39.7–43.6% (mean 41.6%); head length 19.5–22.0% (mean 20.4%). *Percentages of head length*: head depth 42.2–51.2% (mean 47.0%); head width 59.5–67.7% (mean 62.8%); snout length 43.6–51.2% (mean 46.7%). Paravertebral scale width 3.4–3.9% (mean 3.7%) of snout-vent length; dorsolateral scale width 84.3–103.5% (mean 95.8%) of paravertebral scale width.

Boldly striped, *C. bitaeniatus* has a simple body pattern of longitudinally aligned, dark and pale stripes. These consist of a light grey vertebral stripe/zone, black dorsolateral, cream laterodorsal, black upper lateral and light grey midlateral stripes. A dark brown lower lateral stripe may occur on posterior half of body (Fig. 147).

Distribution. Endemic to Ile Europa, southern Mozambique Channel, Reunion, Africa.

Remarks. Abundant from the shoreline to the centre of the 28 km² island (Brygoo 1986).

***Cryptoblepharus boutonii* (Desjardin, 1831)**
(Fig. 148)

Type material examined. *Scincus boutonii* Desjardin, 1831. SYNTYPE: ZMB 8722, Fouquet Island, Mauritius. K. Möbius.

Non-type material examined. See Appendix 4.

Description (12 specimens). A medium sized (40–45 mm SVL), long-legged, deep-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–6 (mean 5.1), modally 5; enlarged upper ciliaries 3–4 (mean 3.1), modally 3; anterior loreal usually largest; supralabials 7–8 (mean 7.2), modally 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.5), modally 6; nuchals 2–4 (mean 3.3), modally 4.

Midbody scale rows 24–26 (mean 25.7), modally 26; paravertebrals 48–54 (mean 50.0), modally 49; subdigital lamellae smooth, 14–16 below fourth finger (mean 15.1) modally 15, 19–22 below fourth toe (mean 20.0) modally 20; 12–14 supradigital lamellae above fourth finger (mean 12.9) modally 13, 15–17 above fourth toe (mean 15.9) modally 15; palmar and plantar scales rounded; plantars 12–15 (mean 13.7), modally 14; palmars 11–13 (mean 11.4), modally 11.

Snout-vent length to 42.0 mm (mean 37.0 mm). *Percentages of snout-vent length*: body length 45.5–54.3% (mean 50.9%); tail length 124.8–148.0% (mean 136.4%); forelimb length 33.3–39.5% (mean 35.9%); hindlimb length 41.2–50.3% (mean 45.0%); forebody length 38.7–43.7% (mean 41.3%); head length 19.7–22.8% (mean 20.7%). *Percentages of head length*: head depth 41.8–47.8% (mean 45.0%); head width 54.1–65.0% (mean 61.6%); snout length 41.0–50.8% (mean 45.4%). Paravertebral scale width 2.6–3.2% (mean 3.0%) of snout-vent length; dorsolateral scale width 81.3–94.5% (mean 89.0%) of paravertebral scale width.

A grey *Cryptoblepharus* with a complex body pattern of longitudinally aligned zones, spots and specks. Dorsally, a grey vertebral zone is bordered by paravertebral series of blackish spots and vague broad, light grey, laterodorsal zones (Fig. 148).

Distribution. Mauritius and nearby islets, Mascarene Islands, Africa. On Mauritius *C. boutonii* has been recorded from Cap Malhéreux, Pointe Lafayette and Rock Mécusson (basalt outcrop on Palmar Beach), and from islets Coin de Mire (Gunner's Quoin), de la Passe, Forquet, and Round Island (Brygoo 1986).

Remarks. Desjardin (1831) based his description on two individuals that were collected from ground among rocks, in the district of Flacq.

***Cryptoblepharus caudatus* (Sternfeld, 1918)**
(Fig. 149)

Type material examined. *Ablepharus boutoni caudatus* Sternfeld, 1918. LECTOTYPE: SMF 15592, Juan de Nova Island, Reunion, Africa. A. Voeltzkow, 1897. PARALECTOTYPES: SMF 15593-97, SMF 15600, BMNH 1946.8.15.76,

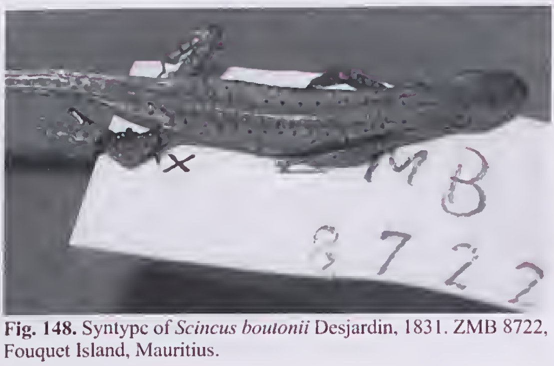

Fig. 148. Syntype of *Scincus boutonii* Desjardin, 1831. ZMB 8722, Fouquet Island, Mauritius.

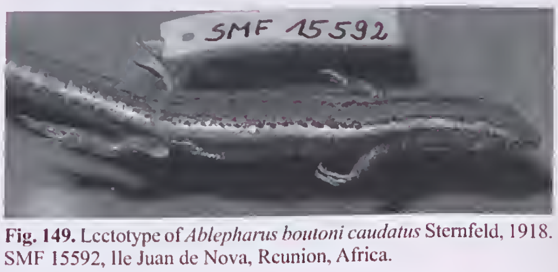

Fig. 149. Lectotype of *Ablepharus boutoni caudatus* Sternfeld, 1918. SMF 15592, Ile Juan de Nova, Reunion, Africa.

Juan de Nova Island, Reunion, Africa. A. Voeltzkow, 1897.

Description (8 specimens). A large (45–50 mm SVL), very short-legged, very deep-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 4–5 (mean 4.9), modally 5; enlarged upper ciliaries 3; posterior loreal usually largest; supralabials 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.2), modally 6; nuchals 2–3 (mean 2.2), modally 2.

Midbody scale rows 24–28 (mean 26.1), modally 26; paravertebrals 55–60 (mean 56.9), modally 55; subdigital lamellae smooth, 13–16 below fourth finger (mean 14.6) modally 15, 17–20 below fourth toe (mean 18.4) modally 19; 12–13 supradigital lamellae above fourth finger (mean 12.4) modally 12, 15–17 above fourth toe (mean 16.1) modally 17; palmar and plantar scales rounded; plantars 10–13 (mean 12.2), modally 13; palmars 10–13 (mean 11.4), modally 11.

Snout-vent length to 48.7 mm (mean 43.9 mm). *Percentages of snout-vent length*: body length 51.3–58.5% (mean 54.4%); tail length 138.8–150.8% (mean 144.9%); forelimb length 27.5–31.1% (mean 30.9%); hindlimb length 37.5–42.6% (mean 39.4%); forebody length 38.3–42.3% (mean 40.2%); head length 17.6–20.3% (mean 19.1%). *Percentages of head length*: head depth 49.1–54.5% (mean 50.5%); head width 60.5–72.6% (mean 68.4%); snout length 42.2–49.1% (mean 46.2%). Paravertebral scale width 4.0–4.8% (mean 4.5%) of snout-vent length; dorsolateral scale width 82.9–92.8% (mean 87.4%) of paravertebral scale width.

A brownish *Cryptoblepharus* with a complex body pattern of longitudinally aligned stripes, spots and specks. Dorsally, a broad, brown vertebral zone is bordered by ragged, narrow, black dorsolateral stripes and prominent broad, pale, smooth-edged laterodorsal stipes (Fig. 149).

Distribution. Endemic to Ile Juan de Nova, Mozambique Channel, Reunion, Africa.

Remarks. Only known from the type-series, collected by A. Voeltzkow in 1897. Voeltzkow (1897) stated "belebt in grosser Anzahl die Dünen" (= enliven the dunes in large numbers).

Cryptoblepharus cognatus (Boettger, 1881)

(Fig. 150)

Type material examined. *Ablepharus boutoni cognatus* Boettger, 1881. HOLOTYPE: SMF 15548, Nosy Bé Island, Madagascar. A. Stumpff; 1881. PARATYPE?: SMF 15549, Nosy Bé Island, Madagascar. A. Stumpff, 1881.

Non-type material examined. See Appendix 4.

Description (4 specimens). A medium sized (40–44 mm SVL), short-legged, shallow-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5; enlarged upper ciliaries 3; loreals usually subequal; supralabials 6–7 (mean 6.6), modally 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.2), modally 6; nuchals 4–7 (mean 5.0), modally 4.

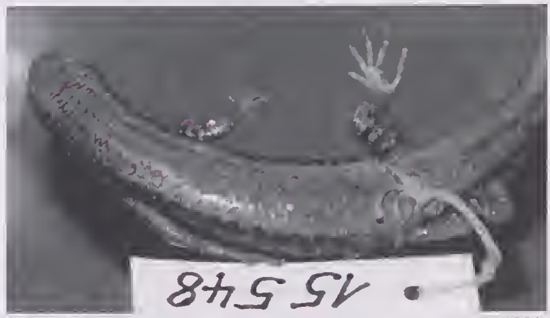

Fig. 150. Lectotype of *Ablepharus boutoni cognatus* Boettger, 1881. SMF 15548, Nosy Bé, Madagascar.

Midbody scale rows 22; paravertebrals 49–51 (mean 50.0), modally 50; subdigital lamellae smooth, 13–15 below fourth finger (mean 14.0) modally 14, 17–18 below fourth toe (mean 17.7) modally 18; 12–14 supradigital lamellae above fourth finger (mean 13.0) modally 13, 16 above fourth toe; palmar and plantar scales rounded; plantars 8–12 (mean 10.2), modally not available; palmars 7–10 (mean 8.7), modally 9.

Snout-vent length to 43.8 mm (mean 41.1 mm). *Percentages of snout-vent length*: body length 53.6–54.2% (mean 54.0%); tail length 131.4% (n = 1); forelimb length 31.0–37.7% (mean 33.7%); hindlimb length 40.1–48.0% (mean 42.8%); forebody length 38.3–40.6% (mean 39.4%); head length 19.0–20.5% (mean 19.7%). *Percentages of head length*: head depth 39.6–44.9% (mean 42.6%); head width 57.8–62.9% (mean 59.8%); snout length 43.5–47.3% (mean 45.3%). Paravertebral scale width 4.2–5.0% (mean 4.5%) of snout-vent length; dorsolateral scale width 73.9–85.6% (mean 80.6%) of paravertebral scale width.

A greyish *Cryptoblepharus* with a complex, longitudinally aligned body pattern of broad zones, spots and specks. Dorsally, a broad, grey vertebral zone has only vague indication of stripes anteriorly. Indistinct, narrow, pale laterodorsal stripes border prominent dark upper lateral zone (Fig. 150).

Distribution. Endemic to Nosy Bé and nearby islands, off the north-western coast of Madagascar. Recorded from Ambariobe at South Rock and from Tany Kely, a small islet off Nosy Bé (Brygoo 1986). Andreone *et al.* (2003) in a herpetofaunal survey of Nosy Bé and 'satellite islands', located *C. cognatus* on: Nosy Bé, Nosy Ambariobe, Nosy Fanihy, Nosy Mitsio, Nosy Sakatia and Nosy Tanikely.

Remarks. The status of SMF 15549 as a paratype is uncertain. Collection data is identical to that of the holotype and it is noted as a paratype in the SMF catalogue, however, in the original description Boettger (1881) states that his diagnosis is based on a single specimen.

Fricke (1970) studied the ecology of *C. cognatus* and observed that the taxon "….descended daily into the intertidal zone to feed there on insects, crustaceans and fish (juvenile *Periophthalmus kohlreuteri*). The pattern of activity of the animals is related to the movements of the tides. The lizards have a definite home range and migrate between intertidal feeding area and resting place on land along pathways established by experience. They return to their home even if released at about 200 m from their home range because they seem to acquire a knowledge of the surrounding by occasional exploratory visits. The tendency to establish a home range and homing behaviour are considered as adaptations for life in the intertidal zone, but the lizard remains a purely terrestrial animal".

Cryptoblepharus gloriosus (Stejneger, 1893)
(Figs 151–153)

Description (21 specimens). A medium sized (33–44 mm SVL), littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–6 (mean 5.2), modally 5; enlarged upper ciliaries 2–4 (mean 3.0), modally 3; posterior loreal usually largest; supralabials 7; fifth supralabial subocular; infralabials 6–7 (mean 6.7), modally 7; nuchals 2–5 (mean 2.7), modally 2.

Midbody scale rows 20–24 (mean 22.7), modally 24; paravertebrals 46–55 (mean 50.3), modally 52; subdigital lamellae smooth, 13–16 below fourth finger (mean 15.1) modally 15, 16–21 below fourth toe (mean 19.0) modally 19; 12–14 supradigital lamellae above fourth finger (mean 12.8) modally 13, 12–17 above fourth toe (mean 16.1) modally 16; palmar and plantar scales rounded; plantars 10–17 (mean 12.3), modally 13; palmars 9–14 (mean 10.8), modally 10.

Snout-vent length to 43.7 mm (mean 37.7 mm). *Percentages of snout-vent length*: body length 47.7–59.6% (mean 52.0%); tail length indeterminate; forelimb length 27.8–37.70% (mean 34.2%); hindlimb length 37.0–47.3% (mean 42.6%); forebody length 37.6–44.5% (mean 40.7%); head length 18.2–21.8% (mean 20.2%). *Percentages of head length*: head depth 36.9–50.9% (mean 45.1%); head width 57.1–66.5% (mean 60.6%); snout length 40.7–49.5% (mean 44.9%). Paravertebral scale width 3.4–5.1% (mean 4.0%) of snout-vent length; dorsolateral scale width 70.6–96.3% (mean 81.6%) of paravertebral scale width.

Boldly striped, *C. gloriosus* has a simple body pattern of longitudinally aligned, dark and pale zones and stripes.

Distribution. Islands of the Mozambique Channel between Africa and northern Madacascar, from Ile Glorieuses, Mayotte and Mwali Islands.

Subspecies. *Cryptoblepharus gloriosus* is a polytypic taxon composed of three allopatric subspecies: *Cryptoblepharus gloriosus gloriosus* (Stejneger, 1893); *Cryptoblepharus gloriosus mayottensis* Mertens, 1928; *Cryptoblepharus gloriosus mohelicus* Mertens, 1928

Cryptoblepharus gloriosus gloriosus (Stejneger, 1893)
(Fig. 151)

Type material examined. *Ablepharus gloriosus* Stejneger, 1893. HOLOTYPE: USNM 20463, Glorioso Islands, Mozambique Channel Islands, Africa. W. Abbott, January 1873. PARATYPES: USNM 204644-466, Glorioso Islands, Mozambique Channel Islands, Africa. W. Abbott, January 1873.

Non-type material examined. See Appendix 4.

Description (5 specimens). A medium sized (40–44 mm SVL), very short-legged, shallow-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact: supraciliaries 5–6 (mean 5.3), modally 5; enlarged upper ciliaries 2–4 (mean 2.9), modally 3; posterior loreal usually largest; supralabials 7; fifth supralabial subocular; infralabials 6–7 (mean 6.2), modally 6; nuchals 2–5 (mean 2.6), modally 2.

Midbody scale rows 20–22 (mean 21.0), modally 22; paravertebrals 47–54 (mean 50.6), modally 51; subdigital lamellae smooth, 15–16 below fourth finger (mean 15.6) modally 16, 16–21 below fourth toe (mean 19.0) modally 19; 12–13 supradigital lamellae above fourth finger (mean 12.2) modally 12, 12–17 above fourth toe (mean 15.6) modally 16; palmar and plantar scales rounded; plantars 12–17 (mean 13.8), modally 13; palmars 10–14 (mean 12.0), modally indeterminate.

Snout-vent length to 43.7 mm (mean 39.8 mm). *Percentages of snout-vent length*: body length 49.7–59.6% (mean 54.7%); tail length indeterminate; forelimb length 27.7–33.0% (mean 30.1%); hindlimb length 37.0–40.8% (mean 39.0%); forebody length 37.7–41.3% (mean 39.2%); head length 18.2–20.1% (mean 19.0%). *Percentages of head length*: head depth 36.9–46.8% (mean 42.5%); head width 58.0–66.4% (mean 60.6%); snout length 40.6–45.2% (mean 43.6%). Paravertebral scale width 3.7–5.1% (mean 4.5%) of snout-vent length; dorsolateral scale width 70.6–87.9% (mean 80.7%) of paravertebral scale width.

Boldly striped, *C. g. gloriosus* has a simple body pattern of longitudinally aligned, dark and pale zones and stripes. These consist of a broad brown vertebral zone, black dorsolateral, cream laterodorsal, black upper lateral, cream mid-lateral and brown lower lateral stripes (Fig. 151). Palmar and plantar surfaces blackish (Stejneger 1893).

Comparison with conspecifics. Distinguished from *C. g. mayottensis* and *C. g. mohelicus* by having shorter forelimbs (mean % of SVL: 30.1 instead of 35.4 or more). Further distinguished from *C. g. mayottensis* by fewer midbody scale rows (mode 22 instead of 24), more palmar scales (mode 12 instead of 10) and larger size (mean SVL 39.8 instead of 36.5 mm). Further distinguished from *C. g. mohelicus* by shorter snout (mean % of head length: 43.6 instead of 47.3), more paravertebral (mode 51 instead of 47) and plantar (mode 13 instead of 11) scales.

Distribution. Endemic to Glorioso Islands, Mozambique Channel, Reunion, Africa.

Fig. 151. *Cryptoblepharus g. gloriosus* (Stejneger, 1893). BMNH 1953.1.12.23, Glorioso Islands, Mozambique Channel Islands, Africa.

***Cryptoblepharus gloriosus mayottensis* Mertens, 1928**
(Fig. 152)

Type material examined. *Cryptoblepharus boutonii mayottensis* Mertens, 1928. HOLOTYPE: ZMB 19451, Mayotte Island, Comoro Islands, Africa. A. Voeltzkow, 1905. PARATYPES: ZMB 19451 A to I, SMF 15537, Mayotte Island, Comoro Islands. Africa. A. Voeltzkow, 1905.

Description (11 specimens). A small (<40 mm SVL), long-legged, deep-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–6 (mean 5.3), modally 5; enlarged upper ciliaries 3; posterior loreal usually largest; supralabials 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.9), modally 7; nuchals 2–4 (mean 2.8), modally 2.

Midbody scale rows 22–24 (mean 23.4), modally 24; paravertebrals 48–55 (mean 51.7), modally 52; subdigital lamellae smooth, 13–16 below fourth finger (mean 14.6) modally 15, 18–20 below fourth toe (mean 18.7) modally 18; 12–14 supradigital lamellae above fourth finger (mean 12.9) modally 13, 15–17 above fourth toe (mean 16.2) modally 16; palmar and plantar scales rounded; plantars 10–14 (mean 12.3), modally 13; palmars 9–12 (mean 10.4), modally 10.

Snout-vent length to 39.9 mm (mean 36.5 mm). *Percentages of snout-vent length*: body length 48.6–56.5% (mean 51.5%); tail length 152.8–162.4% (mean 157.6%); forelimb length 32.0–37.7% (mean 35.7%); hindlimb length 39.8–47.3% (mean 44.4%); forebody length 37.6–43.1% (mean 40.8%); head length 19.3–21.2% (mean 20.5%). *Percentages of head length*: head depth 43.6–50.9% (mean 46.6%); head width 57.1–66.5% (mean 61.1%); snout length 40.9–48.0% (mean 44.9%). Paravertebral scale width 3.4–3.8% (mean 3.6%) of snout-vent length; dorsolateral scale width 73.3–87.3% (mean 80.3%) of paravertebral scale width.

A dark *Cryptoblepharus* with a simple body pattern of straight-edged, longitudinally aligned, dark and pale zones and stripes. These consist of a narrow, dark brown vertebral zone, broad black dorsolateral, narrow cream laterodorsal, broad black upper lateral, narrow cream mid-lateral and dark lower lateral stipes (Fig. 152).

Comparison with conspecifics. Distinguished from *C. g. gloriosus* by having longer forelimbs (mean % of SVL: 35.7 instead of 30.1), more midbody scale rows (mode 24 instead of 22), fewer palmar scales (mode 10 instead of 12) and smaller size (mean SVL 36.5 instead of 39.8 mm). Distinguished from *C. g. mohelicus* by shorter snout (mean % of head length: 44.9 instead of 47.3), more paravertebral (mode 52 instead of 47) and plantar (mode 13 instead of 11) scales and fewer fourth toe subdigital lamellae (mode 18 instead of 20).

Distribution. Endemic to Mayotte Island, Comoro Islands. Africa.

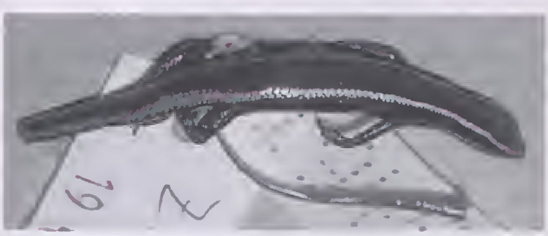

Fig. 152. Paralectotype of *Cryptoblepharus boutonii mayottensis* Mertens, 1928. ZMB 19451, Mayotte, Comoro Islands, Africa.

***Cryptoblepharus gloriosus mohelicus* Mertens, 1928**
(Fig. 153)

Type material examined. *Cryptoblepharus boutonii mohelicus* Mertens, 1928. HOLOTYPE: ZMB 33125 (ex 19450), Miremani, Mohéli (Mwali) Island, Comoro Islands, Africa. A. Voeltzkow, 1905. PARATYPES: ZMB 19036, 33125, 57179, SMF 22177 Miremani, Mohéli (Mwali) Island, Comoro Islands, Africa. A. Voeltzkow, 1905.

Description (5 specimens). A small (<40 mm SVL), short-legged, shallow-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5; enlarged upper ciliaries 3; posterior loreal usually largest; supralabials 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.6), modally 7; nuchals 2–3 (mean 2.4), modally 2.

Midbody scale rows 22–24 (mean 22.8), modally 22; paravertebrals 46–48 (mean 47.0), modally 47; subdigital lamellae smooth, 15–16 below fourth finger (mean 15.7) modally 16, 19–20 below fourth toe (mean 19.7) modally 20; 13 supradigital lamellae above fourth finger, 16–17 above fourth toe (mean 16.7) modally 17; palmar and plantar scales rounded; plantars 10–12 (mean 11.0), modally indeterminate; palmars 9–11 (mean 10.2), modally 11.

Snout-vent length to 39.7 mm (mean 38.8 mm). *Percentages of snout-vent length*: body length 47.7–52.4% (mean 49.6%); tail length 146.9% (n = 1); forelimb length 34.4–36.1% (mean 35.4%); hindlimb length 39.3–44.7% (mean 41.9%); forebody length 41.5–44.5% (mean 42.7%); head length 20.1–21.8% (mean 21.0%). *Percentages of head length*: head depth 38.5–50.8% (mean 44.1%); head width 57.2–60.0% (mean 58.4%); snout length 45.7–49.5% (mean 47.3%). Paravertebral scale width 3.6–4.3% (mean 4.0%) of snout-vent length; dorsolateral scale width 77.4–96.3% (mean 85.0%) of paravertebral scale width.

A dark *Cryptoblepharus* with a body pattern of straight-edged, longitudinally aligned, dark and pale zones and

Fig. 153. Holotype of *Cryptoblepharus boutonii mohelicus* Mertens, 1928. ZMB 33125, Miremani, Mwali, Comoro Islands, Africa.

stripes, with some dark and pale speckling. The type series are all poorly preserved, being hard and discoloured, however, they show indications of a dark brown vertebral zone, black dorsolateral, cream laterodorsal, black upper lateral, cream mid-lateral and dark lower lateral stipes (Fig. 153). Mertens (1928) described the taxon as a half melanotic form.

Comparison with conspecifics. Distinguished from *C. g. gloriosus* by having longer forelimbs (mean % of SVL: 35.4 instead of 30.1), fewer paravertebral (mode 47 instead of 51) and plantar scales (mode 11 instead of 13) and longer snout (mean % of head length: 47.3 instead of 43.6). Distinguished from *C. g. mayottensis* by longer snout (mean % of head length: 47.3 instead of 44.9), fewer paravertebral (mode 47 instead of 52) and plantar (mode 11 instead of 13) scales and more fourth toe subdigital lamellae (mode 20 instead of 18).

Distribution. Endemic to Mwali Island, Comoro Islands, Africa.

Cryptoblepharus quinquetaeniatus (Günther, 1874)
(Fig. 154)

Type material examined. *Ablepharus quinquetaeniatus* Günther, 1874. SYNTYPES: BMNH 1946.8.18.51-52, west coast of Africa. Captain Parry. *Cryptoblepharus boutonii degrijsi* Mertens, 1928a. HOLOTYPE: SMF 15547, Anjouan, Comoro Islands, Africa. A. Voeltzkow, 1905. *Cryptoblepharus boutonii degrijsi* Mertens, 1928a. PARATYPES: SMF 15538, SMF 15540-41, ZMB 19034 (19034B), ZMB 57160-164 (formerly part of 19034). BMNH 1946.8.15.83, Anjouan, Comoro Islands, Africa. A. Voeltzkow, 1905.

Description (12 specimens). A medium sized (40–44 mm SVL), short-legged, shallow-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5; enlarged upper ciliaries 3; posterior loreal usually largest; supralabials 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.7), modally 7; nuchals 2–6 (mean 3.5), modally 2.

Midbody scale rows 22–24 (mean 22.5), modally 22; paravertebrals 49–56 (mean 52.0), modally 50; subdigital lamellae smooth, 14–18 below fourth finger (mean 15.9) modally 16, 20–23 below fourth toe (mean 21.1) modally 21; 12–14 supradigital lamellae above fourth finger (mean 13.0) modally 13, 15–18 above fourth toe (mean 16.7) modally 17; palmar and plantar scales rounded; plantars 12–14 (mean 12.5), modally 12; palmars 10–12 (mean 11.3), modally 12.

Snout-vent length to 43.5 mm (mean 39.0 mm). *Percentages of snout-vent length*: body length 49.2–55.6% (mean 52.1%); tail length 124.6–129.6% (mean 127.8%); forelimb length 31.1–36.0% (mean 34.1%); hindlimb length 40.4–46.7% (mean 43.2%); forebody length 37.2–44.5% (mean 40.5%); head length 18.8–21.7% (mean 20.2%). *Percentages of head length*: head depth 37.9–54.1% (mean 43.3%); head width 53.9–62.6% (mean 57.8%); snout length 42.8–47.6% (mean 45.4%). Paravertebral scale width 3.9–4.5% (mean 4.1% %) of snout-vent length; dorsolateral scale width 73.3–88.5% (mean 78.0%) of paravertebral scale width.

Simply patterned with five very narrow, silvery-white, longitudinal stripes on a black background (Mertens, 1931; Brygoo, 1986). As indicated in Fig. 154, the type specimens examined had a red to reddish-brown ground colour which was probably an artefact of preservation (Brygoo, 1986), being similar to the condition described for *C. ater*.

Distribution. Endemic to Nzwane (Anjouan), Comoro Islands, Africa.

Remarks. This study follows Brygoo (1986) in merging *C. quinquetaeniatus* and *C. degrijsi* but, on the grounds of priority of publication, proposes that *C. b. degrijsi* Mertens, 1928 be treated as a junior synonym of *C. b. quinquetaeniatus* (Günther 1874).

Cryptoblepharus voeltzkowi (Sternfeld, 1918)
(Fig. 155)

Type material examined. *Ablepharus boutoni voeltzkowi* Sternfeld, 1918. LECTOTYPE: SMF 15584, Majunga, Madagascar. A. Voeltzkow, 1893. PARALECTOTYPE: SMF 15585, Majunga, Madagascar. A. Voeltzkow, 1893.

Description (2 specimens). A medium sized (40–44 mm SVL), very long-legged, very deep-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5; enlarged upper ciliaries 3; posterior loreal largest; supralabials 6–7 (mean 6.7), modally indeterminate; fifth supralabial usually subocular; infralabials 6; nuchals 2–6 (mean 4.0), modally indeterminate.

Midbody scale rows 24; paravertebrals 47–52 (mean 49.5), modally indeterminate; subdigital lamellae smooth, 15–16 below fourth finger (mean 15.5) modally indeterminate, 20–22 below fourth toe (mean 21.0) modally indeterminate; 13 supradigital lamellae above fourth finger, 16–17 above fourth toe (mean 16.5) modally indeterminate; palmar and plantar scales rounded; plantars 10; palmars 8–9 (mean 8.5), modally indeterminate.

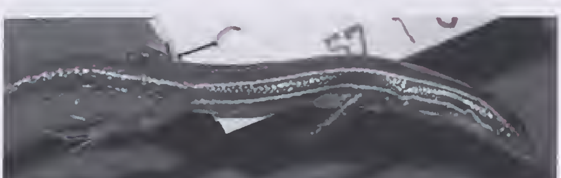

Fig. 154. *Cryptoblepharus quinquetaeniatus*, illustrated by paratype of *Cryptoblepharus boutonii degrijsi* Mertens, 1928. ZMB 57163, Nzwane (Anjouan), Comoro Islands, Africa.

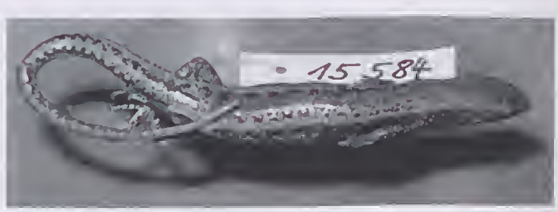

Fig. 155. Lectotype of *Ablepharus boutoni voeltzkowi* Sternfeld, 1918. SMF 15584, Mahajanga (Majunga), Madagascar, Africa.

Snout-vent length to 42.2 mm (mean 39.9 mm). *Percentages of snout-vent length*: body length 49.7–50.9% (mean 50.3%); tail length 143.5% (n = 1); forelimb length 34.5–36.0% (mean 35.2%); hindlimb length 46.2–47.8% (mean 47.0%); forebody length 39.7–42.2% (mean 41.0%); head length 20.2–20.9% (mean 20.5%). *Percentages of head length*: head depth 47.0–50.4% (mean 48.7%); head width 63.1–64.4% (mean 63.7%); snout length 42.7–43.3% (mean 43.0%). Paravertebral scale width 3.5–3.7% (mean 3.6%) of snout-vent length; dorsolateral scale width 87.1–88.7% (mean 87.9%) of paravertebral scale width.

A grey *Cryptoblepharus* with a complex body pattern of longitudinally aligned zones, stripes, spots and specks. Dorsally, a broad, brown-grey vertebral zone is bordered by ragged, narrow, discontinuous black dorsolateral and pale grey laterodorsal stipes. The blackish upper lateral zone is flecked with pale spots and coalesces with greyish lower lateral zone and pale venter (Fig. 155).

Distribution. Endemic to Madagascar, where it is known from the coastal regions of Mahajanga (Majunga) in the northwest, Morombe / Toliara (Tuléar) in the south-west (Brygoo 1986), and Tolagnaro (= Fort Dauphin) on the southeastern coast (Andreone and Greer 2002).

Remarks. A littoral dwelling, saxicoline species. Brygoo (1986) suggests the disjunct distribution probably results from lack of collecting in intervening areas.

INDO-PACIFIC REGION TAXA

Twenty four taxa are recognised from the region encompassing Indonesia (Fig. 156), New Guinea and islands of the Pacific Ocean (to the west coast of South America) (Fig. 157). Comprised of 17 monotypic and three polytypic species, as well as one subspecific component of an Australian taxon, the generic content for the region is: *C. baliensis baliensis*; *C. baliensis sumbawanus*; *C. burdeni*; *C. cursor cursor*; *C. cursor larsonae* ssp. nov.; *C. egeriae*; *C. eximius*; *C. furvus* sp. nov.; *C. intermedius*; *C. keiensis*; *C. leschenault*; *C. litoralis vicinus* ssp. nov.; *C. nigropunctatus*; *C. novaeguineae*; *C. novocaledonicus*; *C. novohebridicus*; *C. poecilopleurus paschalis*; *C. poecilopleurus poecilopleurus*; *C. renschi*; *C. richardsi* sp. nov.; *C. rutilus*; *C. schlegelianus*; *C. xenikos* sp. nov. and *C. yulensis* sp. nov.

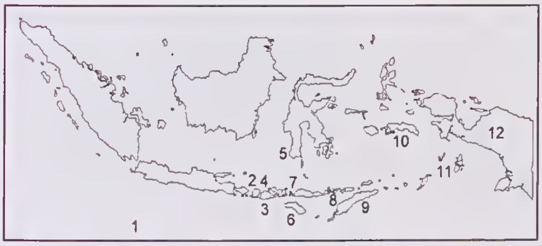

Fig. 156. Map of the Indo-Pacific region indicating general distributions of Indonesian taxa: 1, *Cryptoblepharus egeriae* (Christmas Island); 2, *C. b. baliensis* (Bali, Lombok, Java); 3, *C. b. sumbawanus* (Sumbawa); 4, *C. c. cursor* (Lombok); 5, *C. c. larsonae* (Sulawesi); 6, *C. renschi* (Sumba, Komodo); 7, *C. burdeni* (Komodo); 8, *C. leschenault* (Flores, Timor); 9, *C. schlegelianus* (Timor); 10, *C. intermedius* (Maluku Province); 11, *C. keiensis* (Kai Islands); 12, *C. novaeguineae* (New Guinea, Aru Islands).

Fig. 157. Map of the West-Pacific region indicating general distributions of Pacific Ocean taxa: 1, *Cryptoblepharus nigropunctatus* (Ogasawara-gunto, Japan); 2, *C. rutilus* (Palau Islands); 3, *C. novaeguineae* (New Guinea, Aru Islands); 4, *C. xenikos* sp. nov. (Trans-Fly region, New Guinea); 5, *C. yulensis* sp. nov. (southern New Guinea); 6, *C. furvus* sp. nov. (Normanby Island, New Guinea); 7, *C. richardsi* sp. nov. (Misima Island, New Guinea); 8, *C. novocaledonicus* (New Caledonia); 9, *C. novohebridicus* (Vanuatu); 10, *C. eximius* (Fiji); 11, *C. p. poecilopleurus* (widespread through Pacific Islands to South America); 12, *C. poecilopleurus paschalis* (off map - Easter Island, Chile).

Key to Indo-Pacific *Cryptoblepharus* taxa

1 a. Interparietal and frontoparietals fused; supralabial scales usually seven 2
b. Interparietal distinct from fused frontoparietals; supralabial scales usually eight .... *C. egeriae*

2 a. Mode of 28 or less midbody scale rows; body pattern simple or complex, but normally longitudinally aligned.. 3
b. Mode of 30 midbody scale rows; reduced body pattern of scattered, irregular pale flecks on dark background.. *C. burdeni*

3 a. Mode of 26 or less midbody scale rows 5
b. Mode of 28 midbody scale rows............................. 4

4 a. Paravertebral scales usually 57; palmar scales usually 13; plantar scales usually 16 .... *C. poecilopleurus paschalis*
b. Paravertebral scales usually 54; palmar scales usually 12; plantar scales usually 13 .... *C. poecilopleurus poecilopleurus*

5 a. Mode of 24 or less midbody scale rows 15
b. Mode of 26 midbody scale rows............................. 6

6 a. Boldly striped body pattern; plantar scales usually 13 or less; size medium to small (max. SVL <44 mm). 8
b. Reduced melanotic body pattern; plantar scales usually 15 or more; size relatively large (max. SVL >45 mm)... 7

7 a. Paravertebral scales usually 51; nuchal scales usually 2; fourth finger subdigital lamellae usually 16; hindlimb relatively long (mean 45.2% of SVL); head relatively large (mean depth 47.1% width 62.6% of head length).................. *C. litoralis vicinus* ssp. nov.
b. Paravertebral scales usually 60; nuchal scales usually 4; fourth finger subdigital lamellae usually 19; hindlimb relatively short (mean 42.4% of SVL); head relatively small (mean depth 42.9% width 56.7% of head length)..................................*C. furvus* sp. nov.

8 a. Supraciliary scales usually 5; body pattern complex with broad vertebral zone of ground colour......... 12
b. Supraciliary scales usually 6; body pattern simple with prominent, pale or dark, narrow vertebral stripe.... 9

9 a. Paravertebral scales usually 48 or more; fourth finger subdigital lamellae usually 17 or less; fourth toe subdigital lamellae usually 22; head relatively long and narrow (mean length 21% or more of SVL, width <62% of head length); snout relatively short (mean <46% of head length).. 10
b. Paravertebral scales usually 46; fourth finger subdigital lamellae usually 19; fourth toe subdigital lamellae usually 23; head relatively short and wide (mean length 20.1% of SVL, width 64.3% of head length); snout relatively long (mean 47.1% of head length) ....
.... *C. intermedius*

10 a. Dark dorsolateral stripe obscure and ragged on posterior half of body; forebody relatively long (mean 43% of SVL); head relatively long (mean 21.8% of SVL)
.... 11
b. Dark dorsolateral stripe broad and smooth edged to hindlimbs; forebody relatively short (mean 42.1% of SVL); head relatively long (mean 21.0% of SVL)...
.... *C. leschenault*

11 a. Limbs relatively long (mean forelimb 35.5% hindlimb 44.2% of SVL); pale vertebral stripe forks into two obscure, narrow, pale paravertebral stripes bordering dark vertebral stripe ....*C. baliensis baliensis*
b. Limbs relatively short (mean forelimb 33.0% hindlimb 41.3% of SVL); pale vertebral stripe extends from rostral to hindlimbs .... *C. baliensis sumbawanus*

12 a. Paravertebral scales usually 50 or more; fourth toe subdigital lamellae usually 19 or more; forelimbs relatively long (mean >34% of SVL) 13
b. Paravertebral scales usually 46; fourth toe subdigital lamellae usually 16; forelimbs relatively short (mean 28.6% of SVL).............................. *C. schlegelianus*

13 a. Fourth finger subdigital lamellae usually 17 or more; fourth toe subdigital lamellae usually 21 or more; forebody relatively long (mean 42% or more of SVL)...
.... 14
b. Fourth finger subdigital lamellae usually 15; fourth toe subdigital lamellae usually 19; forebody relatively short (mean 38% of SVL).......................................
....................................*C. cursor larsonae* ssp. nov.

14 a. Fourth finger subdigital lamellae usually 19; head relatively deep (mean 45% of head length); paravertebral scales relatively narrow (mean 3.6% of SVL); size relatively small (mean SVL, 34.9 mm) ....
.... *C. eximius*
b. Fourth finger subdigital lamellae usually 17; head relatively shallow (mean 40% of head length); paravertebral scales relatively wide (mean 4.4% of SVL); size relatively large (mean SVL, 38.6 mm).............
.... *C. richardsi* sp. nov.

15 a. Mode of 22 or less midbody scale rows 21
b. Mode of 24 midbody scale rows.......................... 16

16 a. Paravertebral scales usually 53 or less; fourth toe subdigital lamellae usually 21 or less; palmar scales usually 12 or less; plantar scales usually 13 or less; size medium to small (max. SVL <42 mm).......... 17
b. Paravertebral scales usually 57; fourth toe subdigital lamellae usually 24; palmar scales usually 14; plantar scales usually 16; size large (max. SVL 51.1 mm)...
.... *C. nigropunctatus*

17 a. Supraciliary scales usually five; palmar scales usually 10 or more; plantar scales usually 11 or more...... 19
b. Supraciliary scales usually six; palmar scales usually 9 or less; plantar scales usually 10 or less 18

18 a. Fourth finger subdigital lamellae usually 17; hindlimb relatively long (mean 42.2% of SVL); head relatively deep (mean 46.9% of head length); body pattern with prominent, narrow, pale vertebral stripe...*C. renschi*
b. Fourth finger subdigital lamellae usually 15; hindlimb relatively short (mean 39.5% of SVL); head relatively shallow (mean 42.4% of head length); body pattern with broad vertebral zone of ground colour ....
....*C. yulensis* sp. nov.

19 a. Fourth finger subdigital lamellae usually 16 or less; palmar scales usually 11 or less; plantar scales usually 12 or less; size medium (max. SVL <38 mm); pale midlateral stripe present..20
b. Fourth finger subdigital lamellae usually 18; palmar scales usually 12; plantar scales usually 13; size relatively large (max. SVL 41.2 mm); pale midlateral stripe absent .... *C. novocaledonicus*

20 a. Paravertebral scales usually 50; fourth toe subdigital lamellae usually 18; nuchal scales usually 4; limbs relatively long (mean forelimb 35.0% hindlimb 44.9% of SVL) .... *C. cursor cursor*
b. Paravertebral scales usually 52; fourth toe subdigital lamellae usually 21; nuchal scales usually 6; limbs relatively short (mean forelimb 33.2% hindlimb 41.3% of SVL) .... *C. novohebridicus*

21 a. Fourth finger subdigital lamellae usually 18; fourth toe subdigital lamellae usually 23 or more; palmar scales usually 10 or more 22
b. Fourth finger subdigital lamellae usually 16; fourth toe subdigital lamellae usually 19; palmar scales usually 9.. *C. xenikos* sp. nov.

22 a. Supraciliary scales usually six; midbody scale rows usually 22 23
b. Supraciliary scales usually five; midbody scale rows usually 20 .... *C. rutilus*

23 a. Paravertebral scales usually 47; nuchal scales usually 2; complex body pattern of zones, stripes and flecks on gray or brown background........ *C. novaeguineae*
b. Paravertebral scales usually 50; nuchal scales usually 4; simple body pattern of alternating dark and pale stripes .... *C. keiensis*

Cryptoblepharus baliensis Barbour, 1911

(Plate 4.1; Figs 158–159)

Description (20 specimens). A medium sized (40–44 mm SVL), deep-headed, arboreal *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–7; enlarged upper ciliaries 3–4; posterior loreal usually largest; supralabials 7–8; fifth supralabial usually subocular; infralabials 5–7; nuchals 2–6.

Midbody scale rows 24–28, usually 26; paravertebrals 45–55; subdigital lamellae smooth, 16–19 below fourth finger, 19–24 below fourth toe; 11–14 supradigital lamellae above fourth finger, 14–18 above fourth toe; palmar and plantar scales rounded; plantars 10–13; palmars 8–12.

Snout-vent length to 41.7 mm. *Percentages of snout-vent length*: body length 46.1–52.9%; tail length 135.3–139.7%; forelimb length 28.1–39.5%; hindlimb length 37.4–47.4%; forebody length 38.4–45.4%; head length 19.1–23.3%. *Percentages of head length*: head depth 43.1–51.9%; head width 52.3–66.0%; snout length 42.5–47.6%. Paravertebral scale width 4.0–5.1% of snout-vent length; dorsolateral scale width 63.0–86.3% of paravertebral scale width.

Boldly striped, *C. baliensis* has a simple body pattern of longitudinally aligned, dark and pale stripes.

Distribution. Central Indonesia, from Java, Bali, Lombok and Sumbawa.

Subspecies. *Cryptoblepharus baliensis* is a polytypic taxon comprised of two allopatric subspecies: *Cryptoblepharus baliensis baliensis* Barbour, 1911; *Cryptoblepharus baliensis sumbawanus* Mertens, 1928a

Cryptoblepharus baliensis baliensis Barbour, 1911

(Plate 4.1; Fig. 158)

Type material examined. *Cryptoblepharus boutonii baliensis* Barbour, 1911. HOLOTYPE: MCZ 7480, Buleleng, Bali Island, Indonesia. T. Barbour, 1906-7.

Non-type material examined. See Appendix 4.

Description (10 specimens). Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–7 (mean 6.0), modally 6; enlarged upper ciliaries 3–4 (mean 3.3), modally 3; posterior loreal usually largest; supralabials 7; fifth supralabial subocular; infralabials 5–7 (mean 6.1), modally 6; nuchals 2–3 (mean 2.1), modally 2.

Fig. 158. Holotype of *Cryptoblepharus boutonii baliensis* Barbour, 1911. MCZ 7480, Buleleng, Bali Island, Indonesia.

Midbody scale rows 24–28 (mean 26.0), modally 26; paravertebrals 46–53 (mean 49.4), modally 48; subdigital lamellae smooth, 16–19 below fourth finger (mean 17.1) modally 17, 19–24 below fourth toe (mean 21.8) modally 22; 11–13 supradigital lamellae above fourth finger (mean 12.5) modally 13, 16–18 above fourth toe (mean 16.5) modally 16; palmar and plantar scales rounded; plantars 10–13 (mean 11.2), modally 11; palmars 9–12 (mean 10.9), modally 11.

Snout-vent length to 41.7 mm (mean 38.6 mm). *Percentages of snout-vent length*: body length 46.1–52.4% (mean 49.1%); tail length 139.7% (n = 1); forelimb length 31.0–39.5% (mean 35.5%); hindlimb length 38.7–47.4% (mean 44.2%); forebody length 38.4–45.4% (mean 43.0%); head length 19.1–22.9% (mean 21.8%). *Percentages of head length*: head depth 43.1–51.9% (mean 47.2%); head width 52.3–66.0% (mean 60.6%); snout length 42.7–47.3% (mean 44.7%). Paravertebral scale width 4.0–5.1% (mean 4.5%) of snout-vent length; dorsolateral scale width 63.0–80.7% (mean 73.2%) of paravertebral scale width.

Cryptoblepharus b. baliensis has a simple body pattern of longitudinally aligned, dark and pale stripes. A broad, black vertebral stripe on the body and tail forks at the forelimb into two black paravertebral stripes that border a short pale mid-dorsal stripe on the head and neck. The broad, pale laterodorsal zones may be immaculate or contain traces of dark dorsolateral stripes. The dark upper lateral zones are speckled with pale spots and flecks. A vague, pale mid-lateral stripe may be present from labials to forelimb (Fig. 158). In life, specimens may be bluish with black markings (Plate 4.1, K. Martin pers comm.).

Distribution. Central Indonesia, where it is known from Madura and Parang Island off northern Java, eastern Java, Saobi Island in the Kangean island group, Buleleng district of northern Bali and at Ekas, Laboehan Hadji, Narmada and Selong on Lombok (Mertens 1964).

Remarks. Mertens (1930) observed *C. b. baliensis* on large trees lining the way from the temple to the sea at Sangsit, and on trees at Boelocleng and Gitgit (ca. 400–500 m). McKay (2006) records it as inhabiting trees in monsoon forest.

***Cryptoblepharus baliensis sumbawanus* Mertens, 1928**
(Fig. 159)

Type material examined. *Cryptoblepharus boutonii sumbawanus* Mertens, 1928. HOLOTYPE: SMF 22096, Sumbawa Besar, Sumbawa, Indonesia. R. Mertens, 1927. PARATYPES: SMF 22199, Batoe Doelang, west Sumbawa, Indonesia. R. Mertens, 1927; SMF 22178-84, BMNH 1946.8.15.85, Sumbawa Besar, Sumbawa, Indonesia. R. Mertens, 1927.

Description (10 specimens). Postnasals absent; prefrontals usually in broad contact; supraciliaries 6; enlarged upper ciliaries 3–4 (mean 3.0), modally 3; posterior loreal usually largest; supralabials 7–8 (mean 7.3), modally 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.0), modally 6; nuchals 2–6 (mean 3.1), modally 2.

Midbody scale rows 24–28 (mean 25.9), modally 26; paravertebrals 45–55 (mean 48.8), modally 50; subdigital lamellae smooth, 16–19 below fourth finger (mean 17.4) modally 17, 20–22 below fourth toe (mean 21.4) modally 22; 12–14 supradigital lamellae above fourth finger (mean 13.0) modally 13, 14–18 above fourth toe (mean 16.1) modally 17; palmar and plantar scales rounded; plantars 10–12 (mean 11.0), modally 11; palmars 8–12 (mean 10.0), modally 10.

Snout-vent length to 41.1 mm (mean 38.5 mm). *Percentages of snout-vent length*: body length 46.4–52.9% (mean 50.4%); tail length 135.3–137.4% (mean 136.4%); forelimb length 28.1–35.5% (mean 33.0%); hindlimb length 37.4–43.2% (mean 41.3%); forebody length 40.3–44.7% (mean 43.2%); head length 20.1–23.3% (mean 21.9%). *Percentages of head length*: head depth 44.9–51.7% (mean 47.3%); head width 57.4–63.1% (mean 60.6%); snout length 42.5–47.6% (mean 45.8%). Paravertebral scale width 4.3–4.9% (mean 4.5%) of snout-vent length; dorsolateral scale width 73.8–86.3% (mean 78.7%) of paravertebral scale width.

Boldly striped, *C. b. sumbawanus* has a simple body pattern of longitudinally aligned, dark and pale stripes. Dorsally, these consist of pale vertebral, dark dorsolateral and pale laterodorsal stripes. The dark upper lateral zone is usually speckled with pale spots and flecks. A vague pale mid-lateral stripe may be present (Fig. 159).

Distribution. Sumbawa, Indonesia. Known from Sumbawa Besar, Batoedoelang and Batoe Lanteh (800–900 m) in the west of the island (Mertens 1928a).

Remarks. Mertens (1930) found *C. b. sumbawanus* on large trees of dry monsoon forest at Sumbawa Besar, where it was abundant, and on trees of luxuriant rain forest at nearby Semongkat Atas.

***Cryptoblepharus burdeni* Dunn, 1927**
(Fig. 160)

Type material examined. *Cryptoblepharus boutonii burdeni* Dunn, 1927. HOLOTYPE: AMNH 32006, east coast of Padar Island, Nusa Tenggara Timur, Indonesia. Burden East Indian Expedition, 7 July 1926. PARATYPES: AMNH 32013–014, SMF 55452–453, east coast of Padar Island, Nusa Tenggara Timur, Indonesia. Burden East Indian Expedition, 7 July 1926.

Description (5 specimens). A large (45–50 mm SVL), long-legged, very shallow-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–6 (mean 5.1), modally 5; enlarged upper ciliaries 3; loreals usually subequal; supralabials 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.1), modally 6; nuchals 2–3 (mean 2.2), modally 2.

Midbody scale rows 30–32 (mean 30.8), modally 30; paravertebrals 51–58 (mean 53.4), modally 51; subdigital lamellae smooth, 15–18 below fourth finger (mean 15.8) modally 15, 17–21 below fourth toe (mean 18.8) modally 17; 12–14 supradigital lamellae above fourth finger (mean 12.8) modally 13, 15–17 above fourth toe (mean 15.6) modally 15; palmar and plantar scales rounded; plantars 9–11 (mean 9.8), modally 9; palmars 7–10 (mean 8.4), modally 8.

Snout-vent length to 45.6 mm (mean 43.9 mm). *Percentages of snout-vent length*: body length 52.3–54.8% (mean 53.2%); tail length 132.9–136.9% (mean 134.9%); forelimb length 33.1–35.1% (mean 34.0%); hindlimb length 43.1–45.5% (mean 44.4%); forebody length 39.2–44.3% (mean 41.4%); head length 20.6–22.0% (mean 21.3%). *Percentages of head length*: head depth 35.4–40.6% (mean 37.4%); head width 55.2–59.9% (mean 57.6%); snout length 43.7–45.6% (mean 44.5%). Paravertebral scale width 3.0–3.4% (mean 3.2%) of snout-vent length; dorsolateral scale width 91.7–99.3% (mean 96.1%) of paravertebral scale width.

A dark *Cryptoblepharus* (Fig. 160), described by Auffenberg (1980) as "Entire upper surface metallic dark brown to nearly black, with scattered, irregular lighter flecks. Some individuals nearly uniform brassy brown with slightly darker edge to each scale, sometimes forming faint interrupted longitudinal lines. Ventral surface always an almost

Fig. 159. Holotype of *Cryptoblepharus boutonii sumbawanus* Mertens, 1928. SMF 22096, Batoe Doelang, Sumbawa Besar, Sumbawa Island, Indonesia.

Fig. 160. Paratype of *Cryptoblepharus boutonii burdeni* Dunn, 1927. SMF 55453, west coast of Padar Island, Indonesia.

uniform bluish-grey to grey; palmar surfaces very dark, soles lighter".

Distribution. Central Indonesia, on rocky shores of Padar, Komodo and nearby islets, also observed on rocky headlands of extreme western Flores (Auffenberg, 1980).

Remarks. A saxicoline, littoral species. Dunn (1927) stated: "… on rocks at the tide line on the east coast of Padar. … in great numbers, …. On the wave-cut bench of rock, beset with small pools, and alive with *Periopthalmus* and crabs of various kinds, and wet by the waves of the rising tide, these tiny lizards scuttled about unconcerned by their larger neighbours. When I tried to catch some with my hands they ran into the water of the pools and two were caught there, clinging under water to the rocks". Auffenberg (1980) never found specimens over 20 metres from the water's edge, or in places that lacked small sea cliffs or rock outcrops.

Cryptoblepharus cursor Barbour, 1911

(Plate 4.2; Figs 161–162)

Description. A small (<40 mm SVL), long-legged, very deep-headed, arboreal *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5; enlarged upper ciliaries 3; posterior loreal usually largest; supralabials 7; fifth supralabial subocular; infralabials 5–6 (mean 5.8), modally 6; nuchals 2–4 (mean 3.4), modally 4.

Midbody scale rows 24–26 (mean 25.4), modally 26; paravertebrals 49–56 (mean 52.0), modally 50; subdigital lamellae smooth, 14–15 below fourth finger (mean 14.9), modally 15; 18–19 below fourth toe (mean 18.7), modally 19; 11–12 supradigital lamellae above fourth finger (mean 11.2) modally 11, 14–15 above fourth toe (mean 14.5); ; palmar and plantar scales rounded; plantars 11–15 (mean 13.3), modally 13; palmars 10–12 (mean 11.0), modally 11.

Snout-vent length to 39.5 mm. *Percentages of snout-vent length*: body length 47.8–58.2% (mean 51.7%); tail length 155.0–159.0% (mean 157.0%); forelimb length 32.8–36.2% (mean 34.9%); hindlimb length 42.7–45.8% (mean 44.3%); forebody length 35.8–41.8% (mean 38.8%); head length 20.0–20.8% (mean 20.2%). *Percentages of head length*: head depth 47.3–55.7% (mean 50.4%); head width 59.7–68.2% (mean 64.5%); snout length 40.5–47.1% (mean 44.0%). Paravertebral scale width 4.0–5.0% of snout-vent length (mean 4.6%); dorsolateral scale width 83.2–89.3% of paravertebral scale width (mean 85.1%).

A brownish *Cryptoblepharus* with a simple body pattern of longitudinally aligned zones and stripes. Dorsally, a broad, brown vertebral zone is bordered by indistinct, narrow, discontinuous black dorsolateral stripes and distinct, moderately broad, creamish laterodorsal stipes. The dark upper lateral zone is sparsely flecked with pale spots and a pale mid-lateral stripe extends from labials to hindlimb. This pattern is most distinct anteriorly, noticeably fading on posterior third of body (Plate 4.2, Figs 161 and 162).

Distribution. Central Indonesia; from Lombok, Tengah Kepulauan, Bali and islands off south-west Sulawesi.

Remarks. Mertens (1934, 1964) tentatively placed material from "Bone Tamboeng, Spermonde-Archipel" and "Kleine Insel bei Makassar" (= "Bonetambung Island" northwest of Macassar, and "small island near Macassar"), approximately 450 km northeast of Lombok, with this taxon. Examination of the specimen SMF 22192 (Fig. 162) from near Macassar (= Ujung Pandang) and three additional specimens (NTM R21145-147; Plate 4.2) from Samalona Island (ca. 4 km west of Ujung Pandang) indicated similarity to *C. cursor* in appearance. They differ, however, in midbody scale rows (26 versus 24), head proportions, forebody length and dorsal scale widths. Pending collection of more material of both forms, the north-eastern form is treated as an allopatric subspecies.

Subspecies. *Cryptoblepharus cursor* is a polytypic taxon comprised of two allopatric subspecies: *Cryptoblepharus cursor cursor* Barbour, 1911; *Cryptoblepharus cursor larsonae* ssp. nov.

Cryptoblepharus cursor cursor Barbour, 1911

(Fig. 161)

Type material examined. *Cryptoblepharus boutonii cursor* Barbour, 1911. HOLOTYPE: MCZ 7479, Ampenan, Lombok Island, Nusa Tenggara Barat, Indonesia. T. Barbour, 1907.

Description (1 specimen). Postnasals absent; prefrontals usually in broad contact; supraciliaries 5; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 5; nuchals 4.

Midbody scale rows 24; paravertebrals 50; subdigital lamellae smooth, 15 below fourth finger, 18 below fourth toe; 11 supradigital lamellae above fourth finger, 14 above fourth toe; palmar and plantar scales rounded; plantars 12; palmars 11.

Snout-vent length 36.9 mm. *Percentages of snout-vent length*: body length 50.9%; tail length 159.0%; forelimb length 35.0%; hindlimb length 44.9%; forebody length 41.8%; head length 20.8%. *Percentages of head length*: head depth 55.7%; head width 59.7%; snout length 43.1%. Para-

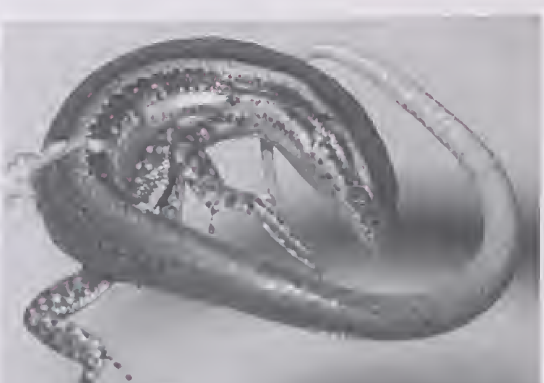

Fig. 161. Holotype of *Cryptoblepharus boutonii cursor* Barbour, 1911. MCZ 7479, Ampenan, Lombok Island, Indonesia.

vertebral scale width 4.0% of snout-vent length; dorsolateral scale width 89.3% of paravertebral scale width.

Colouration and pattern as described above for species (see Fig. 161).

Distribution. Central Indonesia, from Ampenan, Ekas, Laboehan Hadji, Narmada and Selong on Lombok Island (Mertens 1930). Also recorded from Tengah Kepulauan, northeast of Lombok (de Rooij 1915; Mertens 1964). Whitten and McCarthy (1993) and Mckay (2006) record it as occurring on Bali.

Remarks. An arboreal species which hides in holes and crannies in bark, also observed on the ground (Mertens 1930). McKay (2006) describes it as a littoral form, inhabiting debris and vegetation clumps on beaches and foreshores, that commonly basks and forages on beaches above the high tide mark.

Cryptoblepharus cursor larsonae ssp. nov.

(Plate 4.2; Fig. 162)

Type material examined. *Cryptoblepharus cursor larsonae* Horner. HOLOTYPE: NTM R21145, Samalona Island, south Sulawesi, Indonesia, 05°08'S 119°21'E. H. Larson, 31 August 1989. PARATYPES: INDONESIA: NTM 21146-147, same data as holotype; SMF 22192, island near Macassar, Sulawesi. S. Muller and H. Macklot, 1830's (ex Leiden Museum).

Diagnosis. Distinguished from congeners by combination of: fused interparietal and modal values of five supraciliary scales, 26 midbody scale rows, 53 paravertebral scales, 19 fourth toe subdigital lamellae; 15 fourth finger subdigital lamellae; 14 plantar scales, and four nuchal scales. Mean values of head depth 49.1% of head length, head width 65.7% of head length, snout length 44.3% of head length, forebody length 38.1% of snout-vent length, forelimb length 34.8% of snout-vent length and hindlimb length 44.2% of snout-vent length.

Description (4 specimens). Postnasals absent; prefrontals usually in broad contact; supraciliaries 5; enlarged upper ciliaries 3; posterior loreal usually largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2–4 (mean 3.2), modally 4.

Midbody scale rows 25–26 (mean 25.7), modally 26; paravertebrals 49–56 (mean 52.5), modally indeterminate; subdigital lamellae smooth, 14–15 below fourth finger (mean 14.8) modally 15, 18–19 below fourth toe (mean 18.9) modally 19; 11–12 supradigital lamellae above fourth finger (mean 11.3) modally 11, 14–15 above fourth toe (mean 14.6) modally 15; palmar and plantar scales rounded; plantars 11–15 (mean 13.6), modally indeterminate; palmars 10–12 (mean 11.0), modally 11.

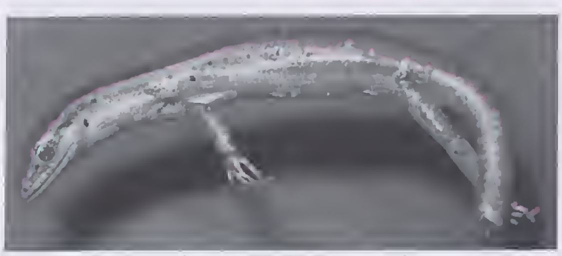

Fig. 162. Paratype of *Cryptoblepharus cursor larsonae* ssp. nov., SMF 22192, island near Macassar (=Ujung Pandang), Sulawesi, Indonesia.

Snout-vent length to 39.5 mm (mean 36.8 mm). *Percentages of snout-vent length:* body length 47.8–58.2% (mean 51.9%); tail length 155.0% (n = 1); forelimb length 32.8–36.2% (mean 34.8%); hindlimb length 42.7–45.8% (mean 44.2%); forebody length 35.8–39.9% (mean 38.1%); head length 20.0–20.5% (mean 20.2%). *Percentages of head length*: head depth 47.3–51.9% (mean 49.1%); head width 62.2–68.2% (mean 65.7%); snout length 40.5–47.1% (mean 44.3%). Paravertebral scale width 4.5–5.0% (mean 4.8%) of snout-vent length; dorsolateral scale width 83.2–84.0% (mean 83.7%) of paravertebral scale width.

Details of holotype. Adult female, NTM R.21145 (discoloured by preserving fluid). Postnasals absent; prefrontals in broad contact (fused); supraciliaries 5; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 4. Midbody scale rows 26; paravertebrals 50; subdigital lamellae smooth, 15 below fourth finger; 19 below fourth toe; supradigital lamellae 11 above fourth finger; 15 above fourth toe; palmars and plantars rounded, plantars 15; palmars 11. Snout-vent length 31.9 mm; body length 15.2 mm; tail length 49.4 mm; forelimb length 11.5 mm; hindlimb length 13.6 mm; forebody length 12.7 mm; head length 6.5 mm; head depth 3.1 mm; head width 4.5 mm; snout length 2.9 mm.

Colouration and pattern. Ground colour brown, patterned with longitudinally aligned, simple body pattern dominated by broad, brown vertebral zone, bordered by indistinct, narrow, discontinuous black dorsolateral stripes and distinct, moderately broad, creamish laterodorsal stipes. Pattern is most distinct anteriorly, noticeably fading on posterior third of (Plate 4.2, Fig. 162). Most specimens conform to the following description.

Dorsal ground colour brown, with broad, vertebral zone extending from head onto tail. Vertebral zone immaculate, as wide as paired paravertebral scales and brown in colour. Indistinct black dorsolateral stripes extend from supraoculars to posterior half of body. Inner margin of dark paravertebral stripes slightly ragged. Prominent, narrow, creamish to white laterodorsal stripes extend from above eye onto tail base. Pale laterodorsal stripes rough edged and without patterning, about as wide as laterodorsal scale. Head concolorous with vertebral zone, usually immaculate or with dark margins to shields. Laterally, head patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Labials creamish, patterned with fine dark margins to scales.

Comparison with congeners. *Cryptoblepharus cursor larsonae* ssp. nov. is distinguished from most south-west Indian Ocean taxa by having 26 midbody scale rows. It shares 26 midbody scale rows only with *C. boutonii* and *C. caudatus,* but can be further distinguished from *C. boutonii* by larger head (mean , head depth 49.1% versus 45.0%; head width 65.7% versus 61.6% of head length) and more paravertebral scales (modally 53 versus 50) and from *C. caudatus* by fewer paravertebral scales (modally 53 versus 55), longer limbs (mean FL 34.8% versus 30.9%; RL 44.2% versus 39.49% of snout-vent length) and smaller size (mean SVL, 36.8 versus 43.9 mm).

Among Indo-Pacific taxa, distinguished from *C. keiensis, C. novaeguineae, C. renschi* and *C. yulensis* sp. nov. by more midbody scale rows (modally 26 versus 24 or less) and fewer supraciliary scales (five versus six); from *C. egeriae* and *C. poecilopleurus paschalis* by fewer midbody scale rows (modally 26 versus 28) and fewer supraciliary scales (five versus six); from *C. novohebridicus* and *C. rutilus* by fewer midbody scale rows (modally 26 versus 24) and more paravertebral scales (modally 53 versus 51 or less); from *C. burdeni* and *C. p. poecilopleurus* by fewer midbody scale rows (modally 26 versus 28 or more) and smaller size (mean SVL, 36.8 versus >43 mm); from *C. nigropunctatus* and *C. novocaledonicus* by more midbody scale rows (modally 26 versus 24) and fewer subdigital lamellae (modally FTL 15 versus 18; HTL 19 versus 21 or more(modally 53 versus 51 or less); from *C. baliensis, C. intermedius* and *C. leschenault* by fewer supraciliary scales (five versus six) and more paravertebral scales (modally 53 versus 50 or less); from *C. schlegelianus* by more paravertebral (modally 53 versus 46), palmar (modally 11 versus 8) and plantar scales (modally 14 versus 11); from *C. furvus* sp. nov. by fewer paravertebral scales (modally 53 versus 58) and subdigital lamellae (modally FTL 15 versus 19; HTL 19 versus 23); from *C. litoralis vicinus* ssp. nov. by smaller size (mean SVL, 36.8 versus 41.3 mm) and fewer subdigital lamellae (modally FTL 15 versus 16; HTL 19 versus 22); from *C. eximius* by fewer paravertebral scales (modally 53 versus 54), shorter limbs (mean FL 34.8% versus 35.8%; RL 44.2% versus 45.1% of snout-vent length) and deeper head (mean 49.1% versus 45.2% of head length); from *C. xenikos* sp. nov. and *C. richardsi* sp. nov. by deeper, wider head (mean HH 49.1% versus 40.2% or less of head length; HW 65.7% versus 57.8% or less of head length), fewer fourth finger supradigital scales (modally 11 versus 12 and 13) and absence of distinct continuous black dorsolateral stripes. Most similar in appearance to conspecific *C. cursor cursor* but distinguished by more midbody scale rows (modally 26 versus 24), paravertebral scales (modally 53 versus 50) and head proportions (mean , head depth 49.1% versus 55.7%; head width 65.7% versus 59.7% of head length).

Among Australian taxa, distinguished from members of lineage 1 by having five supraciliaries (versus 6), and from most members of lineage 2 by more midbody scale rows (modally 26 versus 24 or less) and paravertebral scales (modally 53 versus 45–51). Those members of lineage 2 with 26 or more midbody scale rows are *C. gurrmul* sp. nov. and *C. litoralis*. Distinguished from the two Australian subspecies of *C. litoralis* by fewer paravertebral scales (modally 53 versus 55 or more), smaller size (mean SVL, 36.8 versus >39 mm), more plantar scales (modally 14 versus 11) and deeper head (mean 49.1% versus >43% of head length); from *C. gurrmul* sp. nov. by fewer midbody scale rows (modally 26 versus 28) and more palmar (modally 11 versus 7) and plantar scales (modally 14 versus 7).

Distribution. Islands off south-west Sulawesi. Known from Bonetambung Island (Mertens 1934), an unidentified small island near Ujung Pandang (possibly Samalona) (Mertens 1934), and Samalona Island.

Sympatry and geographic variation. Small sample size prevents analysis of geographic variation. Cases of sympatry are unknown.

Habits and habitats. The specimens from Samalona Island were collected on the strand-line, amongst coral litter on a sandy beach (H. Larson pers. comm.).

Etymology. Named for Helen Larson, Curator of Fishes at the Museum and Art Gallery of the Northern Territory, in recognition of her collection of the type series from Samalona Island.

Cryptoblepharus egeriae Boulenger, 1889
(Plate 4.3; Fig. 163)

Type material examined. *Ablepharus egeriae* Boulenger, 1889. SYNTYPES: BMNH 1946.8.15.86-88 (formerly 88.6.28.9-11), Christmas Island, Indian Ocean. J.J. Lister, 1887.

Non-type material examined. See Appendix 4.

Description (10 specimens). A large (45–50 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–6 (mean 5.9), modally 6; enlarged upper ciliaries 3–6 (mean 3.8), modally 3; loreals usually subequal; supralabials 8; sixth supralabial usually subocular; infralabials 6–7 (mean 6.7), modally 7; nuchals 2–7 (mean 3.4), modally 2.

Midbody scale rows 26–29 (mean 27.3), modally 28; paravertebrals 57–61 (mean 59.4), modally 61; subdigital lamellae smooth, 18–21 below fourth finger (mean 19.0) modally 18, 21–24 below fourth toe (mean 22.7) modally 23; 14–16 supradigital lamellae above fourth finger (mean 14.7) modally 15, 17–22 above fourth toe (mean 18.5) modally 18; palmar and plantar scales rounded; plantars 9–12 (mean 10.4), modally 10; palmars 9–12 (mean 10.0), modally 9.

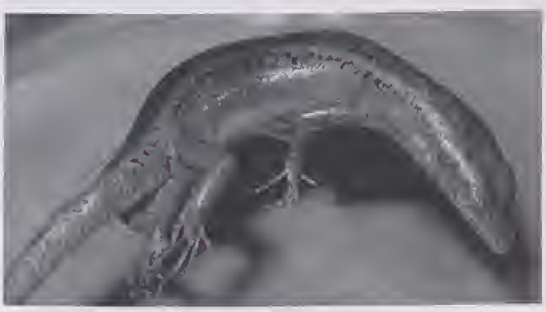

Fig. 163. *Cryptoblepharus egeriae* (Boulenger, 1888). SMF 22127 (ex. BMNH), Christmas Island, Indian Ocean.

Snout-vent length to 47.7 mm (mean 45.7 mm). *Percentages of snout-vent length*: body length 48.4–54.1% (mean 51.4%); tail length 156.0–167.8% (mean 161.7%); forelimb length 33.0–37.9% (mean 35.6%); hindlimb length 34.0–48.1% (mean 43.0%); forebody length 40.5–46.3% (mean 42.8%); head length 19.8–22.6% (mean 21.5%). *Percentages of head length*: head depth 37.2–49.6% (mean 43.9%); head width 54.0–63.0% (mean 57.6%); snout length 41.3–46.5% (mean 43.8%). Paravertebral scale width 3.9–4.3% (mean 4.1%) of snout-vent length; dorsolateral scale width 80.0–91.4% (mean 87.0%) of paravertebral scale width.

Complex body pattern of longitudinally aligned zones, stripes, spots and specks with a characteristic blue tail (Plate 4.3, Fig. 163). Dorsally, a narrow, grey-brown vertebral zone is bordered by ragged, narrow, black dorsolateral and creamish laterodorsal stipes. The blackish upper lateral zones are flecked with pale spots and coalesces with mottled, greyish lower lateral zone. Tail distinctly blue (Plate 4.3).

Distribution. Endemic to Christmas Island, Indian Ocean (ca. 320 km south of Java).

Remarks. The only *Cryptoblepharus* with interparietal distinct from the large, single frontoparietal shield. Cogger *et al* (1983b) noted "common in household gardens and roadside vegetation between Flying Fish Cove and Rocky Point; basks on stone or brick walls, fences, ornamental trees, shrubs and coconut palms; also seen on fallen tree trunks associated with clearings in primary rainforest; iridescent blue tail is a feature of both sexes and is brightest in juveniles, the intensity of colour diminishing in large adults".

Cryptoblepharus eximius Girard, 1857
(Plate 4.4; Fig. 164)

Non-type material examined. See Appendix 4.

Description (8 specimens). A small (<40 mm SVL), long-legged, deep-headed *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 4–5 (mean 4.9), modally 5; enlarged upper ciliaries 3; anterior loreal usually largest; supralabials 6–7 (mean 6.9), modally 7; fifth supralabial usually subocular; infralabials 6–8 (mean 6.9), modally 7; nuchals 2–6 (mean 2.9), modally 2.

Midbody scale rows 24–26 (mean 25.0), modally 26; paravertebrals 50–55 (mean 53.6), modally 54; subdigital lamellae smooth, 15–19 below fourth finger (mean 17.4) modally 19, 19–23 below fourth toe (mean 20.9) modally 22; 11–14 supradigital lamellae above fourth finger (mean 12.7) modally 13, 14–18 above fourth toe (mean 16.3) modally 17; palmar and plantar scales rounded; plantars 11–16 (mean 13.1), modally 13; palmars 10–13 (mean 11.2), modally 11.

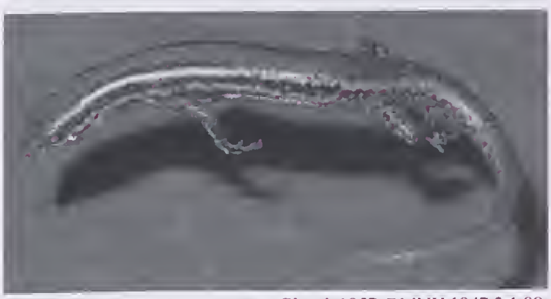

Fig. 164. *Cryptoblepharus eximius* Girard, 1857. BMNH 1947.3.1.88, Cicia, Lau, Fiji.

Snout-vent length to 36.4 mm (mean 34.9 mm). *Percentages of snout-vent length*: body length 47.9–58.2% (mean 51.3%); tail length 141.7% (n = 1); forelimb length 32.4–39.3% (mean 35.8%); hindlimb length 40.6–51.3% (mean 45.1%); forebody length 41.0–43.8% (mean 42.8%); head length 20.8–22.0% (mean 21.5%). *Percentages of head length*: head depth 39.1–48.0% (mean 45.2%); head width 56.3–66.7% (mean 62.2%); snout length 43.2–48.8% (mean 45.8%). Paravertebral scale width 3.3–3.8% (mean 3.6%) of snout-vent length; dorsolateral scale width 67.3–95.2% (mean 82.7%) of paravertebral scale width.

Body brownish, with a complex pattern of longitudinally aligned zones, stripes, spots and specks. Dorsally, a broad, brown vertebral zone is bordered by narrow, discontinuous black dorsolateral and distinct, narrow, creamish laterodorsal stipes. The dark upper lateral zone is usually sparsely flecked with pale spots and a pale mid-lateral stripe extends from labials to hindlimb. Patterning is most distinct anteriorly, noticeably fading on posterior third of body (Plate 4.4, Fig. 164).

Distribution. Endemic to Fiji islands, Oceania. Zug (1991) states "... along the coast of many Fijian islands, but not in Rotuma".

Remarks. Predominantly a coastal species (Zug 1991), but does occupy habitats distant from the shore (Zug 1991; Shea 1995b). Locally abundant (Zug 1991; Shea 1995b), *C. eximius* is recorded from strand vegetation, coral rubble, rock outcrops on beaches, closed forest on a steep rocky slope, walls of abandoned concrete-block house, bare sand and sunny patches of deep leaf litter in coastal closed forest (Shea 1995b). Zug (1991) suggests that egg deposition may be communal, with probable clutches being found beneath rock slabs in the Nausori Highlands, interspersed with eggs of the gekkonid *Lepidodactylus lugubris*.

Cryptoblepharus furvus sp. nov.
(Figs 165–167)

Type material examined. *Cryptoblepharus furvus* Horner. HOLOTYPE: AM R129828, Guleguleu, Normanby Island, Milne Bay, New Guinea, 10°06'S 151°15'E. 23 December 1988. PARATYPES: NEW GUINEA: AM R129809, R129827, R129829-830, R129833-835, R129838-842, R129844-846, Guleguleu, Normanby Island, Milne Bay, 10°06'S 151°15'E. 23 December 1988.

Diagnosis (16 specimens). A large (45–50 mm SVL), short-legged, shallow-headed, littoral *Cryptoblepharus*, distinguished from congeners by combination of: modal values of five supraciliary scales, 26 midbody scale rows, 60 paravertebral scales, 19 subdigital lamellae under the fourth finger, 23 subdigital lamellae under the fourth toe, 12 palmar scales, 15 plantar scales and 4 nuchal scales. Mean values of 42.4 mm snout-vent length and head width 56.7% of head length; anterior loreal largest in series, and indistinct pale dorsolateral stripes.

Description. Postnasals absent; prefrontals in broad contact (100%); supraciliaries 5–6 (mean 5.0), modally 5; enlarged upper ciliaries 3–4 (mean 3.1), modally 3; anterior loreal largest (100%); supralabials 6–8 (mean 7.0), modally 7; fifth supralabial usually subocular (88%), occasionally fourth (6%) or sixth (6%); infralabials 6–7 (mean 6.0), modally 6; nuchals 2–8 (mean 3.9), modally 4; bilateral posttemporals usually 2+2 (57%), occasionally 2+3 (31%), or 3+3 (12%).

Midbody scale rows 26; paravertebrals 53–62 (mean 57.7), modally 60; subdigital lamellae smooth, 17–22 below fourth finger (mean 18.8) modally 19, 20–25 below fourth toe (mean 22.4) modally 23; 12–15 supradigital lamellae above fourth finger (mean 13.2) modally 13, 15–19 above fourth toe (mean 17.0) modally 16; palmar and plantar scales rounded, without calli and skin visible between scales (Fig. 165); plantars 10–15 (mean 13.3), modally 15; palmars 10–15 (mean 12.3), modally 12.

Snout-vent length to 47.0 mm (mean 42.3 mm). *Percentages of snout-vent length*: body length 49.1–58.0% (mean 53.6%); tail length 143.4% (n = 1); forelimb length 31.7–37.9% (mean 34.1%); hindlimb length 37.4–48.4% (mean 42.4%); forebody length 37.3–44.0% (mean 40.6%); head length 18.8–21.4% (mean 20.1%). *Percentages of head length*: head depth 38.1–48.0% (mean 42.9%); head width 53.8–58.5% (mean 56.7%); snout length 42.7–49.1% (mean 45.5%). Paravertebral scale width 3.7–4.7% (mean 4.1%) of snout-vent length; dorsolateral scale width 72.3–93.9% (mean 79.3%) of paravertebral scale width.

Lenticular scale organs 4–12 (mean 7.4%), modally 7.

Details of holotype. Adult male, AM R129828 (Fig. 166). Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; anterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 4. Midbody scale rows 26; paravertebrals 60; subdigital lamellae smooth, 20 below fourth finger; 21 below fourth toe; supradigital lamellae 13 above fourth finger; 19 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 13; palmars 12. Snout-vent length 37.8 mm; body length 19.0 mm; tail not original; forelimb length 13.7 mm; hindlimb length 17.9 mm; forebody length 15.9 mm; head length 8.0 mm; head depth 3.5 mm; head width 4.6 mm; snout length 3.5 mm.

Colouration and pattern. Ground colour grey-black to dark brown-black, patterned with longitudinally aligned, complex body pattern dominated by dark brown vertebral zone, black dorsolateral and pale laterodorsal stripes. In alcohol, type series are blackish, with obscure pale dorso-

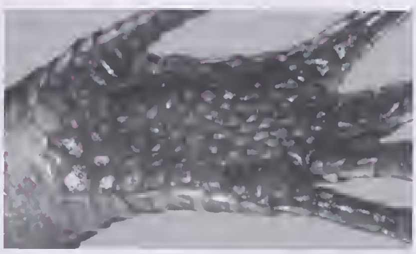

Fig. 165. Ventral surface of foot of *Cryptoblepharus furvus* sp. nov., showing dark, ovate plantar scales (AM R129844, Normanby Island, Milne Bay, Papua New Guinea). Scale: x20.

Fig. 166. Holotype of *Cryptoblepharus furvus* sp. nov. AMR 129828, Guleguleu Village area, Normanby Island, Milne Bay, Papua New Guinea. Scale bar = 10 mm.

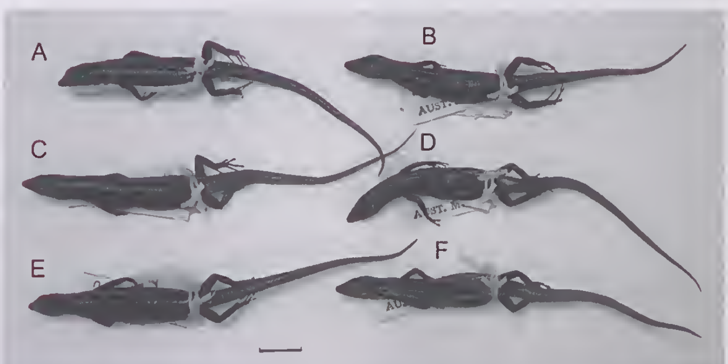

Fig. 167. *Cryptoblepharus furvus* sp. nov., Guleguleu Village area, Normanby Island, Milne Bay, Papua New Guinea. Australian Museum preserved material. **A**, R129828; **B**, R129846; **C**, R129844; **D**, R129827; **E**, R129840; **F**, R129839. Scale bar = 10 mm

lateral stripes (Fig. 167A–F). Most specimens conform to the following description.

Dorsal ground colour grey-black to dark brown-black, with dark brown vertebral zone extending from head to hindlimb. Vertebral zone as wide as paired paravertebral scales, dark brown with blackish speckling, and bordered by broad black dorsolateral stripes from neck to hindlimbs. Obscure, pale grey laterodorsal stripes extend from above eye onto tail, narrow and smooth edged, about width of laterodorsal scales, tapering anteriorly into narrow stripes extending to eye and posteriorly to form tail ground colour. Head concolorous with vertebral zone, usually patterned with dark margins to shields or with random dark specks. Laterally, head is patterned with continuation of dark upper lateral zone, extending above ear, through eye to loreals. Labials pale grey, with dark margins to scales.

Flanks have blackish upper lateral zone, variable in width, extending from loreals onto tail and forming outer border to pale laterodorsal stripes. Obscurely flecked with pale specks and short streaks, upper lateral zone may be represented by narrow broken black stripe but typically is about two lateral scales wide and coalesces gradually into pale grey lower lateral zone. Lower lateral zone is peppered with small pale and/or dark spots and streaks and coalesces into paler venter. Tail concolorous with body, patterned with broken continuations of vertebral and upper lateral zones. Limbs and toes concolorous with body, patterned with pale and dark speckling. Ventral surfaces blue-grey to off-white. Palmar and plantar scales dark grey to dark brown.

Sex ratio and sexual dimorphism. Sex ratio favoured females (9:7), but was not significantly different from parity ($X^2 = 0.25$). Both sexes mature at approximately 41.0 mm snout-vent length. Adults average 42.4 mm snout-vent length and females are larger than males (maximum SVL = 47.0 versus 43.8 mm).

Comparison with congeners. *Cryptoblepharus furvus* sp. nov. is distinguished from south-west Indian Ocean taxa by having more paravertebral scales (modally 60 versus 54 or less) and by number of midbody scale rows. It shares 26 midbody scale rows only with *C. boutonii* and *C. caudatus*, but can be further distinguished from these by more subdigital lamellae under the fourth finger (modally 19 versus 15) and fourth toe (modally 23 versus 20 or less).

Among Indo-Pacific taxa, distinguished from *C. C. cursor, C. keiensis, C. novaeguineae, C. novocaledonicus, C. novohebridicus, C. renschi, C. rutilus* and *C. yulensis* sp. nov. by having more midbody scale rows (modally 26 versus 24 or less) and paravertebral scales (modally 60 versus 54 or less); from *C. burdeni* and *C. p. poecilopleurus* by fewer midbody scale rows (modally 26 versus 28 or more) and more paravertebral scales (modally 60 versus 54 or less); from *C. baliensis, C. intermedius* and *C. leschenault* by more paravertebral scales (modally 60 versus 50 or less) and fewer supraciliary scales (modally 5 versus 6); from *C. egeriae* and *C. p. paschalis* by fewer midbody scale rows (modally 26 versus 28) and fewer supraciliary scales (modally 5 versus 6); from *C. nigropunctatus* by more midbody scale rows (modally 26 versus 24), more paravertebral scales (modally 60 versus 57) and narrower head (mean 56.7% versus 65.7% of head length); from *C. c. larsonae* ssp. nov. and *C. eximius* by more paravertebral scales (modally 60 versus 54 or less) and greater size (mean SVL, 42.4 versus 37.0 mm or less); from *C. schlegelianus* by more paravertebral scales (modally 60 versus 46) and fourth toe subdigital lamellae (23 versus 16); from *C. xenikos* sp. nov. and *C. richardsi* sp. nov. by greater size (mean SVL, 42.4 versus 38.6 mm or less), more paravertebral (modally 60 versus 53 or less) and fourth finger supradigital scales (modally 19 versus 17 or less) and by anterior loreal usually being largest (instead of posterior loreal). Most similar to *C. litoralis vicinus* ssp. nov. (see below).

Among Australian taxa, distinguished from members of lineage 1 by having five supraciliaries (versus 6), and from all members of lineage 2 by more paravertebral scales (modally 60 versus 57 or less) and from most by number of midbody scale rows (modally 26 versus 24 or less). Further distinguished from *C. gurrmul* sp. nov. by fewer midbody scale rows (modally 26 versus 28) and more plantar scales (modally 15 versus 7). Most similar to taxa within the *C. litoralis* complex with which it shares 26 midbody scale rows and semi-melanotic colouration. Distinguished from: *C. litoralis vicinus* ssp. nov. by mean number of paravertebrals (58 versus 51), nuchal scales (4 versus 2), plantar scales (15 versus 16) and relative size of loreals (anterior largest versus both subequal); from *C. litoralis horneri* and *C. litoralis litoralis* it can be distinguished by number of fourth finger subdigital lamellae (19 versus 16), fourth toe subdigital lamellae (23 versus 20), palmar scales (12 versus 11 and 10), plantar scales (15 versus 11) and condition of pale stripes (broad and distinct versus obscure).

Distribution. Type series collected in the vicinity of Guleguleu Village, mid-eastern coast of Normanby Island, D'Entrecasteaux Islands, Milne Bay, Papua New Guinea.

Sympatry and Geographic variation. Cases of sympatry unknown. Taxon known from a single locality.

Habits and habitats. Unknown.

Etymology. From the Latin adjective *furvus*, meaning dark or dusky; in reference to this taxon's semi-melanotic colouration.

Cryptoblepharus intermedius de Jong, 1926

(Fig. 168)

Type material examined. *Ablepharus boutoni intermedius* de Jong, 1926. LECTOTYPE: ZMA 10972, Rana, Buru Island, Maluku Province, Indonesia. L. Toxopeus, 1921–22. PARALECTOTYPE: ZMA 10973, same data as lectotype.

Description (2 specimens). A medium sized (40–44 mm SVL), short-legged, deep-headed *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 6; enlarged upper ciliaries 3; posterior loreal

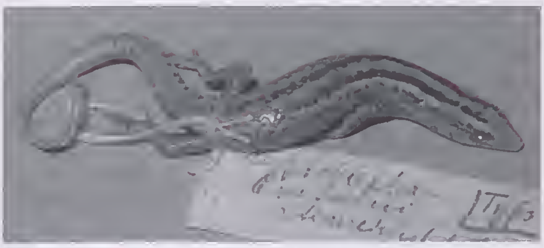

Fig. 168. Lectotype of *Ablepharus boutoni intermedius* de Jong, 1926. ZMA 10972, Rana, Buru Island, Maluku Province, Indonesia.

usually largest; supralabials 7; fifth supralabial usually subocular; infralabials 7; nuchals 2.

Midbody scale rows 25–26 (mean 25.5), modally indeterminate ; paravertebrals 44–48 (mean 46.0), modally indeterminate; subdigital lamellae smooth, 19–20 below fourth finger (mean 19.2) modally indeterminate, 23 below fourth toe; 13–14 supradigital lamellae above fourth finger (mean 13.5) modally indeterminate, 18–19 above fourth toe (mean 18.5) modally indeterminate; palmar and plantar scales rounded; plantars 10–11 (mean 10.5), modally indeterminate; palmars 9–10 (mean 9.5), modally indeterminate.

Snout-vent length to 42.7 mm (mean 42.4 mm). Percentages of snout-vent length: body length 47.3–54.5% (mean 50.9%); tail length indeterminate; forelimb length 34.6–35.0% (mean 34.8%); hindlimb length 41.9–43.1% (mean 42.5%); forebody length 41.7–43.7% (mean 42.7%). Percentages of head length: head length 19.7–20.5% (mean 20.1%); head depth 44.5–49.5% (mean 47.0%); head width 62.0–66.5% (mean 64.3%); snout length 47.0–47.3% (mean 47.1%). Paravertebral scale width 4.3–4.7% (mean 4.5%) of snout-vent length; dorsolateral scale 78.2–104.0% (mean 95.5%) of paravertebral scale width.

Cryptoblepharus intermedius has a complex body pattern of longitudinally aligned zones, stripes, spots and specks. Dorsally, a narrow, pale brown vertebral zone is bordered by ragged, narrow, black dorsolateral stripes and creamish laterodorsal stipes. The dark brown upper lateral zone is flecked with pale spots and coalesces with mottled, pale brown lower lateral zone. Body patterning is most distinct anteriorly, noticeably fading on posterior third of body (Fig. 168).

Distribution. Islands of the Maluku Province, Indonesia. Known from Buru, Ambon, Seram and Haruku islands (Mertens 1931). Mertens (1931) also considers it to occur on the Barat Daya island chain, specifically Serua, Nila, Teun Babar and Tanimbar islands.

Remarks. Mertens (1964) considered *C. intermedius* a synonym of *C. keiensis*, simply stating that he could not separate the two "races". Although sample sizes are small, this study supports the recognition of *C. intermedius*. Comparison shows that *C. intermedius* is not as distinctly striped as *C. keiensis*, particularly in lacking the prominent pale mid-lateral stripe of *C. keiensis*. The two taxa also differ in size (mean SVL, 42.4 versus 38.4 mm), midbody scale rows (modally 26 versus 22), fourth toe supradigital scales (modally 18 versus 15), paravertebral scale width (mean 4.5 versus 3.6% of SVL) and though not statistically significant, number of paravertebral scales (modally 46 versus 50).

Cryptoblepharus keiensis Roux, 1910

(Plate 4.5; Fig. 169)

Type material examined. *Ablepharus boutoni keiensis* Roux, 1910. PARATYPES: SMF 15521-22, Kei-Dulah, H. Merton and J. Roux, 30 May 1908; SMF 15524, Warka, Great Kai Island, H. Merton and J. Roux, 5 June 1908; SMF 15526-28, Langgur, Kai Islands, H. Merton and J. Roux, 30 May 1908; SMF 15529, Elat, Great Kai Island, H. Merton and J. Roux, 4 June 1908.

Description (7 specimens). A small (<40 mm SVL), short-legged, shallow-headed *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–6 (mean 5.9), modally 6; enlarged upper ciliaries 3; posterior loreal usually largest; supralabials 7; fifth supralabial usually subocular; infralabials 6; nuchals 3–4 (mean 3.9), modally 4.

Midbody scale rows 22–24 (mean 22.3), modally 22; paravertebrals 48–51 (mean 49.9), modally 50; subdigital lamellae smooth, 16–19 below fourth finger (mean 18.0) modally 18, 21–24 below fourth toe (mean 23.0) modally 24; 12–13 supradigital lamellae above fourth finger (mean 12.3) modally 12, 14–17 above fourth toe (mean 15.6) modally 15; palmar and plantar scales rounded; plantars 8–10 (mean 9.3), modally 9; palmars 9–10 (mean 9.6), modally 10.

Snout-vent length to 39.5 mm (mean 38.4 mm). *Percentages of snout-vent length*: body length 51.3–53.7% (mean 53.0%); tail length indeterminate; forelimb length 30.0–37.1% (mean 33.5%); hindlimb length 38.4–44.7% (mean 41.8%); forebody length 40.0–42.8% (mean 41.5%); head length 19.1–21.8% (mean 20.5%). *Percentages of head length*: head depth 40.2–47.6% (mean 43.3%); head width 53.1–70.6% (mean 61.3%); snout length 43.1–47.1% (mean 45.5%). Paravertebral scale width 3.5–3.7% (mean 3.6%) of snout-vent length; dorsolateral scale width 72.8–97.2% (mean 86.3%) of paravertebral scale width.

Fig. 169. Paratypes of *Ablepharus boutoni keiensis* Roux, 1910. SMF 15526-528, Langgur, Kai Islands, Maluku Province, Indonesia.

Boldly striped, *C. keiensis* has a simple body pattern of longitudinally aligned, dark and pale stripes. These consist of pale vertebral, laterodorsal and mid-lateral stripes, and dark dorsolateral, upper lateral and lower lateral stripes (Plate 4.5 and Fig. 169).

Distribution. Kai Besar, Maluku Province, Indonesia. Recorded from Dullah Island, Langgur on Kai Kecil, Warka, Banda Elat and Cape Pattinson on Kai Besar.

Cryptoblepharus leschenault Cocteau, 1832
(Figs 170–171)

Type material examined. *Ablepharis* (sic) *leschenault* Cocteau, 1832. SYNTYPE: MNHP 3091, Java. M. Leschenault. SYNTYPES of *Ablepharus boutonii furcata* Weber, 1890: ZMA 10815, ZMA 10830a, ZMA 10831 (Fig. 171), Endeh, Flores, Indonesia. M. Weber, 1888; BMNH 1946.8.18.57, Sikka, East Flores, Indonesia. M. Weber, 1988.

Non-type material examined. See Appendix 4.

Description (15 specimens). A medium sized (40–44 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–7 (mean 6.1), modally 6; enlarged upper ciliaries 3; posterior loreal usually largest; supralabials 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.2), modally 6; nuchals 2–6 (mean 2.3), modally 2.

Midbody scale rows 24–28 (mean 25.6), modally 26; paravertebrals 44–54 (mean 49.2), modally 50; subdigital lamellae smooth, 15–19 below fourth finger (mean 17.4) modally 16, 18–25 below fourth toe (mean 22.0) modally 22; 11–14 supradigital lamellae above fourth finger (mean 12.9) modally 13, 13–19 above fourth toe (mean 16.1) modally 16; palmar and plantar scales rounded; plantars 9–13 (mean 10.8), modally 11; palmars 8–11 (mean 9.5), modally 10.

Snout-vent length to 43.9 mm (mean 38.9 mm). *Percentages of snout-vent length*: body length 45.0–53.1% (mean 50.2%); tail length 151.8–156.1% (mean 154.0%); forelimb length 29.9–36.0% (mean 33.1%); hindlimb length 34.8–44.6% (mean 41.0%); forebody length 39.7–45.0% (mean 42.1%); head length 18.9–23.2% (mean 21.0%). *Percentages of head length*: head depth 33.7–52.4% (mean 44.0%); head width 58.2–66.5% (mean 61.4%); snout length 42.2–48.3% (mean 45.6%). Paravertebral scale width 3.3–5.0% (mean 4.0%) of snout-vent length; dorsolateral scale width 73.3–96.5% (mean 84.1%) of paravertebral scale width.

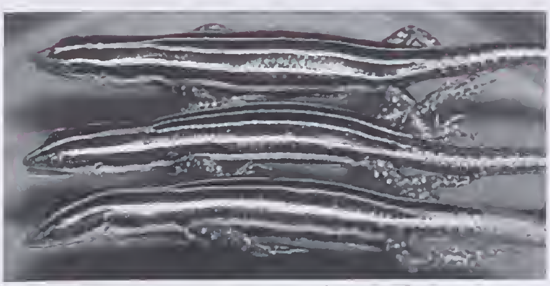

Fig. 170. *Cryptoblepharus leschenault* (Cocteau, 1832). SMF 22193-195, Endeh, Flores Island, Indonesia.

Fig. 171. Syntype of *Ablepharus boutonii furcata* Weber, 1890. ZMA 10831, Endeh, Flores Island, Indonesia.

Boldly striped, *C. leschenault* has a simple body pattern of longitudinally aligned, narrow pale stripes on a dark ground colour. These consist of: a mid-dorsal stripe on the head and neck, which thereafter forks into two narrow paravertebral stripes, laterodorsal and mid-lateral stripes (Figs 170 and 171).

Distribution. Islands of the Nusa Tenggara Timur and Kepulauan Barat Daya groups, Indonesia. Recorded from Alor, Lomblen, Groot-Bastaard, Wetar and Damma islands, and Endeh, Wolo Waro, Sikka and Larentoeka on Flores (Mertens 1930) and from Semau island and Timor by Brongersma (1942).

Remarks. Mertens (1930) observed this species near Endeh, on Flores, noting populations on coconut-palms in the hinterland and on big, individual bread-friut trees (*Dipterocarpus*). The bread-fruit trees housed up to 10 individuals at times. Brongersma (1942) cites S. Müller as observing "a few in the flotsam washed ashore by the surf on the sandy beaches on the north coast of Samao".

The original description gives "Java" as the type locality for *C. leschenault*. Mertens (1964) argues that the taxon does not occur on Java and that the collector (Jean Leschenault de la Tour, botanist on the voyage of the Géographe and Naturaliste 1801-1803) spent considerable time in Kupang, Timor (see Marchant 1982) before arriving in Java. Mertens (1964) suggests, therefore, that Timor should be designated as the type locality of *C. leschenault*. Brongersma (1942) records sympatry between *C. leschenault* and *C. schlegelianus* on "Samao Island" (= Semau Island) off Kupang, Timor.

Cryptoblepharus nigropunctatus Hallowell, 1860
(Fig. 172)

Non-type material examined. See Appendix 4.

Description (2 specimens). A very large (<50 mm SVL), short-legged, very deep-headed *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6–7 (mean 6.2); nuchals 2.

Midbody scale rows 24; paravertebrals 56–58 (mean 57.0); subdigital lamellae smooth, 18–19 below fourth finger (mean 18.5), 23–25 below fourth toe (mean 24.0);

Fig. 172. *Cryptoblepharus nigropunctatus* (Hallowell, 1860). SMF 22124, Haha shima, Ogasawara-gunto (Bonin Islands), Kanto region, Japan.

13 supradigital lamellae above fourth finger, 15–17 above fourth toe (mean 16.0); palmar and plantar scales rounded; plantars 16–17 (mean 16.5); palmars 14–15 (mean 14.5).

Snout-vent length to 51.1 mm (mean 47.3 mm). *Percentages of snout-vent length*: body length 53.1–56.7% (mean 54.9%); tail length 160.9% (n = 1); forelimb length 31.0–35.3% (mean 33.1%); hindlimb length 41.4–41.8% (mean 41.6%); forebody length 38.8–43.6% (mean 41.2%); head length 19.3–20.9% (mean 20.1%). *Percentages of head length*: head depth 47.0–54.0% (mean 50.5%); head width 63.8–67.5% (mean 65.7%); snout length 41.2–44.0% (mean 42.6%). Paravertebral scale width 4.2–5.0% (mean 4.6%) of snout-vent length; dorsolateral scale width 68.0–96.5% (mean 81.6%) of paravertebral scale width.

A dark *Cryptoblepharus* with an obscure body pattern of longitudinally aligned zones, spots and specks. Dorsally, a broad, grey-brown vertebral zone is patterned by vague narrow, discontinuous black paravertebral stripes. Pale laterodorsal stripes are represented by vague, narrow, discontinuous wavy lines. The dark upper lateral zone is flecked with pale spots and coalesces into brownish lower lateral zone (Fig. 172).

Distribution. Ogasawara-gunto (Bonin Islands), Kanto region, Japan. Recorded from Haha shima, Chichi shima (Mertens, 1931) and Minami-Tori-shima (Marcus Island) (Mertens, 1933).

Remarks. Suzuki and Nagoshi (1999) supply information on the habits of *C. nigropunctatus*, observing that the taxon primarily inhabits grassland and forest edges and only occasionally is found near the coast. It principally forages on the ground, and most specimens were observed on the ground or concrete walls, with few being found on plants.

Population density of *C. nigropunctatus* in the Ogasawara Islands has been adversely affected by the introduced anoline lizard *Anolis carolinensis carolinensis*, with *C. nigropunctatus* now absent from areas where the *Anolis* occurs in high density (Suzuki and Nagoshi 1999).

Cryptoblepharus novaeguineae Mertens, 1928
(Figs 173–176)

Cryptoblepharus boutonii aruensis Mertens, 1928a: 87; Mertens, 1964: 107.

Cryptoblepharus boutonii novaeguinae Mertens, 1928a: 87; Mertens, 1964: 107.

Cryptoblepharus boutonii pallidus Mertens, 1928a: 88 (syn. nov.).

Fig. 173. Holotype of *Cryptoblepharus boutonii aruensis* Mertens, 1928. SMF 15517, Papakoela, Kobroor Island, Aru Island group, Maluku Province, Indonesia.

Fig. 174. Holotype of *Cryptoblepharus boutonii novaeguineae* Mertens, 1928. NHMB 8343, Mamberamo, West Papua, New Guinea.

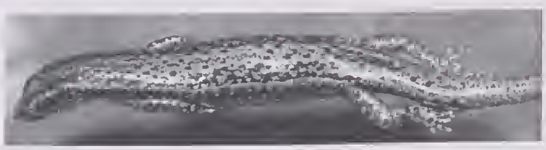

Fig. 175. Paratype of *Cryptoblepharus boutonii novaeguineae* Mertens, 1928. SMF 15606, Simbang, West Papua, New Guinea.

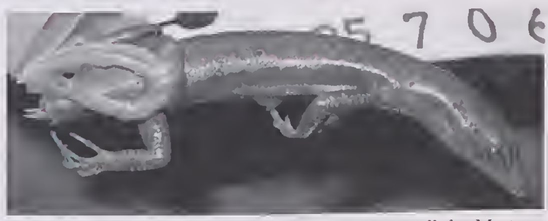

Fig. 176. Holotype of *Cryptoblepharus boutonii pallidus* Mertens, 1928. ZMB 25706, Sepik area, New Guinea.

Type material examined. *Cryptoblepharus boutonii aruensis* Mertens, 1928a. HOLOTYPE: SMF 15517 (Fig. 173), Papakoela, Kobroor Island, Aru Island Group, Maluku Province, Indonesia. H. Merton and J. Roux, 1908. *Cryptoblepharus boutonii novaeguineae* Mertens, 1928a. HOLOTYPE: NHMB 8343 (Fig. 174), Mamberamo, West Papua, New Guinea. P. Wirz, 1922. *Cryptoblepharus boutonii pallidus* Mertens, 1928a. HOLOTYPE: ZMB 25706 (Fig. 176), Sepik area, north New Guinea. Bürgers, 1912. *Cryptoblepharus boutonii aruensis* Mertens, 1928a. PARATYPES: NHMB 6201-202, SMF 15518, Papakoela, Kobroor Island, Aru Island Group, Maluku Province, Indonesia. H. Merton and J. Roux, 1908. SMF 15515-516, Seltoetti, Kobroor Island, Aru Island Group, Maluku Province, Indonesia. H. Merton and J. Roux, 1908. *Cryptoblepharus boutonii novaeguineae* Mertens, 1928a. PARATYPES: NHMB 8342, Mamberamo, West Papua, New Guinea. P. Wirz, 1922;

NHMB 9322, Sentani area, West Papua, New Guinea. P. Wirz, 1922

Non-type material examined. See Appendix 4.

Description (14 specimens). A small (<40 mm SVL), short-legged, shallow-headed *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–6 (mean 5.7), modally 6; enlarged upper ciliaries 3–4 (mean 3.0), modally 3; loreals usually subequal; supralabials 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.4), modally 6; nuchals 2.

Midbody scale rows 22; paravertebrals 44–53 (mean 47.0), modally 47; subdigital lamellae smooth, 15–19 below fourth finger (mean 17.4) modally 18, 19–24 below fourth toe (mean 22.0) modally 23; 11–15 supradigital lamellae above fourth finger (mean 13.0) modally 12, 15–17 above fourth toe (mean 15.7) modally 16; palmar and plantar scales rounded; plantars 8–12 (mean 10.7), modally 11; palmars 8–13 (mean 10.4), modally 10.

Snout-vent length to 39.2 mm (mean 35.6 mm). *Percentages of snout-vent length*: body length 45.4–56.0% (mean 51.8%); tail length 124.3–133.1% (mean 129.2%); forelimb length 31.9–40.0% (mean 35.6%); hindlimb length 37.7–45.2% (mean 46.2%); forebody length 39.0–43.9% (mean 41.3%); head length 18.8–22.6% (mean 20.8%). *Percentages of head length*: head depth 35.8–48.4% (mean 41.8%); head width 54.7–64.2% (mean 60.8%); snout length 42.3–48.0% (mean 45.0%). Paravertebral scale width 3.8–5.7% (mean 4.7%) of snout-vent length; dorsolateral scale width 68.0–99.5% (mean 78.0%) of paravertebral scale width.

A grey to grey/brown *Cryptoblepharus* with a complex body pattern of longitudinally aligned stripes/zones, spots and specks. Dorsally, a greyish vertebral zone is bordered by ragged, dark grey-brown dorsolateral stripes and ragged, pale grey laterodorsal stipes. The dark brown upper lateral zone is flecked with pale spots and coalesces with pale venter. Intensity of body pattern is variable, ranging through boldly striped (Figs 173 and 174), heavily flecked (Fig. 175), to reduced and obscure (Fig. 176).

Distribution. New Guinea, where it is known from Mamberamo, Sentani and Ajamaroe in West Papua, Sepik area, Simbang and Port Moresby in Papua New Guinea, and Aru Kepulauan, Maluku Province, Indonesia.

Cryptoblepharus novocaledonicus Mertens, 1928
(Figs 177–178)

Type material examined. *Cryptoblepharus boutonii novocaledonicus* Mertens, 1928. HOLOTYPE: SMF 15520 (Fig. 177), Hienghiène, New Caledonia, Oceania. F. Sarasin and J. Roux, 1911. PARATYPES: NHMB 7217-218, NHMB 7220-221 (Fig. 178), same data as holotype; NHMB 7212, Médu, Maré Island, Loyalty Islands. F. Sarasin and J. Roux, 1911; NHMB 7213, NHMB 7215-216, Poum, New Caledonia, Oceania. F. Sarasin and J.Roux, 1911.

Description (9 specimens). A medium sized (40–44 mm SVL), long-legged, deep-headed, littoral *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 4–5 (mean 4.9), modally 5; enlarged upper ciliaries 3; loreals usually subequal; supralabials 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.8), modally 7; nuchals 2–6 (mean 3.1), modally 2.

Midbody scale rows 24–26 (mean 24.7), modally 24; paravertebrals 48–59 (mean 54.6), modally 53; subdigital lamellae smooth, 16–19 below fourth finger (mean 17.7) modally 18, 19–24 below fourth toe (mean 21.1) modally 21; 12–14 supradigital lamellae above fourth finger (mean 12.9) modally 13, 15–18 above fourth toe (mean 16.0) modally 15; palmar and plantar scales rounded; plantars 11–15 (mean 12.9), modally 13; palmars 10–13 (mean 11.8), modally 12.

Snout-vent length to 41.2 mm (mean 37.6 mm). *Percentages of snout-vent length*: body length 47.2–56.1% (mean 50.8%); tail length 145.6% (n = 1); forelimb length 32.8–38.7% (mean 35.7%); hindlimb length 42.5–47.3% (mean 45.3%); forebody length 40.9–43.7% (mean 42.7%); head length 20.2–22.3% (mean 21.2%). *Percentages of head length*: head depth 43.1–51.6% (mean 46.7%); head width 58.4–65.1% (mean 62.1%); snout length 43.9–47.8% (mean 45.7%). Paravertebral scale width 3.5–4.1% (mean 3.8%) of snout-vent length; dorsolateral scale width 81.8–92.2% (mean 86.7%) of paravertebral scale width.

Dorsal surface brown, with an obscure body pattern of longitudinally aligned zones, spots and specks. The dark brown vertebral zone, speckled with pale spots and flecks, is bordered by obscure, wavy, discontinuous black paravertebral stripes and anteriorly prominent, pale laterodorsal stripes. The dark upper lateral zone is prominently flecked with pale spots and coalesces into brownish lower lateral zone (Figs 177 and 178).

Distribution. New Caledonia and the Loyalty Islands, Oceania. Recorded from many coastal localities on New Caledonia (Sadlier 1975; Bauer and Vindum 1990), includ-

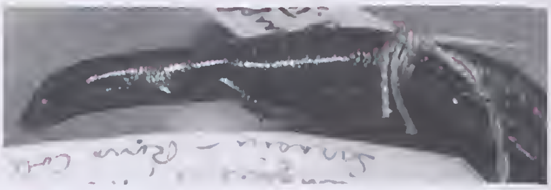

Fig. 177. Holotype of *Cryptoblepharus boutonii novocaledonicus* Mertens, 1928. SMF 15520, Hienghiène, New Caledonia, Oceania.

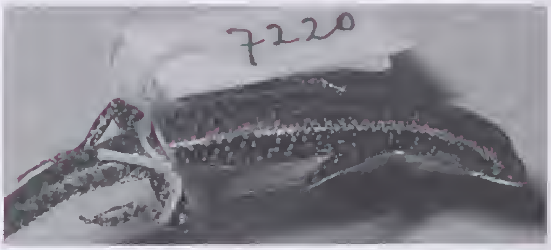

Fig. 178. Paratype of *Cryptoblepharus boutonii novocaledonicus* Mertens, 1928. NHMB 7220, Hienghiène, New Caledonia, Oceania.

ing Ile des Pins (Bauer and Sadlier 1994) and from Ouvéa, Lifou and Maré Islands of the Loyalty Islands (Sadlier and Bauer 1997).

Remarks. A saxicoline, coastal species associated with "outcropping limestone pavement within the spray zone" (Bauer and Sadlier 1994) and rocky beach fronts, boulders and rock ledges around headlands (Sadlier 1975). Sadlier (1975) gives detailed information on morphology and habits.

Cryptoblepharus novohebridicus Mertens, 1928
(Plate 4.6; Fig. 179)

Type material examined. *Cyproblepharus boutonii novohebridicus* Mertens, 1928. HOLOTYPE: NHMB 6787, Malo (Island), Sanma Province, Vanuatu (New Hebrides), Oceania. Dr F. Opeiser, 1911. PARATYPES: NHMB 6786, NHMB 6788, same data as holotype: NHMB 6789, Aoba (Island), Penama Province, Vanuatu (New Hebrides), Oceania. Dr F. Opeiser, 1911.

Description (4 specimens). A small (<40 mm SVL), short-legged, very deep-headed *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 4–5 (mean 4.7), modally 5; enlarged upper ciliaries 3; loreals usually subequal; supralabials 6–7 (mean 6.9), modally 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.7), modally 7; nuchals 5–8 (mean 6.2), modally 6.

Midbody scale rows 22–24 (mean 23.5), modally 24; paravertebrals 50–53 (mean 51.5), modally indeterminate; subdigital lamellae smooth, 15–16 below fourth finger (mean 15.7) modally 16, 19–21 below fourth toe (mean 20.2) modally 21; 12–14 supradigital lamellae above fourth finger (mean 13.0) modally 13, 16–17 above fourth toe (mean 16.2) modally 16; palmar and plantar scales rounded; plantars 11–14 (mean 12.2), modally 11; palmars 8–10 (mean 9.5), modally 10.

Snout-vent length to 37.0 mm (mean 35.3 mm). *Percentages of snout-vent length*: body length 47.6–54.7% (mean 52.0%); tail length 126.5–140.6% (mean 133.5%); forelimb length 31.2–34.3% (mean 33.2%); hindlimb length 39.4–43.1% (mean 41.3%); forebody length 41.4–43.5% (mean 42.2%); head length 20.3–21.5% (mean 21.0%). *Percentages of head length*: head depth 46.8–49.1% (mean 48.0%); head width 59.1–61.0% (mean 60.4%); snout length 43.7–50.3% (mean 47.5%). Paravertebral scale width 4.0–5.1% (mean 4.4%) of snout-vent length; dorsolateral scale width 64.1–85.5% (mean 76.5%) of paravertebral scale width.

Dorsal surface brown, patterned with longitudinally aligned stripes and zones. Brown vertebral zone is speckled with dark brown flecks and is bordered by narrow, blackish-brown dorsolateral and prominent whitish laterodorsal stipes. The dark brown upper lateral zone is usually sparsely flecked with pale spots and is separated from the brown lower lateral zone by a prominent, whitish mid-lateral stripe which extends from labials to hindlimb (Plate 4.6, Fig. 179).

Distribution. Vanuatu, Oceania. Recorded from Malo, Aoba, Ambryn, Efaté, Mérig, and Malecula islands (Mertens 1931).

Remarks. A coastal species associated with coral litter, palm trunks and dead timber. Very abundant in areas of suitable habitat (pers. obs.).

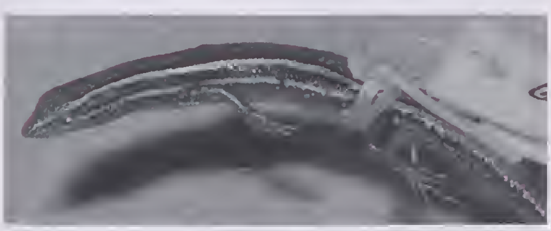

Fig. 179. Holotype of *Cryptoblepharus boutonii novohebridicus* Mertens, 1928. NHMB 6787, Malo Island, Vanuatu (New Hebrides), Oceania.

Cryptoblepharus poecilopleurus (Wiegmann, 1834)
(Plates 4.7–4.8; Figs 180–182)

Description (24 specimens). A very large (>50 mm SVL), short-legged, deep-headed *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–6; enlarged upper ciliaries 2–4; posterior loreal usually largest; supralabials 7–8; fifth or sixth supralabial subocular; infralabials 5–7; nuchals 2–5.

Midbody scale rows 26–30, usually 28; paravertebrals 49–60; subdigital lamellae smooth, 15–20 below fourth finger, 19–26 below fourth toe; 12–15 supradigital lamellae above fourth finger, 14–18 above fourth toe; palmar and plantar scales rounded; plantars 11–16; palmars 10–15.

Snout-vent length to 50.6 mm. *Percentages of snout-vent length*: body length 48.7–60.2%; tail length 137.5–148.1%; forelimb length 29.8–36.5%; hindlimb length 37.5–45.4%; forebody length 36.0–43.6%; head length 17.6–22.4%. *Percentages of head length*: head depth 40.0–52.5%; head width 58.0–66.3%; snout length 41.7–48.3%. Paravertebral scale width 3.0–4.6% of snout-vent length; dorsolateral scale width 77.9–94.1% of paravertebral scale width.

Dorsal surface brown-grey to greenish brown, with a complex body pattern of longitudinally aligned zones, stripes, spots and specks. Brownish vertebral zone, obscurely speckled with dark and pale spots and flecks, is bordered by ragged, narrow, black dorsolateral and moderately broad creamish laterodorsal stipes. The blackish upper lateral zone is flecked with pale spots and coalesces with the mottled, brownish lower lateral zone. Posterior half of tail russet.

Distribution. Widespread through the islands of Oceania, to the west coast of the South American mainland.

Subspecies. *Cryptoblepharus poecilopleurus* is a polytypic taxon comprised of two allopatric subspecies: *Cryptoblepharus poecilopleurus paschalis* Garman, 1908; *Cryptoblepharus poecilopleurus poecilopleurus* Wiegmann, 1835.

Cryptoblepharus poecilopleurus paschalis Garman, 1908

(Plate 4.7; Fig. 180)

Type material examined. *Cryptoblepharus poecilopleurus paschalis* Garman, 1908. SYNTYPES: MCZ 6995-998 MCZ 7001-003, Easter Island, Valparaiso region, Chile, South America. Expedition to the eastern tropical Pacific, ex "Albatross", 1904-1905.

Non-type material examined. See Appendix 4.

Description (8 specimens). Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–6 (mean 5.5), modally 6; enlarged upper ciliaries 3; posterior loreal usually largest; supralabials 7–8 (mean 7.6), modally 8; sixth supralabial usually subocular; infralabials 6–7 (mean 6.5), modally 6; nuchals 2–4 (mean 2.9), modally 2.

Midbody scale rows 27–30 (mean 28.3), modally 28; paravertebrals 56–60 (mean 57.9), modally 57; subdigital lamellae smooth, 17–19 below fourth finger (mean 18.1) modally 18, 22–26 below fourth toe (mean 23.9) modally 24; 13–14 supradigital lamellae above fourth finger (mean 13.1) modally 13, 15–17 above fourth toe (mean 16.4) modally 17; palmar and plantar scales rounded; plantars 13–16 (mean 14.9), modally 16; palmars 12–15 (mean 13.5), modally 13.

Snout-vent length to 50.6 mm (mean 43.1 mm). *Percentages of snout-vent length*: body length 48.7–60.2% (mean 55.2%); tail length 137.5–148.1% (mean 143.9%); forelimb length 31.2–35.9% (mean 32.9%); hindlimb length 38.1–44.9% (mean 41.1%); forebody length 36.9–45.2% (mean 40.9%); head length 18.6–22.4% (mean 20.2%). *Percentages of head length*: head depth 40.0–52.2% (mean 46.3%); head width 58.0–66.3% (mean 61.9%); snout length 42.7–48.3% (mean 45.6%). Paravertebral scale width 3.4–4.6% (mean 4.0%) of snout-vent length; dorsolateral scale width 77.9–87.3% (mean 83.0%) of paravertebral scale width.

Colouration and pattern as described above (see Plate 4.7 and Fig. 180).

Distribution. Endemic to Isla de Pascua (Easter Island), Oceania (Valparaiso region, Chile, South America).

Remarks. Type series were collected under rocks, Garman (1908) notes that some specimens taken under rocks were "… very dark ones, slaty on the belly, on which the light lines are almost invisible".

Fig. 180. Syntype of *Cryptoblepharus poecilopleurus paschalis* Garman, 1908. MCZ 7002, Isla de Pascua (Easter Island), Chile.

Cryptoblepharus poecilopleurus poecilopleurus (Wiegmann, 1834)

(Plate 4.8; Figs 181–182)

Type material examined. *Ablepharus poecilopleurus* Wiegmann, 1834. LECTOTYPE: ZMB 1349 (Fig. 181), island near Pisacoma, Peru. F. Meyen. PARALECTOTYPES: ZMB 57181-182, same data as lectotype.

Non-type material examined. See Appendix 4.

Description (16 specimens). Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–6 (mean 5.1), modally 5; enlarged upper ciliaries 2–4 (mean 3.0), modally 3; posterior loreal usually largest; supralabials 7–8 (mean 7.2), modally 7; fifth supralabial usually subocular; infralabials 5–7 (mean 6.2), modally 6; nuchals 2–5 (mean 2.9), modally 2.

Midbody scale rows 26–30 (mean 28.3), modally 28; paravertebrals 49–59 (mean 54.4), modally 54; subdigital lamellae smooth, 15–20 below fourth finger (mean 16.9) modally 17, 19–25 below fourth toe (mean 21.9) modally 22; 12–15 supradigital lamellae above fourth finger (mean 13.2) modally 13, 14–18 above fourth toe (mean 16.2) modally 16; palmar and plantar scales rounded; plantars 11–15 (mean 12.7), modally 13; palmars 10–13 (mean 11.3), modally 12.

Snout-vent length to 49.3 mm (mean 44.1 mm). *Percentages of snout-vent length*: body length 49.2–57.6% (mean 53.9%); tail length 144.0% (n = 1); forelimb length 29.8–36.5% (mean 33.1%); hindlimb length 37.5–45.4% (mean 40.6%); forebody length 36.0–43.6% (mean 40.5%); head length 17.6–20.9% (mean 19.9%). *Percentages of head*

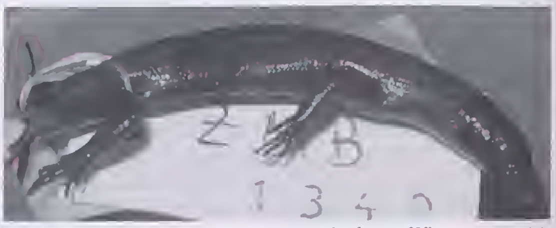

Fig. 181. Lectotype of *Ablepharus poecilopleurus* Wiegmann, 1834. ZMB 1349, island near Pisacoma, Peru.

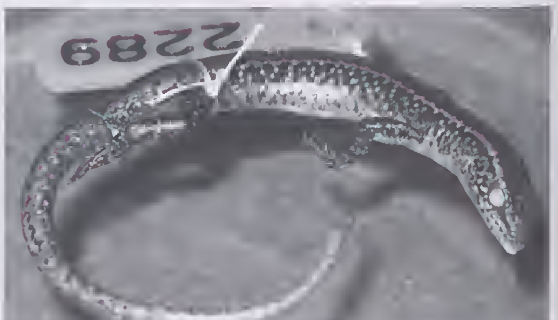

Fig. 182. *Cryptoblepharus poecilopleurus poecilopleurus* Wiegmann, 1834. BMNH 1976.2289, near Coyhaique, Chile.

length: head depth 43.2–52.5% (mean 46.9%); head width 59.3–65.8% (mean 62.9%); snout length 41.7–48.3% (mean 44.7%). Paravertebral scale width 3.0–4.1% (mean 3.3%) of snout-vent length; dorsolateral scale width 78.2–94.1% (mean 87.2%) of paravertebral scale width.

Colouration and pattern as described above (see Plate 4.8, Figs 181 and 182).

Distribution. Widespread through the islands of Oceania. Known from the Austral, Cook, Gilbert, Hawaiian, Line, Mariana, Marquesa, Marshall, Palau, Phoenix, Pitcairn, Samoa, Society, Tahiti, Tonga, Tuamotu and Wake island groups and/or islands (Adler *et al.* 1995; Burt and Burt 1932; Crombie and Steadman 1986; Hunsaker and Breese 1967; McCann 1974; McCoid *et al.* 1995; McGregor 1904; McKeown 1978; Mertens 1931; Oliver and Shaw 1953; Pregill 1993; Rodda *et al.* 1991; Snyder 1919; Wiles and Conry 1990; Wiles and Guerrero 1996; Wiles *et al.* 1989).

Occasional records indicate *C. p. poecilopleurus* occurs on the west coast of the South American mainland. The type locality is "islands near Pisacoma, Peru" (Wiegmann 1835), Duméril and Duméril (1851; cited in Mertens 1931) note a specimen from "Puna Island, near Guayaquil, Ecuador", and Boulenger (1887) cites a third locality as "Bahia, Smithsonian Institution" which may relate to USNM 063494, collected in Peru by the U.S. Exploring Expedition. A fourth record (BMNH 1976-2289) (Fig. 182) was collected near "Coyhaique, Chile" in 1976 .

Remarks. A saxicoline and/or arboreal species, largely associated with littoral habitats. Information on habits is given by McKeown (1978) and on reproduction by McGregor (1904).

Cryptoblepharus renschi Mertens, 1928
(Fig. 183)

Type material examined. *Cryptoblepharus boutonii renschi* Mertens, 1928. HOLOTYPE: SMF 22095, Kambaniroe, near Waingapu, Sumba Island, Indonesia. R. Mertens, 1927. PARATYPES: SMF22209-11, same data as holotype.

Non-type material examined. See Appendix 4.

Description (6 specimens). A small (<40 mm SVL), short-legged, deep-headed, arboreal *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5–6 (mean 5.7), modally 6; enlarged upper ciliaries 3–4 (mean 3.2), modally 3; posterior loreal usually largest; supralabials 7; fifth supralabial usually subocular; infralabials 6; nuchals 2.

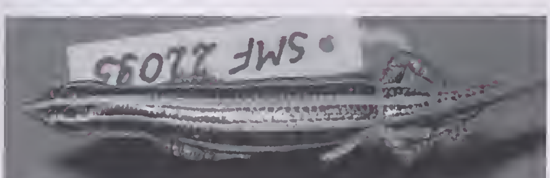

Fig. 183. Holotype of *Cryptoblepharus boutonii renschi* Mertens, 1928. SMF 22095, Kambaniroe, near Waingapu, Sumba Island, Indonesia.

Midbody scale rows 22–26 (mean 24.3), modally 24; paravertebrals 44–53 (mean 49.5), modally 52; subdigital lamellae smooth, 14–17 below fourth finger (mean 16.5) modally 17, 18–24 below fourth toe (mean 20.7) modally 20; 12–13 supradigital lamellae above fourth finger (mean 12.2) modally 12, 14–16 above fourth toe (mean 15.2) modally 15; palmar and plantar scales rounded; plantars 9–12 (mean 10.3), modally 10; palmars 9–11 (mean 9.5), modally 9.

Snout-vent length to 39.5 mm (mean 35.8 mm). *Percentages of snout-vent length*: body length 48.1–56.7% (mean 51.3%); tail length 153.5% (n = 1); forelimb length 30.5–35.7% (mean 33.0%); hindlimb length 38.8–45.6% (mean 42.2%); forebody length 38.6–44.3% (mean 41.4%); head length 20.2–22.3% (mean 21.0%). *Percentages of head length*: head depth 41.0–50.1% (mean 46.9%); head width 58.4–65.4% (mean 62.3%); snout length 44.0–46.8% (mean 44.9%). Paravertebral scale width 4.8–6.4% (mean 5.3%) of snout-vent length; dorsolateral scale width 66.7–84.0% (mean 74.8%) of paravertebral scale width.

Boldly striped, *C. renschi* has a simple body pattern of longitudinally aligned, narrow, pale stripes on a dark ground colour. These consist of a vertebral stripe on the head and body, laterodorsals from supraoculars to tail and mid-lateral stripes from labials to hindlimb (Fig. 183).

Distribution. Western islands of Nusa Tenggara Timur Province, Indonesia. Known from Kambaniroe (near Waingapu) (Mertens 1928b) and Kambera (Mertens 1964) on Sumba, and Komodo and Padar islands (Mertens 1964). Auffenberg (1980) records it from Pulau Longo (off Komodo) and reports observing a specimen near Nggoer, western Flores. McKay (2006) records it from eastern Karangasem and Nusa Lembongan on Bali.

Remarks. An arboreal species associated with savanna habitats, where it is found on trees or under bark (Auffenberg 1980). Auffenberg (1980) gives detailed information on morphology and habits. McKay (2006) notes that it also inhabits trees in monsoon forests and is abundant in gardens and on building walls at Karangasem.

Cryptoblepharus richardsi sp. nov.
(Plate 4.9; Figs 184–186)

Type material examined. *Cryptoblepharus richardsi* Horner. HOLOTYPE: SAMA R62449, Foreshore by Misima Mine, Misima Island, Louisiade Archipelago, Milne Bay Province, Papua New Guinea, 10°41'29"S 152°47'45"E. coll. S. Richards, 3 November 2002. On beach, rocks and foreshore vegetation. PARATYPES: PAPUA NEW GUINEA: SAMA 62447-448, same data as holotype except 10 November 2002; SAMA 62450–455, same data as holotype; UPNG 10043, Lagua Camp, Misima Island, 10°41'40"S 152°49'43"E. coll. S. Richards, 26 October 2002. On limestone rock at seafront, 1730 hours; UPNG 10044-045, same data as holotype.

Diagnosis (11 specimens). A medium sized (32–43 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*, distinguished from congeners by combination of: fused

Fig. 184. Ventral surface of foot of *Cryptoblepharus richardsi* sp. nov. showing dark, ovate plantar scales (SAM R62448, Misima Island, Papua New Guinea). Scale: x20.

Fig. 185. Holotype of *Cryptoblepharus richardsi* sp. nov., SAM R62449, Misima Island, Papua New Guinea.

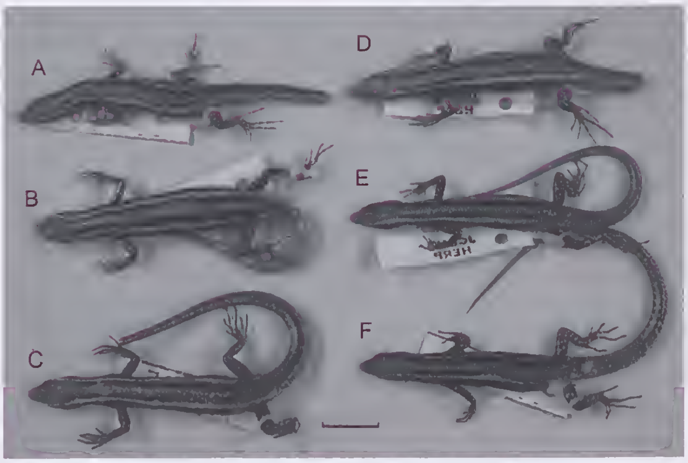

Fig. 186. *Cryptoblepharus richardsi* sp. nov., Misima Island, Papua New Guinea. Preserved material. **A**, UPNG 10044; **B**, SAM 62451; **C**, SAM R62453; **D**, SAM R62452; **E**, SAM R62449 (holotype); **F**, SAM R62447. Scale bar = 10 mm.

interparietal and frontoparietal shields and medium size (maximum SVL <44 mm); modal values of five supraciliary scales, 26 midbody scale rows, 53 paravertebral scales, 17 fourth finger subdigital lamellae, 21 fourth toe supradigital lamellae, 12 palmar and 14 plantar scales; mean values of: head depth 40.2% of head length, forebody length 42.0% of SVL, forelimb length 34.4% of SVL, hindlimb length 46.1% of SVL, paravertebral scale width 4.4% of SVL; and boldly striped body pattern with prominent dark dorsolateral stripes and broad vertebral zone of ground colour.

Description (11 specimens). Postnasals absent; prefrontals usually in broad contact (82%), occasionally in narrow contact (9%) or separated (9%); supraciliaries 4–5 (mean 5.0), modally 5; enlarged upper ciliaries 3–4 (mean 3.2), modally 3; posterior loreal usually largest (56%), often loreals are subequal (44%); supralabials 7–8 (mean 7.1), modally 7; fifth supralabial usually subocular (91%), occasionally sixth (9%); infralabials 6 (100%); nuchals 2–6 (mean 4.2), modally 4; bilateral posttemporals usually 2+2 (91%), occasionally 2+3 (9%).

Midbody scale rows 24–28 (mean 25.5), modally 26; paravertebrals 52–58 (mean 54.5), modally 53; subdigital lamellae smooth, 15–20 below fourth finger (mean 17.5) modally 17, 20–25 below fourth toe (mean 21.8) modally 21; 13–14 supradigital lamellae above fourth finger (mean 13.3) modally 13, 15–18 above fourth toe (mean 16.4) modally 16; palmar and plantar scales ovate, without calli and skin visible between scales (Fig. 184); plantars 10–15 (mean 12.7), modally 14; palmars 10–14 (mean 12.0), modally 12.

Snout-vent length to 43.1 mm (mean 38.6 mm). *Percentages of snout-vent length*: body length 42.2–53.0% (mean 49.0%); tail length 158.2–174.7% (mean 166.5%); forelimb length 32.2–38.0% (mean 34.4%); hindlimb length 43.5–49.1% (mean 46.1%); forebody length 39.8–47.6% (mean 42.0%); head length 20.2–23.1% (mean 21.2%). *Percentages of head length*: head depth 36.3–44.0% (mean 40.2%); head width 54.5–61.9% (mean 57.8%); snout length 43.7–48.8% (mean 46.6%). Paravertebral scale width 3.9–5.0% (mean 4.4%) of snout-vent length; dorsolateral scale width 61.3–91.5% (mean 77.0%) of paravertebral scale width.

Details of holotype. Adult male (Fig. 185), SAMA R62449. Postnasals absent; prefrontals in broad contact;

supraciliaries 5; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 6. Midbody scale rows 24; paravertebrals 56; subdigital lamellae smooth, 15 below fourth finger; 22 below fourth toe; supradigital lamellae 13 above fourth finger; 15 above fourth toe; palmars and plantars rounded, skin visible between scales; plantars 13; palmars 12. Snout-vent length 39.3 mm; body length 19.9 mm; tail missing; forelimb length 13.7 mm; hindlimb length 18.6 mm; forebody length 16.5 mm; head length 8.6 mm; head depth 3.4 mm; head width 4.9 mm; snout length 3.7 mm.

Colouration and pattern. A brownish-grey *Cryptoblepharus*, with longitudinally aligned, simple body pattern dominated by brownish grey vertebral zone and prominent dark dorsolateral and pale laterodorsal stripes (Plate 4.9). Intensity of body patterning is variable, ranging from obscure to prominent (Fig. 186A–F). Most specimens conform to the following description.

Dorsal ground colour brown to grey-brown, with moderately broad vertebral zone extending from above eye to hindlimb. Vertebral zone unpatterned, as wide as single paravertebral scale and brown to grey-brown in colour. Distinct, black dorsolateral stripes extend from above eye onto tailbase, where they merge creating a blackish, ragged, median, tapering stripe on anterior half of tail. Inner margin of dark dorsolateral stripes slightly ragged. Prominent narrow, creamish laterodorsal stripes extend from above eye onto tail. Pale laterodorsal stripes smooth edged and without patterning, about as wide as laterodorsal scale. Head concolorous with vertebral zone or coppery brown, usually with vague dark mottling on scales. Laterally patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Labials creamish, patterned with fine dark margins to scales.

Flanks patterned with brownish-black upper lateral zone, slightly wider than dark dorsolateral stripes, extending from loreals onto tail and forming a smooth outer border to pale laterodorsal stripes. Usually immaculate, but occasionally flecked with pale specks and spots, upper lateral zone is about 2.5 lateral scales wide and borders an indistinct pale mid-lateral stripe extending from labials to hindlimb. Mid-lateral stripe is about 1.5 lateral scales wide and has slightly ragged margins. Dark grey lower lateral zone, often obscure, peppered with small pale and/or dark spots and coalesces into pale venter. Tail concolorous with body, patterned with continuations of blackish dorsolateral stripes, pale laterodorsal stripes and dark upper lateral zone. Limbs and toes concolorous with body, patterned with pale and dark speckling. Venter immaculate off-white. Palmar and plantar surfaces light grey to blackish subdigital lamellae blackish.

Sex ratio and reproductive biology. Sex ratio favoured males (6:5), but was not significantly different from parity ($X^2 = 0.76$). Reproductive biology unavailable.

Comparison with congeners. *Cryptoblepharus richardsi* sp. nov. is distinguished from most south-west Indian Ocean taxa by having a simple striped body pattern. It shares a simple striped body pattern only with *C. bitaeniatus* and *C. gloriosus*, but can be distinguished from these by midbody scale rows (modally 26 versus 22, 24 or 28), more fourth toe subdigital lamellae (modally 21 versus 18–20), more plantar scales (modally 14 versus 11–13) and shallower narrow head (mean HH 40.2% versus 42.5% or more, HW 57.8% versus 58.4% or more of head length).

Among Indo-Pacific taxa, distinguished from *C. baliensis, C. egeriae, C. intermedius, C. keiensis, C. leschenault, C. novaeguineae, C. p. poecilopleurus, C. renschi* and *C. yulensis* sp. nov. by fewer supraciliary scales (five versus six). Further differs from *C. egeriae, C. keiensis, C. novaeguineae, C. p. poecilopleurus, C. renschi* and *C. yulensis* sp. nov. by midbody scale rows (modally 26 versus 22, 24 or 28) and from *C. baliensis, C. intermedius* and *C. leschenault* by more paravertebral scales (modally 53 versus 50 or less).

Differs from *C. burdeni, C. c. cursor, C. xenikos* sp. nov., *C. nigropunctatus, C. novocaledonicus, C. novohebridicus, C. p. paschalis* and *C. rutilus* by midbody scale rows (modally 26 versus 20, 24, 28 or 30), further differs from *C. xenikos* sp. nov., *C. nigropunctatus, C. p. paschalis* and *C. rutilus* by number of paravertebral scales (modally 53 versus 47, 50 or 57), from *C. c. cursor, C. novocaledonicus, C. novohebridicus* by shallow, narrow head (mean HH 40.2% versus 46.7% or more of head length; HW 57.8% versus 59.7% or more of head length) and from *C. burdeni* by more fourth toe subdigital lamellae (modally 21 versus 17) and smaller size (mean SVL 38.6 versus 43.9 mm). Differs from *C. c. larsonae* ssp. nov., *C. eximius* and *C. l. vicinus* ssp. nov. by shallow, narrow head (mean HH 40.2% versus 45.2% or more of head length; HW 57.8% versus 62.2% or more of head length), further differs from *C. c. larsonae* ssp. nov. by longer forebody (mean 42.0% versus 38.1% of SVL), from *C. eximius* by fewer fourth finger subdigital lamellae (modally 17 versus 19) and from *C. l. vicinus* ssp. nov. by fewer plantar scales (modally 14 versus 16) and smaller size (mean SVL 38.6 versus 41.3 mm). Differs from *C. furvus* sp. nov. by fewer paravertebral scales (modally 53 versus 60) and smaller size (mean SVL 38.6 versus 42.4 mm) and from *C. schlegelianus* by more paravertebral scales (modally 53 versus 46) and subdigital lamellae (modally FTL 17 versus 13; HTL 21 versus 16). Most similar in colour and body pattern to *C. xenikos* sp. nov. but readily distinguished by more midbody scale rows (modally 26 versus 22), paravertebral (modally 53 versus 50), palmar (modally 12 versus 9) and plantar scales (modally 14 versus 9), subdigital lamellae (modally FTL 16 versus 17, HTL 21 versus 19) and limb lengths (mean FL 34.4% versus 30.9% of SVL, RL 46.1% versus 39.8% of SVL).

Among Australian taxa, distinguished from members of lineage 1 by having five supraciliaries (versus 6) and simple striped body pattern. Distinguished from most members of lineage 2 by midbody scale rows (modally 26 versus 22 or 24) and paravertebral scales (modally 53 versus 51 or less). It shares 26 or more midbody scale rows and 53 or more paravertebral scales with *C. gurrmul* sp. nov. and *C. litoralis*. Distinguished from the two Australian subspecies of *C. litoralis* by fewer paravertebral scales (modally 53 versus 55 or more), smaller size (mean SVL, 37.6 versus 39.0 mm or more) and wider paravertebral scales (mean 4.4% versus 3.7% or less of SVL) and from *C. gurrmul* sp. nov. by fewer midbody scale rows (modally 26 versus 28) and more palmar (modally 12 versus 7) and plantar scales (modally 14 versus 7).

Cryptoblepharus richardsi sp. nov. is most similar to *C. adamsi* sp. nov., *C. bitaeniatus*, *C. cursor*, *C. eximius*, *C. gloriosus*, *C. xenikos* sp. nov., *C. novohebridicus*, *C. pulcher*, *C. virgatus*, and *C. yulensis* sp. nov. in having combinations of simple striped body patterns with prominent dark dorsolateral stripes and vertebral zone of ground colour. However it differs from these by having more fourth finger (modally 17 versus 15–16) and toe subdigital lamellae (modally 21 versus 18–20), palmar (modally 12 versus 8–11) and plantar scales (modally 14 versus 9–13). Further differs from most by having 26 midbody scales rows. It shares 26 midbody scale rows with *C. c. larsonae* ssp. nov. and *C. eximius* but differs from *C. c. larsonae* ssp. nov. by having longer hindlimbs (mean 46.1% instead of 44.2% of SVL) and shallower head (mean 40.2% instead of 49.1% of SVL) and from *C. eximius* by having a shallower head (mean 40.2% instead of 45.2% of SVL) and wider paravertebral scales (mean 4.4% instead of 3.6% of SVL).

Distribution. Misima Island, Louisiade Archipelago, Papua New Guinea.

Sympatry and geographic variation. Cases of sympatry unknown. Taxon known from a single locality.

Habits and habitats. A coastal form recorded from beach, rocks and foreshore vegetation.

Etymology. Named for Stephen Richards, of the South Australian Museum, in recognition of his collection of the type series from Misima Island.

Cryptoblepharus rutilus (Peters, 1879)
(Fig. 187)

Type material examined *Ablepharus rutilis* Peters, 1879. HOLOTYPE: ZMB 7926, Palau Islands, Oceania. J. Kubary.

Description (1 specimen). A small (<40 mm SVL), long-legged, deep-headed, arboreal *Cryptoblepharus*. Postnasals absent; prefrontals usually in broad contact; supraciliaries 5; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 4.

Midbody scale rows 20; paravertebrals 47; subdigital lamellae smooth, 18 below fourth finger, 23 below fourth toe; 14 supradigital lamellae above fourth finger, 15 above fourth toe; palmar and plantar scales rounded; plantars 10; palmars 11.

Snout-vent length 35.4 mm. *Percentages of snout-vent length*: body length 54.2%; tail length 129.1%; forelimb length 36.5; hindlimb length 44.1%; forebody length 41.4%; head length 20.3%. *Percentages of head length*: head depth 46.7%; head width 58.6; snout length 44.0%. Paravertebral scale width 4.6% of snout-vent length; dorsolateral scale width 73.4% of paravertebral scale width.

The specimen examined (holotype) is in poor condition, with numerous body scales missing (Fig. 187). It appears to have a greenish-brown ground colour, speckled with dark and pale spots and flecks, and obscure dark dorsolateral and pale laterodorsal stripes. In the original description Peters (1879) describes *C. rutilus* as "shiny golden, with a row of black stains on the back". Mertens (1931), describing the holotype, suggests a metallic-bronze, light brown ground colour with obscure stripes.

Distribution. Palau Islands, Oceania.

Remarks. Crombie and Pregill (1999) give information on habits and distribution (as *Cryptoblepharus* sp.). Crombie and Pregill (1999) also observed a more strongly striped, "*poecilopleurus*-like" *Cryptoblepharus* on northern Babeldaob Island, supporting Wiles and Conry's (1990) record of *C. p. poecilopleurus* from the Palau Islands.

Cryptoblepharus schlegelianus Mertens, 1928
(Fig. 188)

Type material examined. *Cryptoblepharus boutonii schlegelianus* Mertens, 1928. HOLOTYPE: SMF 15604, Timor (ex Liebig-Museum, 1854).

Description (1 specimen). A medium sized (40–44 mm SVL), very short-legged, shallow-headed *Cryptoblepharus*. Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; anterior loreal largest; supralabials 7; fifth supralabial usually subocular; infralabials 7; nuchals 4.

Midbody scale rows 26; paravertebrals 46; subdigital lamellae smooth, 13 below fourth finger, 16 below fourth toe; 11 supradigital lamellae above fourth finger, 13 above fourth toe; palmar and plantar scales rounded; plantars 11; palmars 8.

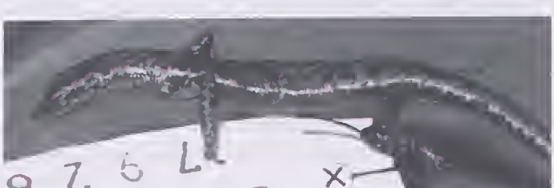

Fig. 187. Holotype of *Ablepharus rutilus* Peters, 1879. ZMB 7926, Palau Islands, Oceania.

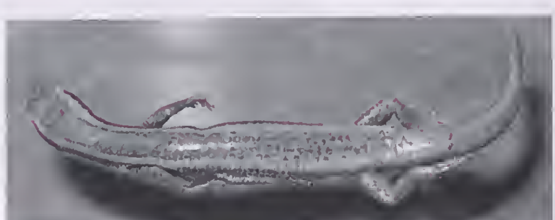

Fig. 188. Holotype of *Cryptoblepharus boutonii schlegelianus* Mertens, 1928. SMF 15604, Timor.

Snout-vent length 40.3 mm. *Percentages of snout-vent length*: body length 50.2%; tail length indeterminate; forelimb length 28.6%; hindlimb length 38.8%; forebody length 36.5%; head length 19.4%. *Percentages of head length*: head depth 39.5%; head width 59.8%; snout length 43.4%. Paravertebral scale width 3.5% of snout-vent length; dorsolateral scale width 81.1% of paravertebral scale width.

The specimen examined (holotype) is in poor condition, with numerous body scales missing (Fig. 188). It appears to have a pale grey ground colour, with very narrow, dark dorsolateral and moderately broad, pale laterodorsal stripes.

Distribution. Timor Island, Nusa Tenggara, Indonesia. Recorded from Semau island, off Kupang Timor, by Brongersma (1942).

Remarks. Brongersma (1942) cites S. Müller as recording that *C. schlegelianus* prefers sandy beaches and was extremely common on the northern beach of Samao (= Semau Island) where it occurred in flotsam such as logs and leaves washed ashore by the surf. *Cryptoblepharus schlegelianus* is sympatric with *C. leschenault* on Semau Island (Brongersma 1942).

Cryptoblepharus xenikos sp. nov.

(Plate 4.10; Figs 189–191)

Type material examined. *Cryptoblepharus xenikos* Horner. HOLOTYPE: SAMA R62458, Aquam Camp, Trans-Fly region, Western Province, Papua New Guinea, 09°05'48"S 141°26'08"E. coll. S. Richards, 1 April 2004. On tree by camp, in afternoon. PARATYPES: PAPUA NEW GUINEA: SAMA R62456-457, Wegamu Camp, Trans-Fly region, Western Province, Papua New Guinea, 08°25'58"S 141°06'46"E. coll. S. Richards, 28 March 2004; SAMA R62459, same data as holotype except 3 April 2004 and 1015 hours; UPNG 10046, same data as holotype.

Diagnosis. A medium sized (32–38 mm SVL), short-legged, shallow-headed, arboreal *Cryptoblepharus*. Distinguished from Indo-Pacific congeners by combination of: fused interparietal and frontoparietal shields, medium size (maximum SVL <44 mm) and modal values of 16

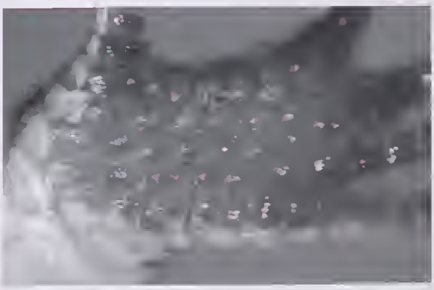

Fig. 189. Ventral surface of foot of *Cryptoblepharus xenikos* sp. nov. showing dark, ovate plantar scales (SAM R62458, Aquam Camp, Trans-Fly region, Papua New Guinea). Scale: x20.

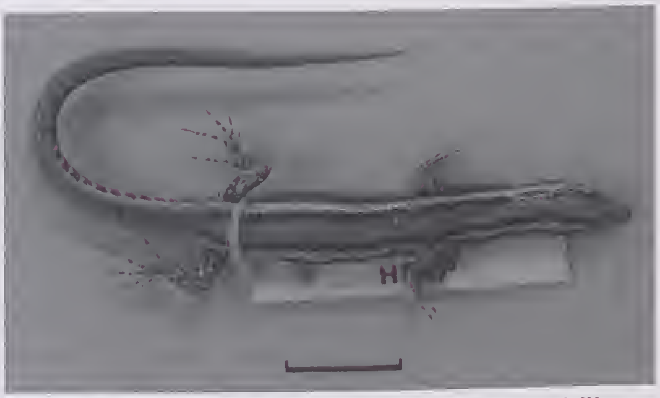

Fig. 190. Holotype of *Cryptoblepharus xenikos* sp. nov., SAM R62458, Wegamu, Trans-Fly region, Papua New Guinea.

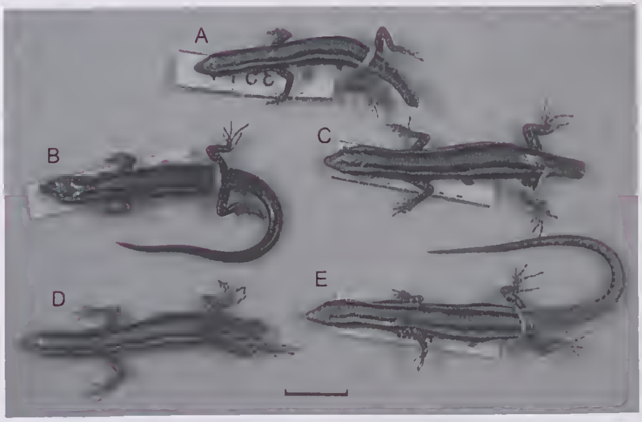

Fig. 191. *Cryptoblepharus xenikos* sp. nov., Trans-Fly region (a, d and e Aquam Camp; b and c Wegamu), Papua New Guinea. Preserved material. **A**, UPNG 10046; **B**, SAM R62456; **C**, SAM R62457; **D**, SAM R62459; **E**, SAM R62458 (holotype). Scale bar = 10 mm.

fourth finger subdigital lamellae, 19 fourth toe supradigital lamellae and 9 palmar.

Description (5 specimens). Postnasals absent; prefrontals in broad contact (100%); supraciliaries 5 (100%); enlarged upper ciliaries 3 (100%); posterior loreal usually largest (60%), often loreals are subequal (40%); supralabials 7–8 (mean 7.1), modally 7; fifth supralabial usually subocular (90%), occasionally sixth (10%); infralabials 6 (100%); nuchals 2–4 (mean 3.0), modally 2; bilateral post-temporals 2+2 (100%).

Midbody scale rows 22 (100%); paravertebrals 46–53 (mean 49.8), modally 50; subdigital lamellae smooth, 14–17 below fourth finger (mean 15.8) modally 16, 17–21 below fourth toe (mean 19.2) modally 19; 12–13 supradigital lamellae above fourth finger (mean 12.2) modally 12, 14–15 above fourth toe (mean 14.6) modally 15; palmar and plantar scales ovate, without calli and skin not visible between scales (Fig. 189); plantars 8–10 (mean 9.0), modally 9; palmars 8–10 (mean 9.0), modally 9.

Snout-vent length to 38.0 mm (mean 35.3 mm). *Percentages of snout-vent length*: body length 48.4–52.8% (mean 50.6%); tail length unknown; forelimb length 27.0–34.4% (mean 30.9%); hindlimb length 36.3–42.4% (mean 39.8%); forebody length 40.7–43.7% (mean 41.9%); head length 19.3–21.2% (mean 20.2%). *Percentages of head length*: head depth 37.3–44.7% (mean 40.1%); head width 54.5–60.5% (mean 57.7%); snout length 48.6–51.7% (mean 50.3%). Paravertebral scale width 4.0–4.8% (mean 4.5%) of snout-vent length; dorsolateral scale width 69.6–90.8% (mean 79.5%) of paravertebral scale width.

Details of holotype. Adult female (Fig. 190), SAMA R62458. Postnasals absent; prefrontals in broad contact; supraciliaries 5; enlarged upper ciliaries 3; posterior loreal largest; supralabials 7; fifth supralabial subocular; infralabials 6; nuchals 2. Midbody scale rows 22; paravertebrals 50; subdigital lamellae smooth, 14 below fourth finger; 17 below fourth toe; supradigital lamellae 12 above fourth finger; 15 above fourth toe; palmars and plantars rounded, skin not visible between scales; plantars 8; palmars 8. Snout-vent length 37.9 mm; body length 18.9 mm; tail missing; forelimb length 10.2 mm; hindlimb length 13.7 mm; forebody length 15.8 mm; head length 7.4 mm; head depth 3.0 mm; head width 4.0 mm; snout length 3.6 mm.

Colouration and pattern. A brownish-grey *Cryptoblepharus*, with longitudinally aligned, simple body pattern dominated by broad, brownish vertebral zone, and prominent dark dorsolateral and pale laterodorsal stripes (Plate 4.10). Intensity of body patterning is variable, ranging from obscure to prominent (Fig. 191A–E). Most specimens conform to the following description.

Dorsal ground colour grey to bronze-brown, with broad vertebral zone extending from above eye to hindlimb. Vertebral zone unpatterned, as wide as single paravertebral scale and grey to bronze-brown in colour. Distinct, black dorsolateral stripes extend from above eye onto tailbase, where they merge creating an obscure blackish, ragged, median, tapering stripe on anterior half of tail. Inner margin of dark dorsolateral stripes slightly ragged. Prominent narrow, creamish laterodorsal stripes extend from above eye onto tail. Pale laterodorsal stripes smooth edged and without patterning, about as wide as laterodorsal scale. Head concolorous with vertebral zone or coppery brown, usually with vague dark mottling on scales. Laterally patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Labials creamish, patterned with fine dark margins to scales.

Flanks patterned with blackish-grey upper lateral zone, slightly wider than dark dorsolateral stripes, extending from loreals onto tail and forming a smooth outer border to pale laterodorsal stripes. Usually immaculate, but occasionally flecked with pale specks and spots, upper lateral zone is about two lateral scales wide and may coalesce gradually into greyish lower lateral zone or have an indistinct pale mid-lateral stripe extending from labials to hindlimb. Mid-lateral stripe (if present) is about 1.5 lateral scales wide and has slightly ragged margins. Dark grey lower lateral zone is often obscure and peppered with small pale and/or dark spots and coalesces into pale venter. Tail concolorous with body, patterned with continuations of blackish dorsolateral stripes, pale laterodorsal stripes and dark upper lateral zone. Limbs and toes concolorous with body, patterned with pale and dark speckling. Venter immaculate off-white. Palmar and plantar surfaces off-white or pale brown, subdigital lamellae dark brown.

Sex ratio and reproductive biology. Sex ratio favoured males (3:2), but was not significantly different from parity ($X^2 = 0.65$). Reproductive biology unavailable.

Comparison with congeners. *Cryptoblepharus xenikos* sp. nov. is distinguished from most south-west Indian Ocean taxa by having a simple striped body pattern. It shares this pattern type only with *C. bitaeniatus* and *C. gloriosus*, but can be distinguished from *C. bitaeniatus* by having fewer midbody scale rows (modally 22 instead of 28) and paravertebral scales (modally 50 instead of 53) and from *C. gloriosus* by fewer palmar (modally 9 instead of 10 or 12) and plantar scales (modally 9 instead of 11 or 13) and shallower head (mean 40.1% instead of 42.5% or more of head length).

Among Indo-Pacific taxa, distinguished from *C. baliensis, C. egeriae, C. intermedius, C. keiensis, C. leschenault, C. novaeguineae, C. p. poecilopleurus, C. renschi* and *C. yulensis* sp. nov. by fewer supraciliary scales (five versus six). Further differs from *C. baliensis, C. egeriae, C. intermedius, C. leschenault, C. p. poecilopleurus, C. renschi* and *C. yulensis* sp. nov. by fewer midbody scale rows (modally 22 versus 24, 26 or 28) and from *C. keiensis* and *C. novaeguineae* by fewer fourth toe subdigital lamellae (modally 19 versus 24 and 23).

Differs from all remaining Indo-Pacific taxa (*C. burdeni, C. c. cursor; C. c. larsonae* ssp. nov., *C. eximius, C. furvus* sp. nov., *C. l. vicinus* ssp. nov., *C. nigropunctatus, C. novocaledonicus, C. novohebridicus, C. p. paschalis, C. rutilus,* *C. schlegelianus* and *C. richardsi* sp. nov.) by midbody scale rows (modally 22 versus 20, 24, 26, 28 or 30) and from most by shallow, narrow head (mean HH 40.1% versus 45.2% or more of head length; HW 57.7% versus 59.7% or more of head length). Shares shallow, narrow head with *C. burdeni, C. furvus* sp. nov., *C. schlegelianus* and *C. richardsi* sp. nov. but further differs from *C. furvus* sp. nov. and *C. richardsi* sp. nov. by fewer paravertebral scales (modally 50 versus 60 and 53), from *C. schlegelianus* by more paravertebral scales (modally 50 versus 46) and from *C. burdeni* by fewer fourth toe subdigital lamellae (modally 19 versus 24) and shorter hindlimbs (mean 39.8% versus 44.4% of SVL). Most similar in colour and body pattern to *C. richardsi* sp. nov. but readily distinguished by fewer midbody scale rows (modally 22 versus 26), paravertebral (modally 50 versus 53), palmar (modally 9 versus 12) and plantar scales (modally 9 versus 14), subdigital lamellae (modally FTL 16 versus 17, HTL 19 versus 21) and limb lengths (mean FL 30.9% versus 34.4% of SVL, RL 39.8% versus 46.1% of SVL).

Among Australian taxa, distinguished from members of lineage 1 by having five supraciliaries (versus 6) and fewer midbody scale rows (modally 22 versus 24 or 26) and from most members of lineage 2 by midbody scale rows (modally 22 versus 24, 26 or 28) and simply striped body pattern. Shares body pattern type with *C. adamsi* sp. nov., *C. pulcher* and *C. virgatus* and 22 midbody scale rows with *C. ustulatus* and *C. virgatus* but differs from these by having shorter forelimbs (mean 30.9% versus 32.1% or more of SVL) and longer snout (mean 50.3% versus 44.1% or less of SVL). Further differs from *C. pulcher, C. ustulatus* sp. nov., and *C. virgatus* by having more paravertebral scales (modally 50 versus 47 or less).

Cryptoblepharus xenikos sp. nov. is most similar to *C. adamsi* sp. nov., *C. bitaeniatus*, *C. cursor, C. eximius, C. gloriosus, C. novohebridicus, C. pulcher, C. virgatus, C. richardsi* sp. nov. and *C. yulensis* sp. nov. in having combinations of simple striped body patterns with prominent dark dorsolateral stripes and vertebral zone of ground colour. However it differs from most of these by having 22 midbody scale rows instead of 24, 26 or 28. It shares 22 midbody scale rows with *C. virgatus* and two subspecies of *C. gloriosus* but differs from *C. virgatus* by having more paravertebral scales (modally 50 instead of 47) and deeper head (mean 40.1% instead of 38.2% of head length) and from *C. gloriosus* by fewer palmar (modally 9 instead of 10 or 12) and plantar scales (modally 9 instead of 11 or 13) and shallower head (mean 40.1% instead of 42.5% or more of head length)

Distribution. Papua New Guinea, from the Trans-Fly region, Western Province.

Sympatry and geographic variation. Cases of sympatry unknown. Sample size too small to analyse geographic variation.

Habits and habitats. An arboreal species, recorded from tree trunks and a large log.

Etymology. From the Greek adjective *xenikos*, in relation to the definition 'concerning the status of a foreigner'.

Cryptoblepharus yulensis sp. nov.

(Fig. 192)

Type material examined. *Cryptoblepharus yulensis* Horner. HOLOTYPE: NHMB 10570, Yule Island, Central Province, Papua New Guinea, 8°49'S 146°32'E. P. Wirz, 1931. PARATYPES – PAPUA NEW GUINEA: NHMB 10568-569, 10572-575, same data as holotype; NHMB 10576-577, Western Province. P. Wirz, 1931; QM J30028-029, Korobosea, Port Moresby, Central Province, 9°29'S 147°11'E, 9 January 1977; QM J30030, Rouna Falls, 4 km west of Sogeri, Central Province, 9°25'S 147°23'E, 1 January 1977; QM J30031-032, Konedobu, Port Moresby, Central Province, 9°28'S 147°09'E, 28 December 1976.

Diagnosis (14 specimens). A medium sized (40–44 mm SVL), very short-legged, shallow-headed *Cryptoblepharus*. Distinguished from congeners by combination of: modal values of six supraciliary scales, 24 midbody scale rows, 53 paravertebral scales, 20 fourth toe subdigital lamellae and 16 fourth finger supradigital lamellae; mean values of head depth 42.4% of head length, forelimb length 32.9% of snout-vent length and hindlimb length 39.5% of snout-vent length, and simple body pattern with broad, brown vertebral zone and lack of speckling or blotches.

Description. Postnasals absent; prefrontals usually in broad contact; supraciliaries 4–6 (mean 5.8), modally 6; enlarged upper ciliaries 2–4 (mean 3.0), modally 3; loreals usually subequal; supralabials 7; fifth supralabial usually subocular; infralabials 6–7 (mean 6.6), modally 7; nuchals 2.

Midbody scale rows 22–26 (mean 23.9), modally 24; paravertebrals 47–55 (mean 51.0), modally 53; subdigital lamellae smooth, 14–18 below fourth finger (mean 15.6) modally 15, 19–23 below fourth toe (mean 20.1) modally 20; 12–13 supradigital lamellae above fourth finger (mean 12.5) modally 13, 15–17 above fourth toe (mean 15.6) modally 16; palmar and plantar scales rounded; plantars 9–12 (mean 9.9), modally 9; palmars 8–10 (mean 9.2), modally 9.

Snout-vent length to 41.9 mm (mean 37.2 mm). *Percentages of snout-vent length*: body length 47.5–54.5% (mean 50.6%); tail length 135.5–145.2% (mean 141.8%); forelimb length 30.0–35.0% (mean 32.9%); hindlimb length

Fig. 192. Holotype of *Cryptoblepharus yulensis* sp. nov., NHMB 10570, Yule Island, Papua New Guinea.

35.1–42.4% (mean 39.5%); forebody length 38.7–45.9% (mean 42.1%); head length 19.6–22.2% (mean 21.3%). *Percentages of head length*: head depth 37.1–48.6% (mean 42.4%); head width 56.2–66.2% (mean 61.1%); snout length 43.6–48.4% (mean 46.0%). Paravertebral and dorsolateral scale widths not measured.

Details of holotype. Adult specimen, NHMB 10570 (Fig. 192). Postnasals absent; prefrontals in broad contact; supraciliaries 6; enlarged upper ciliaries 3; loreals subequal; supralabials 7; fifth supralabial subocular; infralabials 7; nuchals 2. Midbody scale rows 22; paravertebrals 49; subdigital lamellae smooth, 15 below fourth finger; 20 below fourth toe; supradigital lamellae 12 above fourth finger; 15 above fourth toe; palmars and plantars rounded, plantars 9; palmars 9. Snout-vent length 39.0 mm; body length 21.3 mm; tail incomplete; forelimb length 13.1 mm; hindlimb length 15.7 mm; forebody length 16.5 mm; head length 8.7 mm; head depth 4.0 mm; head width 5.4 mm; snout length 3.9 mm.

Colouration and pattern. Ground colour brown, patterned with longitudinally aligned, simple body pattern dominated by broad, brown vertebral zone, and prominent dark dorsolateral and pale laterodorsal stripes (Fig. 192). Most specimens conform to the following description.

Dorsal ground colour brown, with broad, vertebral zone extending from head onto tail. Vertebral zone immaculate, as wide as paired paravertebral scales and brown in colour. Black dorsolateral stripes extend from supraoculars onto tailbase. Inner margin of dark paravertebral stripes slightly ragged. Prominent, narrow, creamish to white laterodorsal stripes extend from above eye onto tail base. Pale laterodorsal stripes smooth edged and without patterning, about as wide as laterodorsal scale.

Head concolorous with vertebral zone, usually immaculate or with dark margins to shields. Laterally, head patterned with continuation of dark upper lateral zone, which extends above ear, through eye to loreals. Labials creamish, patterned with fine dark margins to scales.

Flanks have blackish upper lateral zone, similar in width to pale laterodorsal stripes, extending from loreals onto tail and forming a smooth outer border to pale laterodorsal stripes. Usually immaculate, but occasionally flecked with pale specks and spots, upper lateral zone typically is about two lateral scales wide. Lower lateral zone creamy-brown, peppered with small pale and/or dark spots and coalesces into pale venter.

Tail concolorous with body, patterned with continuations of pale laterodorsal stripes and dark upper lateral zone. Limbs and toes concolorous with body, patterned with pale and dark speckling.

Venter immaculate off-white. Palmar and plantar surfaces light grey to pale brown.

Sex ratio and sexual dimorphism. Unavailable, examined specimens were not definitively sexed.

Comparison with congeners. *Cryptoblepharus yulensis* sp. nov. is distinguished from all south-west Indian Ocean taxa by having more supraciliary scales (modally 6 versus 5).

Among Indo-Pacific taxa, distinguished from: *C. burdeni, C. c. cursor, C. c. larsonae* ssp. nov., *C. eximius, C. furvus* sp. nov., *C. l. vicinus* ssp. nov., *C. nigropunctatus, C. novocaledonicus, C. novohebridicus, C. p. poecilopleurus. C. rutilus* and *C. schlegelianus* by more supraciliary scales (modally 6 versus 5); from *C. novaeguineae* and *C. keiensis* by more midbody scale rows (modally 24 versus 22); from *C. b. baliensis, C. b. sumbawanus, C. egeriae, C. leschenault* and *C. p. paschalis* by fewer midbody scale rows (modally 24 versus 26 or more); from *C. intermedius* by fewer paravertebral scales (modally 53 versus 46), fewer fourth toe subdigital lamellae (modally 20 versus 23) and shallower head (mean 42.4 versus 47.0% of head length); from *C. renschi* by shorter hindlimbs (mean 39.5 versus 42.2% of snout-vent length), shallower head (mean 42.4 versus 46.9% of head length) and broad, brown vertebral zone (versus narrow, pale vertebral stripe). Distinguished from *C. richardsi* sp. nov. by shorter limbs (mean FL 32.9 versus 34.4% of SVL; RL 39.5 versus 46.1% of SVL) and fewer palmar (modally 9 versus 12) and plantar scales (modally 9 versus 14) and from *C. xenikos* sp. nov. by more midbody scale rows (modally 24 versus 22) and shorter snout (mean 46.0 versus 50.3% of head length).

Among Australian taxa, distinguished from members of lineage 2 by having six supraciliaries (versus 5). Distinguished from saxicoline members of lineage 1 (*C. daedalos* sp. nov., *C. juno* sp. nov., *C. megastictus* and *C. wulbu* sp. nov.) by ground colour and body pattern characteristics (brownish, longitudinally aligned pattern versus reddish, randomly speckled or blotched pattern) and by fewer midbody scale rows (modally 24 versus 26). Distinguished from *C. australis, C. buchananii, C. cygnatus* sp. nov., *C. metallicus* and *C. ruber* by ground colour and body pattern characteristics (brownish simple striped body versus greyish complex pattern of stripes, spots and flecks), more infralabial scales (modally 7 instead of 6) and shorter forelimbs (mean % of SVL 32.9 instead of 33.5 mm or more).

Cryptoblepharus yulensis sp. nov. is most similar to *C. adamsi* sp. nov., *C. bitaeniatus, C. cursor, C. eximius, C. gloriosus, C. xenikos* sp. nov., *C. novohebridicus, C. pulcher, C. virgatus,* and *C. richardsi* sp. nov. in having combinations of simple striped body patterns with prominent dark dorsolateral stripes and vertebral zone of ground colour. However it differs from all of these by having more supraciliary scales (modally 6 instead of 5).

Distribution. Southern Papua New Guinea. Known from Korobosea and Konedobu near Port Moresby, Rouna Falls near Sogeri and Yule Island in Central Province, and from an unidentified site in Western Province (NMHB 10576-577).

Sympatry and geographic variation. Small sample size prevents analysis of geographic variation. Cases of sympatry unknown.

Habits and habitats. Unavailable.

Etymology. Named in reference to Yule Island, type locality for this species.

***Cryptoblepharus* sp.**

(Fig. 193)

Material examined (1 specimen). SMF 28061, Botanical Gardens, Bogor, Java, Indonesia. Prof. Harms, 1930.

Remarks. This specimen (Fig. 193) was examined by Mertens (1931), who considered it to have been transported to the collection site by human activity. Later, Mertens (1964) identified the sample as *C. virgatus* and reiterated that its appearance in Bogor could only result from human mediated transport.

A taxonomic assessment of this taxon was not attempted, as Prasetyo (1996) has already determined its distinctiveness (from *C. b. baliensis*) and will publish a description.

Fig. 193. *Cryptoblepharus* sp. SMF 28061, Bogor (Buitenzorg), Java, Indonesia.

DISCUSSION

Data congruence. Horner and Adams (2007) identified 22 Australian genetic OTUs (excluding the hybrid OTU virgA1x3) and this study of morphological data identified 25 Australian taxa. While totals are comparable, these results were incongruent in 45% of cases, with the incongruence consisting of either 'divergent allozyme profile but similar morphology' or 'similar allozyme profile but divergent morphology'.

Divergent allozyme profile but similar morphologies may be explained by convergence in, or stasis of, morphological characters, but there is no obvious explanation for the reverse incongruence (aside from the possibility that particular allozyme loci which may have resolved the incongruence were not identified, or the data may have been compromised by small sample sizes for some taxa).

Geographical proximity of taxa has been associated with discordance (Wiens and Penkrot 2002), where different environmental parameters may drive disjunct populations to diverge morphologically but retain similar genotypes throughout the remainder of the genome. This finding is unlikely to apply to the *Cryptoblepharus* situation, given *C. ruber* and its allozymically similar sister *C. megastictus* are sympatric (although ecologically divergent) and two other pairs of allozymic sister-taxa (*C. pannosus* and *C. adamsi*; *C. metallicus* and *C. australis*) are probably sympatric and ecologically similar.

Horner and Adams (2007) determined that genetic OTUs plagA2 and plagA3 were allozymically (and geographically) near to OTUs plagA1, plagA4 and megaA4 (herein recognised as *C. ruber, C. buchananii* and *C. megastictus*). With relatively low levels of genetic divergence (5% fixed allelic differences) and similarities in body patterning (except for *C. megastictus*) and scale characters, these were considered members of a species-complex that had undergone a recent speciation event in which some participants had not yet differentiated morphologically.

In the case of 'divergent allozyme profiles but similar morphology', studies have indicated that genetic divergence in skinks may proceed more rapidly than morphological evolution (Bruna *et al.* 1996; Donnellan and Aplin 1989; Donnellan and Hutchinson 1990; Hutchinson *et al.* 1990; Hickson *et al.* 1992; Austin 1995) and phenotypic similarities are usually attributed to recent common ancestry (Bruna *et al.* 1996). Of genetic OTUs characterised by 'divergent allozyme profiles but similar morphology' (carnA2, carnA4, plagA1, plagA2 and plagA3; herein referred to *C. tytthos* and *C. ruber*), none had previously been taxonomically distinguished and were treated conservatively. Unable to be diagnosed by morphological characters they were treated (along with their morphologically similar sister-OTUs) as composite species, acknowledged as representing two or more morphologically indeterminate taxa.

Based on allozyme data (Horner and Adams 2007) OTU carnA2 (part of *C. tytthos*) is most closely related to allopatric OTUs carnA3 (*C. ochrus*) and megaB (*C. ustulatus*), but is morphologically indistinguishable from its geographical neighbour OTU carnA4 (also part of *C. tytthos*). Interestingly, the relatively low level of genetic divergence (5% fixed allelic differences) between the allopatric, morphologically divergent OTUs carnA2, carnA3 and megaB, suggest they result from a relatively recent speciation event in which, contrary to the above, morphological evolution has exceeded molecular evolution. However, as OTUs carnA2 and carnA4 are not each other's closest relative (Horner and Adams 2007), their morphological similarity cannot be attributed to a recent speciation event and their incongruence may result from convergence in morphological characters or other indeterminate factors.

As a satisfactory explanation for the data incongruence identified in this study is lacking, it remains for future investigations, with larger sample sizes of incongruent taxa, to elucidate the situation.

Sympatry. Sympatry is commonplace among Australian (and extralimital) *Cryptoblepharus,* occurring both within and between genetic lineages and involving up to four taxa, though two taxa in sympatry is most common. Over evolutionary time sympatry in closely related organisms should, through interbreeding, lead ultimately to a homogeneous population or, through disruptive selection factors (Tregenza and Butlin 1999) instigate marked ecological and morphological differentiation. Australian *Cryptoblepharus* are conservative in morphology, often syntopic and occasionally hybridise, so how is specific identity maintained?

Mechanisms proposed to maintain reproductive isolation in sympatry include both pre- and post-mating factors. Post-mating factors, such as hybrid viability, were unable to be investigated by this study except for the probable discounting of gametic incompatibility and zygotic mortality, as evidenced by two hybrid specimens (NTM R18837 and NTM R18931) being gravid females containing well developed eggs. Similarly, some pre-mating factors such as temporal and ecological isolation can be discounted, as syntopic *Cryptoblepharus* (e.g. *C. ruber* and *C. exochus*) share spatial and temporal regimes and have similar ecological and behavioural patterns.

Hemipenis morphology may play a role in maintaining reproductive isolation, particularly between members of different lineages as evidence suggests a possible divergence in hemipenis proportions between Australian lineages. As hemipenis morphology was not investigated in all Australian *Cryptoblepharus* taxa, further research is required to elucidate any role this factor may play.

Behavioural isolation, where congeners meet but choose members of their own species as partners, may be important for *Cryptoblepharus*. Narrowly sympatric species are often interspecifically territorial or aggressive, although Huey and Pianka (1977) found some species of *Mabuya* are social skinks which frequently occur in large numbers on the same log or tree (as do *C. ruber* and *C. exochus*) with little or no interspecific aggression. Huey and Pianka (1977) suggest the evolution of interspecific aggression might be difficult or impossible in such gregarious species. Cooper and Vitt (1987) found that aggression was present among conspecific males of some sympatric *Eumeces* (Scincidae), but heterospecific males were usually ignored. Such species specific behaviour may account for instances of aggression noted between *Cryptoblepharus* individuals.

Among lizard groups, discriminative abilities may depend on visual, chemical or auditory stimuli or some combination thereof (Cooper and Vitt 1987). Many species (particularly agamids and iguanids) have visual displays that produce species-specific responses, however apart from occasional instances of tail waving, visual display behaviour has not been observed among *Cryptoblepharus*. Some skinks are known to vocalise (O'Connor 2003), however most are silent and as vocalising has not been recorded in *Cryptoblepharus* this is not assumed to play a role in their discriminative abilities.

Skinks characteristically rely heavily on chemosensory systems (Olsson and Shine 1998), using them to discriminate among prey (Cooper and Vitt 1989), in mate recognition (Olsson and Shine 1998), maternal recognition of offspring (Bull *et al.* 1994; Main and Bull 1996), to identify familiar versus unfamiliar conspecific individuals (Cooper 1996) and conspecific versus heterospecific individuals (Cooper and Vitt 1987). In the latter situation Cooper and Vitt (1987) found that agonistic behaviour in male *Eumeces* (*fasciatus* group) is directed primarily to conspecific males, with visually similar heterospecific males usually ignored following chemosensory investigation by tongue-flicking.

Overall, field observations show that sympatry in Australian *Cryptoblepharus* is a common phenomenon in which species distinctiveness is most likely maintained by pre-mating isolating factors. Recognition of conspecific and heterospecific individuals is probably initiated through visual stimuli and then confirmed by chemosensory investigation.

Biogeography. *Cryptoblepharus* is the most wide-ranging scincid genus. Two other highly vagile scincid genera, *Emoia* and *Lipinia,* have similar broad Indo-Pacific distributions (Ineich and Zug 1991; Adler, *et al.* 1995; Austin 1995) and *Emoia* also occurs on the northern tip of Cape York Peninsula, Australia. *Cryptoblepharus*, however, is unique among scincids in including continental Australia and the south-west Indian Ocean region in its distribution.

In the south-west Indian Ocean region, *Cryptoblepharus* occurs on the east coast and adjacent islands of continental Africa (Fig. 142). From northern South Africa at Black Rock, Tongaland coast, northern KwaZulu (Haacke 1977) to Mogadishu, mid-Somalia (Mertens 1931), on islands in the Mozambique Channel (Juan de Nova, Europa and the Comoros), on the southern Seychelle islands of Aldabra, Assumption, Astove, Cosmoledo, Farquhar and Providence (UMMZ records), on Madagascar and Nosy Bé Island, and on Réunion and Mauritius Islands. *Cryptoblepharus* has not been recorded from the northern Seychelles and Amirante Island groups (Mertens 1931; Brygoo 1986).

East of Mauritius, the nearest congener is almost 6,000 kilometres distant, on Christmas Island in the eastern Indian Ocean. From Christmas Island, *Cryptoblepharus* extends eastward through the Lesser Sunda Islands (and at least one of the Greater Sunda Islands, i.e. Samalona Island off Sulawesi) to Timor (Mertens 1931) and onwards through the Maluku island chain (including Kai and Aru islands) to New Guinea (Fig. 156). North of New Guinea *Cryptoblepharus* occurs in the Palau, Caroline, Mariana and Bonin Islands. Eastwards it occurs on the Bismarck Archipelago, Solomon, Vanuatu, New Caledonia, Fiji, Tonga, Samoa, Phoenix, Cook, Society, Tahiti, Austral, Tuamotu, Marquesas, Hawaiian, Pitcairn and Easter Islands (Adler *et al.* 1995; Mertens 1931) (Fig. 157). Adler *et al.* (1995) did not record *Cryptoblepharus* from other Pacific island chains. There are, however, numerous records from Wake, Marshall, Gilbert and the Line island groups in the USNM collection. Additionally, there are literature records of *Cryptoblepharus* from the Gilbert Islands (Kiribati). Garman (1901) described *Ablepharus heterurus* from a specimen collected on Apaiang Island. Mertens (1931) examined a further ten specimens from Tarowa (= Tarawa) (ZMB 9796-9797; NHMB 4755-4756) and determined *A. heterurus* to be invalid, placing it in the synonymy of *C. poecilopleurus*. In the Pacific region, *Cryptoblepharus* has not been recorded from Santa Cruz, Rotuma, Ellice (= Tuvalu) and Wallis-Futuna island groups (Adler *et al.* 1995), leaving a conspicuous void in their tropical Pacific Ocean distribution (Fig. 29).

Additionally, there are scattered records of *C. poecilopleurus* from the west coast of South America. Indeed the type locality of this widespread Pacific taxon is "Perú; gefunden auf den Inseln bei Pisacoma" (Wiegmann 1834). To assess the status of *Cryptoblepharus* on mainland South America, known records are examined in detail.

Wiegmann described *C. poecilopleurus* from three specimens (ZMB 1349, 57181-182) collected by Dr Franz J.F. Meyen who visited Peru and Bolivia in 1831. The type locality, "islands near Pisacoma, Peru", is reasonably specific but Mertens (1931), on zoogeographical grounds, considered the locality an error or that the specimens had been transported there through human mediation. This type locality is also problematical in that only one 'Pisacoma' could be located by the author, and it is situated in the far south of Peru (in the Andes, on the Chilean border) about 180 km inland from the coast and certainly without nearby islands. As *C. poecilopleurus* is generally a littoral species (McKeown 1978), this Pisacoma is highly unlikely to be the collection site. It is tempting to speculate that either Meyen or Wiegmann confused the name with the Peruvian fishing village of Pisco which, incidentally, is the closest port to the Ballestas Islands.

A second South American record was first noted by Duméril and Duméril (1851) in their "Catalogue méthodique de la collection des reptiles du Muséum d'Historie Naturelle" (cited in Mertens 1931). This specimen was not examined by the author, but the locality is given as Puna Island near Guayaquil, Ecuador.

Boulenger (1887) cites a third locality as "Bahia; Smithsonian Institution". Although this locality has been interpreted as Bahia State in Brazil (Garman 1908), the Spanish word Bahía is equivalent to 'Bay' in English, and could refer to many places on the South American coast. A search of USNM records failed to locate a specimen with this locality, however, a record from Peru (USNM 063494) was found that had been collected by the "U.S. Exploring Expedition". Lacking a specific Peruvian locality, it is again tempting to speculate whether this specimen could possibly be from "Bahía Pisco" (= Pisco Bay, Peru), which could have been visited by the Expedition (during the stop-over at Callao) in December, 1839.

The South American records considered so far relate to early nineteenth century collections and suffer from imprecise locality information and subsequent poor reliability, even though competent scientific collectors were usually involved. There is, however, an additional record, which although from an unlikely locality, was collected relatively recently. The specimen (BMNH 1976-2289) was collected near Coyhaique, Chile, in January 1975 by the late S. Jacquemart, an entomologist from the Royal Belgian Institute of Natural Sciences. Coyhaique (45° 28'S 071° 38'W) is a small city located in the deep south of Chile, between Puerto Montt and Punta Arenas. The locality is an unlikely site for *C. poecilopleurus* because it is about 60 kilometres inland from the coast, has a relatively cool climate and represents the most southerly record for the genus. Interestingly, the specimen label carried the following quote, "This appears to be the first record of the species from mainland South America".

Any one of these records can be dismissed as collection locality error or accidental, human aided translocation of individuals. Together, they indicate there is a possibility *Cryptoblepharus* occurs on the west coast of South America. They do not, however, indicate whether the genus is represented by scattered recent arrivals or occurs in well established populations.

Little attempt has been made to speculate on the origin and dispersal patterns of *Cryptoblepharus*. Mertens (1931) suggested an ancestral form evolved in South-east Asia, migrated to Australia where *Cryptoblepharus* evolved and diversified and then, by passive means of dispersal, radiated to its present broad distribution in the Australian/Indo-Pacific regions. The disjunct south-west Indian Ocean distribution was an enigma to Mertens (1931) and he did not offer an explanatory hypothesis, although Fuhn (1969b) considered it a result of immigration from the east.

There are three mechanisms by which *Cryptoblepharus* could have achieved its disjunct, widespread distribution: (1) the ancestral form may have evolved at a time when the regions were connected; (2) they may have naturally dispersed over a long period of time (millions of years); (3) they may have only recently dispersed through human-mediated transport.

Mechanism 1: Africa, Madagascar, South America and Australia were components of the ancient supercontinent Gondwana. Continental drift triggered the fracturing of Gondwana, with landmasses corresponding to the above countries separating about 140 million years before present (Vickers-Rich and Rich 1993). Some lizard taxa have remained virtually unchanged for many millions of years. Losos (2001) reports on two specimens of *Anolis* (Iguanidae) fossilised in amber dating from the Miocene, approximately 20 million years before present, which are virtually indistinguishable from extant *Anolis*. Early skink fossils are known from the Oligocene of North America (approximately 30 million years before present) and have been attributed to the extant genus *Eumeces* (Hutchinson 1992). Baverstock and Donnellan (1990) considered the three Australian groups of lygosomine skinks to have diverged about 60 million years ago. Hutchinson (1992) determined that fossil material from Riversleigh (Queensland) dated at early to mid-Miocene (approximately 20 million years ago), contained examples from the three lygosomine groups, and of the extant genera *Egernia, Tiliqua, Eulamprus* and *Glaphyromorphus* practically indistinguishable from living taxa. To have been present on Gondwana prior to the continental break-up *Cryptoblepha-*

rus must be older than 140 million years, however, judging from the meagre scincid fossil evidence, the genus is not sufficiently ancient to be of Gondwanic origin.

Mechanism 2: *Cryptoblepharus* has many attributes that aid natural dispersal, including low metabolic requirements associated with ectothermy and an adaptation to habitats devoid of fresh water. Greer (1989) suggested that features of the genus, such as arboreality, littoral-dwelling and heliothermy, would facilitate the crossing of open seas. Mertens (1931) considered the small size and adaptability of *Cryptoblepharus* as being useful aids to passive dispersal.

Determination of possible migration paths and radiation patterns firstly requires identification of the centre of origin. The ancestor of the *Eugongylus*-group was probably South-east Asian in origin (Honda *et al.* 2000; Greer 1989), although Hutchinson and Donnellan (1993) suggest a possible Australian origin. Mertens (1931) considered Australia the centre of origin of *Cryptoblepharus*, while Iskandar and Nio (1996) suggested the genus was of Australo-Papuan origin.

It can be assumed that *Cryptoblepharus* has had a long period of evolution (millions of years). Evidence of this includes being found throughout the Australian continent with no clear biogeographic bias (Hutchinson and Donnellan 1993) and by having numerous species spread over a broad distribution (Gibbons 1985). Over such a considerable period of time, dispersal to or from Australia and through the Indo-Pacific region could have been accomplished using islands as 'stepping stones' and rafting on driftwood or vegetation mats. Such dispersal would have been facilitated by sea level changes during the Pleistocene when, for example, 17 000 years ago sea level was 100 metres lower than today (Gibbons 1985). The question remains, however, how did *Cryptoblepharus* colonise the south-west Indian Ocean region?

The most plausible explanation is that from an eastern point of origin (Indonesia or Australia), founder specimens were transported 6000 kilometres to the south-west Indian Ocean region by passive rafting on buoyant vegetation mats (Rocha *et al.* 2006). Achievement of such a feat relies on factors of time, ocean currents and weather conditions. Over-water dispersal of lizards due to hurricane activity was documented by Censky *et al.* (1998), who described how individuals of *Iguana iguana* arrived on the eastern beaches of Anguilla Island in the Caribbean aboard an extensive mat of logs and uprooted trees. Deduced as originating from Guadeloupe (approximately 250 km distant), the vegetation mat was uprooted and deposited in the sea by one of two hurricanes which passed over the area in September 1995. Approximately a month after the first of these hurricanes, iguanas reached the shores of Anguilla (Censky *et al.* 1998). Support for the concept of rafting on buoyant vegetation is supplied by Carranza *et al.* (2000), who analysed mtDNA sequences of the gekkonid genus *Tarentola* and determined that the ancestor of *T. (Neotarentola) americana* was likely to have travelled a distance of at least 6000 kilometres from the west coast of north Africa to Cuba in the West Indies, by transmarine dispersal via the North Equatorial Current.

In the case of *Cryptoblepharus*, it is hypothesised that a severe tropical cyclone deposited a large mat of buoyant vegetation (holding a number of *Cryptoblepharus* individuals) into the seas surrounding Indonesia and/or northern Australia, which then floated approximately 6000 kilometres to the south-west Indian Ocean region. As major eastern (East Australian) and western (Leeuwin) currents off the Australian coast flow strongly southwards and there is only a low frequency transport by currents through northern Australian waters via Torres Strait (Wolanski *et al.* 1988; Wasjsowicz 1999), it is most likely that such a large floating vegetation mat would have originated from Indonesian waters.

Transmarine transport across the Indian Ocean is reliant on interactions between two major ocean currents. The Indonesian Throughflow, a current flowing from the Pacific to the Indian Ocean that weaves through Indonesian Seas transporting large amounts of warm water from the Pacific into the Indian Ocean. These waters contribute to the South Equatorial Current, which is a strong westward flow spanning the entire width of the Indian Ocean. Strong and deep, the South Equatorial Current carries about 50 million cubic metres of water per second or an equivalent flow of about 250 Amazon Rivers (Commonwealth Scientific and Industrial Research Organisation 1999). The Indonesian Throughflow, centred along 12°S, is well represented within the South Equatorial Current thermocline contributing about one third of the total volume (Gordon *et al.* 1997). Measurements made by the Commonwealth Scientific and Industrial Research Organisation (1999) determined the South Equatorial Current has surface currents of about two knots in the core of the flow. Remnants of the Indonesian Throughflow exit the Indian Ocean southward via the Mozambique Channel and the east coast of Madagascar (Song *et al.* 2004).

With strong traits towards arboreality, sociality and littoral dwelling and a preference for exposed habitats, it is possible that any extensive vegetation mat washed from a *Cryptoblepharus* inhabited region could house many individuals. Their small size would facilitate the use of loose bark or hollow limbs as shelter sites, presumably small prey items such as insects and other invertebrates would be found among a raft's vegetation mat and they could also consume small crustaceans, etc. that might colonise the raft during its voyage.

Mechanism 3: Human-mediated transport as principal mechanism of *Cryptoblepharus* dispersal is highly unlikely, although it has almost certainly contributed to colonisation of geologically recent islands and atolls, and possibly accounts for records from the South American west coast. Kluge (1969) supplied a list of features common to lizards whose dispersal was human-aided; typically they are undifferentiated from probable parent stock, are mainly coastal, primarily occur in areas of human settlement and dates of introduction are established. Many *Cryptoblepharus* populations feature the first two of these attributes.

Bauer and Vindum (1990) were unable to age the occupation of *Cryptoblepharus* on New Caledonia, but considered that morphological differentiation within the genus supported unambiguous pre-human occurrence. Pregill (1993) considered the lizard fauna of the islands of central and eastern Polynesia to derive from chance, often multiple, introductions that began with the early Polynesian voyagers, although precultural fossil material from 'Eua, Tonga, identified as *Emoia* spp., suggests a capability for natural dispersal among Pacific island lizards (Pregill 1993). Austin and Zug (1999) investigated genetic and morphological variation in some *Emoia* and determined that *E. tongana* is genetically uniform in Tonga and Samoa, suggesting human mediated recent introductions, while *E. concolor* within the Fijian archipelago shows relatively large genetic divergence, suggesting prehuman intra-archipelago dispersal and isolation.

In summary, it is suggested that a mixed sex group of an early *Cryptoblepharus* survived rafting the South Equatorial Current from Indonesia to either Madagascar or the east coast of Africa. Subsequent colonising of islands in the region could have involved similar voyages or radiation from the original point of colonisation (Rocha *et al.* 2006). Similarly, it is probable that colonisation and radiation though the Indo-Pacific region and Australia was achieved by rafting supplemented by, in the Pacific region, human mediated transport.

CONCLUSION

This study identified considerable species diversity within *Cryptoblepharus*, almost doubling the number of species- and subspecies-level taxa previously recognised. Focused on the Australian region the increase there was fourfold, with analyses of data unequivocally demonstrating that five widely distributed 'species' were complexes of three or more taxa.

Although the study made detailed use of a comprehensive suite of morphological characters and genetic data from Horner and Adams (2007), the number of species ultimately identified is considered a conservative estimate of the true extent of *Cryptoblepharus*. Results obtained from the rigorously investigated Australian subset of populations suggest that similar intensive examinations of taxa from the south-west Indian Ocean and Indo-Pacific regions will reveal greater species diversity than currently recognised. Additionally, allozyme divergence found among some morphologically indeterminate Australian taxa, herein treated as species-complexes, indicates increased sampling will identify more cryptic species. It is also noteworthy that the three most morphologically distinctive Australian *Cryptoblepharus* (*C. fuhni*, *C. gurrmul* and *C. wulbu*) are recent discoveries, restricted to remote localities difficult to access and rarely visited by herpetologists, suggesting that further field work in remote areas will almost certainly result in additional species being discovered.

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APPENDIX 1

Results for Discriminant Function Analyses (DFA). Listed are DFA by number, cluster designations, taxa within each cluster, means of canonical variables for discriminant functions and principal canonical variables used to predict discriminant functions. Numbers in brackets are standardised coefficients for each canonical variable.

DFA	clusters	taxa	means of canonical variables		principal predicting variables	
			DF1	DF2	DF1	DF2
1	1	carnA1, carnA2, carnA3, carnA4, carnA5, carnB, carnC, carnD	-23.0 to -12.6	-14.0 to 0.5	CPS (-0.58) SDL (-0.50) PS (-0.56) BP (-0.1) PLN (-0.10)	SDL (-0.81) PS (0.47) BP (0.31) SC (0.16) PN (-0.09)
	2	plagA1, plagA2, plagA3, plagA4, plagA5, plagB	-2.3 to 5.9	-0.3 to 8.6		
	3	megaA1, megaA2, megaA3, megaA4, megaA5, megaB	19.7 to 23.1	-9.1 to -5.9		
	4	fuhn, litor, oxley	3.1 to 5.9	-6.8 to -2.1		
	5	virgA1, virgA2, virgA3	11.5 to 12.0	1.0 to 1.1		
2	A	carnB	-9.5	-8.0	PS (1.04) SC (0.21) PP (0.19) CPS (0.18) HH (-0.18)	SDL (1.06) PS (0.36) LL (-0.14) SC (-0.13) PP (0.11)
	B	carnA2, carnA3, carnA4, carnC	-9.1 to -5.4	0.5 to 3.1		
	C	carnA1, carnA5	2.2 and 2.5	3.8 and 5.8		
	D	carnD	5.7	-3.8		
3	B1	carnC	-2.1	2.1	PS (-0.84) SDL (0.56) MR (0.34) PLN (0.27) SE (-0.11)	PTS (-0.84) HH (0.49) NS (-0.43) SC (0.40) SE (-0.38)
	B2	carnA3	-1.7	-2.5		
	B3	carnA2, carnA4	2.2 and 2.7	0.1 and 0.2		
4	E	plagB	-6.8	-0.04	SDL (-0.88) CPS (0.48) PLN (-0.20) PTS (0.18) MR (0.14)	HH (0.41) PTS (-0.40) PV (-0.36) CPS (0.33) PS (0.31)
	F	plagA1, plagA2, plagA3, plagA4, plagA5	2.0 to 2.9	-1.6 to 0.8		
5	G	megaA1, megaA2, megaA4, megaA5	-3.5 to -0.4	-0.6 to 2.4	BP (0.88) SC (-0.50) HTS (0.43) SE (-0.28) FTS (-0.19)	PV (0.64) SC (-0.47) HTS (-0.45) BP (-0.36) HW (0.34)
	H	megaA3	-0.5	-4.4		
	I	megaB	4.9	0.3		
6	G1	megaA5	-3.8	0.1	SC (0.99) BP (0.41) HTS(0.26) PTS (-0.20))	HTS (0.81) BP (0.69) PLN (-0.63) PTS (0.45)
	G2	megaA4	1.2	2.5		
	G3	megaA1, megaA2	0.7 and 1.0	-1.7 and 0.4		
7	J	oxley	-10.6	7.5	PN (-0.87) SDL (-0.63) PS (-0.48) MR (-0.35)	HTL (-0.57) PP (-0.49) PN (0.42) PLN (-0.18)
	K	litor	-3.7	-3.3		
	L	fuhn	-1.6	-4.7		
	M	virgA1, virgA2, virgA3	2.3 to 3.0	0.2 to 2.0		
8	L1	fuhn	-8.0	-0.2	CPS (0.88) PV (0.73) PP (-0.43) LL (0.40)	SDL (-0.84) PAL (-0.59) MR (-0.41) PV (0.31)
	K1	horn	1.4	2.2		
	K2	litor	2.8	-0.8		
9	M1	virgB	-2.7	0.9	PP (-0.94) CPS (0.37) FTL (0.36) VS (0.27)	MR (0.63) PS (0.49) PAL (-0.45) CPS (0.41)
	M2	virgA1	-1.9	-0.6		
	M3	virgA3	3.3	2.7		
	M4	virgA2	3.2	-1.9		

DFA	clusters	taxa	means of canonical variables DF1	means of canonical variables DF2	principal predicting variables DF1	principal predicting variables DF2
10	N	*bitaeniatus*	-15.2	4.8	PS (-1.31) HL (-0.45) LL (0.39) PLN (-0.34)	MR (0.95) PV (0.39) SE (0.34) BL (-0.25)
	O	*quinquetaeniatus*	-14.0	-2.6		
	P	*gloriosus, mayottensis, mohelicus*	-7.0 to -4.7	-4.6 to -1.2		
	Q	*africanus, ahli, aldabrae, ater, boutonii, caudatus, cognatus, voeltzkowi*	5.1 to 8.8	-2.6 to 3.7		
11	P1	*gloriosus*	-4.9	-1.7	PV (1.23) MR (1.23) FL (0.96) SFL (-0.89)	HTL (-1.00) PV (-1.00) SFL (0.73) SE (0.50)
	P2	*mohelicus*	-2.0	4.7		
	P3	*mayottensis*	2.8	-0.5		
12	Q1	*boutonii*	-5.0	-2.1	MR (-0.87) PLN (-0.70) LL (0.56) BL (0.42)	NS (-0.77) PAL (0.53) SFL (0.63) FL (-0.59)
	Q2	*caudatus*	-2.4	3.9		
	Q3	*ahli, aldabrae, ater*	0.1 to 2.2	0.6 to 1.9		
	Q4	*voeltzkowi*	-0.3	-3.3		
	Q5	*africanus, cognatus*	2.8 and 4.1	-1.3 and -3.4		
13	Q6	*aldabrae*	-3.7	-0.2	SVL (1.14) SFL (0.66) MR (0.60) FTS (0.56)	HL(1.21) SFL (-0.97) LL (-0.92) PAL (-0.54)
	Q7	*ater*	1.8	2.0		
	Q8	*ahli*	2.7	-2.4		
14	R	Nor, litorPNG	-24.2 to -23.2	5.5 to 4.9	PS (-1.40) BP (-1.16) HH (-0.22) SFL (-0.19)	BP (0.94) FL (0.32) PV (0.30) HL (-0.28)
	S	*baliensis, sumbawanus*	-20.5	-12.2 to -11.7		
	T	*egeriae, paschalis, poecilopleurus*	-15.3 to -15.8	-1.3 to -2.1		
	U	Mis, TransF	-4.9	15.9		
	V	*schlegelianus*	10.6	15.4		
	W	*aruensis, cursor, eximius, intermedius, novaeguineae, pallidus*	12.1 to 14.2	0.8 to 2.0		
	X	*nigropunctatus*	16.7	11.4		
	Y	*keiensis, leschenault, novohebridicus, renschi,* Sam, virgA2PNG	20.4 to 21.9	-5.3 to -6.4		
	Z	*novocaledonicus, rutilus*	25.7 to 25.8	4.4 to 4.5		
	AA	*burdeni*	32.6	11.5		
15	T1	*egeriae*	-8.3	-0.1	SL (-1.29) PV (-0.88) PLN (0.80) HH (0.80)	PAL (0.65) SC (0.46) NS (-0.42) SL (0.32)
	T2	*paschalis*	3.0	2.1		
	T3	*poecilopleurus*	3.7	-0.8		
16	W1	*cursor*	-6.4	-4.2	SC (1.35) FTL (1.25) MR (-0.82) PLN (-0.79)	SVL (-0.98) SE (0.66) SC (-0.98) MR (-0.90)
	W2	*eximius*	-5.7	0.5		
	W3	*intermedius*	3.6	-6.0		
	W4	*aruensis, novaeguineae, pallidus*	2.7 to 4.6	0.0 to 2.0		
17	Y1	*keiensis*	-4.4	-3.4	PLN (2.05) HTL (-1.08) NS (1.08) HH (1.23)	SFL (-1.29) BL (-1.18) MR (0.67) NS (-0.63)
	Y2	*leschenault, renschi,* virgA2PNG	-2.7 to -0.3	0.4 to 3.4		
	Y3	*novohebridicus*	7.9	-7.3		
	Y4	Sam	12.4	5.2		

APPENDIX 2

Phenotypic characters, identified by ANOVA, that discriminate between some pairs of Australian morphological OTUs and/or extralimital taxa. Morphometric variables are allometrically adjusted.

taxon	character		p	mean	N	mode	std.dev
carnA5 vs virgA3	finger subdigital lamellae		0.004***	15.9 vs 15.1	64 vs 23	16 vs 16	1.04 vs 0.97
	palmar scales		0.001***	9.1 vs 7.4	64 vs 23	9 vs 8	0.97 vs 0.95
	plantar scales		0.001***	10.4 vs 9.3	64 vs 23	11 vs 9	1.23 vs 0.70
	posterior temporal scales		0.009**	2.7 vs 2.4	64 vs 23	3 vs 2	0.42 vs 0.41
carnA1 vs carnA5	midbody scale rows		0.001***	24.2 vs 23.7	28 vs 64	24 vs 24	1.04 vs 1.15
	plantar scale condition		0.048*	4.1 vs 4.0	28 vs 64	4 vs 4	0.31 vs 0.12
	subdigital lamellae cond.		0.001***	3.1 vs 3.6	28 vs 64	3 vs 4	0.35 vs 0.49
	posterior temporal scales		0.001***	2.3 vs 2.7	28 vs 64	2 vs 3	0.43 vs 0.41
	plantar pigmentation		0.001***	1.6 vs 1.0	28 vs 64	1 vs 1	1.42 vs 0.00
plagA5 vs carnD	snout-vent length (mm)	♂	0.037*	38.1 vs 39.8	71 vs 60	-	3.78 vs 2.66
		♀	0.001***	39.3 vs 41.2	49 vs 45	-	4.61 vs 4.18
	midbody scale rows		0.001***	24.1 vs 24.9	120v105	24 vs 24	0.92 vs 1.22
	finger subdigital lamellae		0.001***	15.0 vs 15.9	120v105	14 vs 16	1.16 vs 0.91
	toe subdigital lamellae		0.001***	18.1 vs 19.2	120v105	18 vs 19	1.34 vs 1.18
	palmar scales		0.001***	7.7 vs 9.3	120v105	8 vs 9	0.90 vs 0.87
	plantar scales		0.001***	9.6 vs 11.6	120v105	10 vs 12	0.96 vs 1.13
	posterior temporal scales		0.001***	2.4 vs 2.8	120v105	2 vs 3	0.44 vs 0.34
plagA2 vs plagA3	head width (mm)	♂	0.025*	4.9 vs 4.4	7 vs 2	-	0.12 vs 0.20
		♀	0.001***	4.6 vs 4.3	3 vs 3	-	0.17 vs 0.13
'plagA2+plagA3' vs plagA1	forelimb length (mm)	♂	0.012*	12.6 vs 13.2	9 vs 12	-	0.44 vs 0.55
		♀	0.033*	12.6 vs 12.9	6 vs 9	-	0.53 vs 0.49
'plagA1+plagA2+plagA3' vs plagA4	head width (mm)		0.027*	4.7 vs 4.8	36 vs 44	-	0.24 vs 0.20
	finger subdigital lamellae		0.001***	15.7 vs 14.7	36 vs 44	16 vs 14	0.92 vs 1.16
	toe subdigital lamellae		0.001***	18.8 vs 17.9	36 vs 44	18 vs 18	1.28 vs 1.06
	palmar scales		0.029*	7.8 vs 8.2	36 vs 44	8 vs 8	0.84 vs 0.74
	body pattern		0.001***	3.1 vs 3.9	36 vs 44	4 vs 4	1.12 vs 0.63
	laterodorsal stripes		0.001***	5.8 vs 5.2	36 vs 44	6 vs 5	0.40 vs 0.42
'plagA1+plagA2+plagA3' vs plagA5	tail length (mm)	♂	0.001***	51.3 vs 55.4	11 vs 19	-	3.97 vs 4.20
		♀	0.047*	49.3 vs 52.9	9 vs 18	-	3.81 vs 3.34
	paravertebral scales	♂	0.001***	51.7 vs 49.3	21 vs 71	51 vs 49	2.80 vs 2.45
		♀	0.001***	52.9 vs 50.1	15 vs 49	54 vs 48	1.67 vs 2.34
	midbody scale rows		0.014*	24.5 vs 24.0	36vs120	24 vs 24	0.91 vs 0.92
	nuchal scales		0.007**	2.1 vs 2.0	36vs120	2 vs 2	0.50 vs 0.18
	finger subdigital lamellae		0.001***	15.7 vs 15.0	36vs120	16 vs 14	0.92 vs 1.15
	finger supradigital scales		0.033*	13.1 vs 12.9	36vs120	13 vs 13	0.81 vs 0.72
	toe subdigital lamellae		0.005***	18.8 vs 18.1	36vs120	18 vs 18	1.28 vs 1.34
	toe supradigital scales		0.011*	15.7 vs 15.1	36vs120	15 vs 15	1.29 vs 0.94
	posterior temporal scales		0.001***	2.9 vs 2.3	36vs120	3 vs 2	0.29 vs 0.44
	body pattern		0.001***	3.1 vs 3.9	36vs120	4 vs 4	1.12 vs 0.38
plagA4 vs plagA5	snout-vent length (mm)	♂	0.001***	39.6 vs 38.0	19 vs 71	-	3.81 vs 3.78
		♀	0.041*	42.2 vs 39.3	25 vs 49	-	2.63 vs 4.60
	tail length (mm)	♂	0.001***	52.4 vs 55.4	8 vs 19	-	5.68 vs 4.20
		♀	0.042*	48.7 vs 52.9	13 vs 18	-	3.38 vs 3.34
	paravertebral scales	♂	0.001***	51.3 vs 49.3	19 vs 71	50 vs 49	2.81 vs 2.45
		♀	0.001***	52.6 vs 50.1	25 vs 49	52 vs 48	2.27 vs 2.34
	head width (mm)		0.001***	4.8 vs 4.7	44vs120	-	0.19 vs 0.22
	midbody scale rows		0.001***	24.9 vs 24.0	44vs120	24 vs 24	1.14 vs 0.92
	palmar scales		0.001***	8.2 vs 7.7	44vs120	8 vs 8	0.74 vs 0.90
	plantar scale condition		0.001***	2.7 vs 2.9	44vs120	3 vs 3	0.43 vs 0.21
	posterior temporal scales		0.001***	2.9 vs 2.3	44vs120	3 vs 2	0.31 vs 0.44
	laterodorsal stripes		0.001***	5.2 vs 5.8	44vs120	5 vs 6	0.42 vs 0.39

taxon	character		p	mean	N	mode	std.dev
megaA1 vs megaA2	head depth (mm)		0.035*	2.8 vs 2.6	15 vs 29	-	0.25 vs 0.30
	plantar scales		0.008**	13.2 vs 12.0	15 vs 29	13 vs 12	1.29 vs 1.51
	posterior temporal scales		0.001***	2.3 vs 2.8	15 vs 29	2 vs 3	0.40 vs 0.28
	body pattern		0.014*	2.0 vs 2.3	15 vs 29	2 vs 2	0.00 vs 0.47
litor vs horn	paravertebral scale width		0.037*	1.30 vs 1.40	20 vs 13	-	0.13 vs 0.11
	finger supradigital scales		0.035*	13.3 vs 12.8	33 vs 14	14 vs 13	0.70 vs 1.10
	palmar scales		0.001***	11.0 vs 9.5	33 vs 14	11 vs 9	1.13 vs 1.16
	plantar scales		0.018*	11.7 vs 10.9	33 vs 14	11 vs 11	1.17 vs 0.70
	loreal size		0.009**	1.4 vs 2.1	33 vs 14	1 vs 3	0.79 vs 1.02
virgA1 vs virgB	snout-vent length (mm)	♂	0.002***	33.7vs 36.1	24 vs 12	-	2.37 vs 1.48
		♀	ns	36.0 vs 37.0	24 vs 19	-	2.63 vs 2.79
	paravertebral scales	♂	ns	48.0 vs 48.5	24 vs 12	-	2.25 vs 1.73
		♀	0.018*	48.4 vs 50.2	24 vs 19	-	2.51 vs 2.17
	midbody scale rows		0.001***	23.2 vs 24.6	48 vs 31	24 vs 24	1.05 vs 0.88
	finger supradigital scales		0.008**	14.6 vs 15.1	48 vs 31	15 vs 15	0.92 vs 0.82
	toe subdigital lamellae		0.010**	18.1 vs 18.9	48 vs 31	19 vs 19	1.27 vs 0.98
	plantar scales		0.001***	8.9 vs 9.8	48 vs 31	9 vs 10	0.74 vs 0.93
	laterodorsal stripes		0.001***	2.9 vs 3.5	48 vs 31	3 vs 3	0.33 vs 0.89

taxon	character	p	mean	N	mode	std.dev
africanus vs *cognatus*	tail length	0.008**	61.4 vs 53.0 mm	5 vs 1	-	1.60 vs 0.00
	head depth	0.030*	3.8 vs 3.4 mm	10 vs 4	-	0.26 vs 0.20
	paravertebral scale width	0.035*	1.76 vs 1.84 mm	5 vs 4	-	0.10 vs 0.13
	finger subdigital lamellae	0.001***	15.7 vs 14.0	10 vs 4	16 vs 14	0.67 vs 0.82
	toe supradigital scales	0.000***	17.5 vs 16.0	10 vs 4	18 vs 16	1.08 vs 0.00
	toe subdigital lamellae	0.019**	20.3 vs 17.7	10 vs 4	20 vs 18	1.06 vs 0.50
gloriosus vs *mayottensis*	snout-vent length	0.016**	39.8 vs 36.5 mm	5 vs 11	-	2.31 vs 2.24
	forelimb length	0.000***	12.1 vs 13.9 mm	5 vs 11	-	0.89 vs 0.46
	hindlimb length	0.000***	15.7 vs 17.4 mm	5 vs 11	-	0.49 vs 0.58
	head length	0.008**	7.6 vs 8.0 mm	5 vs 11	-	0.34 vs 0.17
	head depth	0.040*	3.4 vs 3.8 mm	5 vs 11	-	0.35 vs 0.24
	midbody scale rows	0.000***	21.0 vs 23.4	5 vs 11	22 vs 24	1.00 vs 0.92
	toe subdigital lamellae	0.030*	19.0 vs 18.7	5 vs 11	19 vs 18	1.87 vs 0.79
	palmar scales	0.027*	12.0 vs 10.4	5 vs 11	12 vs 10	1.58 vs 0.93
gloriosus vs *mohelicus*	forelimb length	0.010**	12.1 vs 14.1 mm	5 vs 3	-	0.89 vs 0.33
	forebody length	0.016**	15.8 vs 17.1 mm	5 vs 3	-	0.46 vs 0.68
	head length	0.024*	7.6 vs 8.4 mm	5 vs 3	-	0.34 vs 0.35
	snout length	0.028*	3.5 vs 3.8 mm	5 vs 3	-	0.14 vs 0.15
	finger supradigital scales	0.024*	12.2 vs 13.0	5 vs 3	12 vs 13	0.45 vs 0.00
mayottensis vs *mohelicus*	forebody length	0.028*	16.1 vs 17.1 mm	11 vs 3	-	0.58 vs 0.68
	head length	0.014**	8.0 vs 8.4 mm	11 vs 3	-	0.17 vs 0.35
	paravertebral scales	0.000***	51.7 vs 47.0	11 vs 5	52 vs 47	1.74 vs 0.71
baliensis vs *sumbawanus*	forelimb length	0.015*	13.4 vs 12.9 mm	20 vs 10	-	0.97 vs 0.82
	hindlimb length	0.008**	16.8 vs 16.2 mm	20 vs 10	-	1.00 vs 0.70
	nuchal scales	0.037*	2.1 vs 3.1	20 vs 10	2 vs 2	0.32 vs 1.37
leschenault vs *renschi*	midbody scale rows	0.047*	25.6 vs 24.3 mm	6 vs 15	26 vs 24	1.12 vs 1.51
	paravertebral scale width	0.000***	1.51 vs 1.91 mm	6 vs 10	-	0.18 vs 0.07
	toe subdigital lamellae	0.044*	22.0 vs 20.7	6 vs 15	22 vs 20	1.63 vs 1.97
paschalis vs *poecilople-urus*	paravertebral scales	0.020*	57.9 vs 54.4	8 vs 16	57 vs 54	1.38 vs 2.96
	supralabial scales	0.021*	7.6 vs 7.2	8 vs 16	8 vs 7	0.50 vs 0.36
	supraciliary scales	0.007**	5.5 vs 5.1	8 vs 16	6 vs 5	0.46 vs 0.17
	palmar scales	0.001***	13.5 vs 11.3	8 vs 16	13 vs 12	0.93 vs 0.95
	plantar scales	0.004***	14.9 vs 12.7	8 vs 16	16 vs 13	1.13 vs 1.06
aruensis vs *novaeguine-ae+pallidus*	forelimb length	0.001***	14.3 vs 13.1	6 vs 8	-	0.65 vs 0.52
	hindlimb length	0.007**	16.9 vs 15.8	6 vs 8	-	0.65 vs 0.60
	finger subdigital lamellae	0.009**	18.3 vs 16.7	6 vs 8	18 vs 17	0.51 vs 1.16

taxon	character	p	mean	N	mode	std.dev
OTUs Mis vs TransF	forelimb length	0.001***	13.2 vs 10.9 mm	11 vs 5	-	1.02 vs 0.60
	hindlimb length	0.000***	17.8 vs 14.0 mm	11 vs 5	-	1.59 vs 0.78
	head length	0.000***	8.2 vs 7.1 mm	11 vs 5	-	0.54 vs 0.24
	snout length	0.013*	3.8 vs 3.6 mm	11 vs 5	-	0.19 vs 0.30
	midbody scale rows	0.000***	25.5 vs 22.0	11 vs 5	26 vs 22	1.21 vs 0.00
	paravertebral scales	0.001***	54.5 vs 49.8	11 vs 5	53 vs 50	1.86 vs 2.49
	finger subdigital lamellae	0.027*	17.5 vs 15.8	11 vs 5	17 vs 16	1.43 vs 1.09
	finger supradigital scales	0.005***	13.3 vs 12.2	11 vs 5	13 vs 12	0.47 vs 0.44
	toe subdigital lamellae	0.005***	21.8 vs 19.2	11 vs 5	21 vs 19	1.47 vs 1.48
	toe supradigital scales	0.000***	16.3 vs 14.6	11 vs 5	16 vs 15	0.92 vs 0.54
	palmar scales	0.000***	12.0 vs 9.0	11 vs 5	12 vs 9	1.26 vs 0.70
	plantar scales	0.000***	12.7 vs 9.0	11 vs 5	12 vs 9	1.49 vs 0.70
OTUs virgA2PNG vs virgA3	snout-vent length	0.001***	39.1 vs 34.3 mm	5 vs 23	-	1.77 vs 2.18
	hindlimb length	0.013*	14.3 vs 15.1 mm	5 vs 23	-	0.65 vs 0.61
	head length	0.032*	7.7 vs 7.4 mm	5 vs 23	-	0.32 vs 0.24
	paravertebral scales	0.003***	52.0 vs 47.8	5 vs 23	na vs 50	1.22 vs 2.79
	finger subdigital lamellae	0.001***	16.8 vs 15.1	5 vs 23	ns vs 16	0.83 vs 0.96
	toe subdigital lamellae	0.001***	20.6 vs 18.5	5 vs 23	20 vs 18	1.51 vs 1.12
	palmar scales	0.001***	9.0 vs 7.4	5 vs 23	9 vs 8	0.70 vs 0.94
	plantar scales	0.001***	10.6 vs 9.3	5 vs 23	10 vs 9	0.89 vs 0.70
OTUs virgA2PNG vs virgA1	snout-vent length	0.005***	39.1 vs 35.6 mm	5 vs 79	-	1.77 vs 2.74
	head length	0.049*	7.7 vs 7.4 mm	5 vs 79	-	0.32 vs 0.34
	paravertebral scales	0.003***	52.0 vs 48.7	5 vs 79	na vs 49	1.22 vs 2.37
	supraciliary scales	0.001***	5.5 vs 5.0	5 vs 79	6 vs 5	0.87 vs 0.18
	finger subdigital lamellae	0.001***	16.8 vs 14.8	5 vs 79	ns vs 15	0.83 vs 0.91
	toe subdigital lamellae	0.001***	20.6 vs 18.4	5 vs 79	20 vs 19	1.51 vs 1.20
	palmar scales	0.001***	9.0 vs 7.8	5 vs 79	9 vs 8	0.70 vs 0.75
	plantar scales	0.003***	10.6 vs 9.2	5 vs 79	10 vs 9	0.89 vs 0.93
OTUs virgA2PNG vs virgA2	snout-vent length	0.006**	39.1 vs 34.8 mm	5 vs 31	-	1.77 vs 3.23
	forebody length	0.028*	15.1 vs 15.8 mm	5 vs 31	-	0.51 vs 0.65
	midbody scale rows	0.001***	24.4 vs 21.8	5 vs 31	24 vs 22	0.89 vs 0.99
	paravertebral scales	0.001***	52.0 vs 47.3	5 vs 31	na vs 47	1.22 vs 2.38
	finger subdigital lamellae	0.008**	16.8 vs 15.7	5 vs 31	ns vs 16	0.83 vs 0.77
	plantar scales	0.037*	10.6 vs 9.4	5 vs 31	10 vs 10	0.89 vs 1.09
virgA2PNG vs leschenault	forelimb length	0.001***	11.8 vs 13.0 mm	5 vs 15	-	0.47 vs 0.63
	hindlimb length	0.003***	14.3 vs 16.1 mm	5 vs 15	-	0.65 vs 1.07
	forebody length	0.001***	15.1 vs 16.5 mm	5 vs 15	-	0.51 vs 0.73
	head length	0.031*	7.7 vs 8.2 mm	5 vs 15	-	0.32 vs 0.42
	head width	0.001***	4.7 vs 5.1 mm	5 vs 15	-	0.16 vs 0.22
	snout length	0.022*	3.6 vs 3.8 mm	5 vs 15	-	0.08 vs 0.12
	midbody scale rows	0.044*	24.4 vs 25.6	5 vs 15	24 vs 26	0.89 vs 1.12
	supraciliary scales	0.033*	5.5 vs 6.1	5 vs 15	6 vs 6	0.87 vs 0.33
virgA2PNG vs renschi	forelimb length	0.038*	11.8 vs 12.8 mm	5 vs 6	-	0.47 vs 0.78
	hindlimb length	0.002***	14.3 vs 16.4 mm	5 vs 6	-	0.65 vs 0.96
	forebody length	0.032*	15.1 vs 16.2 mm	5 vs 6	-	0.51 vs 0.83
	head length	0.037*	7.7 vs 8.2 mm	5 vs 6	-	0.32 vs 0.27
	head depth	0.011**	3.2 vs 3.9 mm	5 vs 6	-	0.36 vs 0.29
	head width	0.005***	4.7 vs 5.0 mm	5 vs 6	-	0.16 vs 0.19
	finger supradigital scales	0.036*	12.8 vs 12.1	5 vs 6	13 vs 12	0.44 vs 0.40
OTUs Nor vs litorPNG	head depth	0.008**	3.2 vs 3.6 mm	16 vs 6	-	0.19 vs 0.33
	head width	0.001***	4.4 vs 4.9 mm	16 vs 6	-	0.11 vs 0.22
	paravertebral scales	0.001***	57.7 vs 50.8	16 vs 6	60 vs na	2.68 vs 3.06
	toe subdigital lamellae	0.023*	22.5 vs 22.1	16 vs 6	23 vs 22	1.50 vs 1.32
	plantar scales	0.003***	13.3 vs 15.5	16 vs 6	15 vs 16	1.50 vs 0.54

taxon	character	p	mean	N	mode	std.dev
OTUs Nor vs litor	head width	0.001***	4.4 vs 4.6 mm	16 vs 33	-	0.11 vs 0.19
	finger subdigital lamellae	0.001***	18.8 vs 15.9	16 vs 33	19 vs 16	1.28 vs 0.92
	toe subdigital lamellae	0.001***	22.5 vs 20.1	16 vs 33	23 vs 20	1.50 vs 1.11
	toe supradigital scales	0.001***	16.9 vs 15.7	16 vs 33	16 vs 16	1.18 vs 0.69
	palmar scales	0.001***	12.3 vs 11.0	16 vs 33	12 vs 11	1.30 vs 1.13
	plantar scales	0.001***	13.3 vs 11.8	16 vs 33	15 vs 11	1.50 vs 1.17
OTUs Nor vs horn	head depth	0.028*	3.2 vs 3.11 mm	16 vs 14	-	0.19 vs 0.18
	paravertebral scales	0.002***	57.7 vs 54.3	16 vs 14	60 vs 54	2.68 vs 2.76
	finger subdigital lamellae	0.001***	18.8 vs 15.8	16 vs 14	19 vs 16	1.28 vs 1.27
	toe subdigital lamellae	0.001***	22.5 vs 19.5	16 vs 14	23 vs 20	1.50 vs 1.56
	toe supradigital scales	0.001***	16.9 vs 15.1	16 vs 14	16 vs 15	1.18 vs 1.24
	palmar scales	0.001***	12.3 vs 9.5	16 vs 14	12 vs 9	1.30 vs 1.16
	plantar scales	0.001***	13.3 vs 10.9	16 vs 14	15 vs 11	1.50 vs 0.70

APPENDIX 3

(A). Summary of morphometric and meristic characters for *Cryptoblepharus* taxa from the Australian region. Sample sizes are in parenthesis.

Character	*C. adamsi* (24)	*C. australis* (105)	*C. buchananii* (44)	*C. cygnatus* (71)	*C. daedalos* (16)	*C. exochus* (29)
midbody scale rows	23.8 ± 1.20 24, 22-26	24.9 ± 1.22 24, 22-28 (104)	24.9 ± 1.15 24, 22-28	23.4 ± 0.82 24, 22-24	25.7 ± 0.70 26, 24-26	24.8 ± 0.94 24, 24-26
paravertebrals	47.8 ± 2.75 50, 43-52	50.1 ± 2.77 52, 43-57 (104)	52.0 ± 2.56 52, 45-57	49.2 ± 2.33 49, 44-54	48.9 ± 2.13 48, 45-54	50.9 ± 2.25 51, 48-57
nuchals	2.1 ± 0.41 2, 2-4	2.1 ± 0.44 2, 2-5	2.2 ± 0.78 2, 2-7	2.1 ± 0.50 2, 2-4	2.4 ± 0.81 2, 2-4	2.2 ± 0.46 2, 2-4
supralabials	7.3 ± 0.42 7, 7-8	7.0 ± 0.18 7, 6-8	7.0 ± 0.15 7, 7-8	7.1 ± 0.31 7, 7-8	7.1 ± 0.27 7, 7-8	7.0 ± 0.00 7, 7
infralabials	6.0 ± 0.00 6, 6	6.1 ± 0.23 6, 6-7 (98)	6.0 ± 0.13 6, 5-7	6.0 ± 0.12 6, 6-7	6.1 ± 0.25 6, 6-7	6.0 ± 0.10 6, 6-7
supraciliaries	5.2 ± 0.41 5, 5-7	6.0 ± 0.25 6, 5-8	6.0 ± 0.31 6, 5-7	6.0 ± 0.12 6, 5-7	6.0 ± 0.29 6, 5-7	5.0 ± 0.10 5, 5-6
ciliaries	3.1 ± 0.25 3, 3-4	3.0 ± 0.17 3, 2-4	3.0 ± 0.08 3, 3-4	3.1 ± 0.36 3, 2-5	3.1 ± 0.25 3, 3-4	3.0 ± 0.00 3, 3
subdigital lamellae (4th finger)	15.1 ± 0.97 16, 13-16	15.9 ± 0.91 16, 14-18	14.7 ± 1.16 14, 13-17	16.2 ± 0.88 16, 15-19 (70)	16.2 ± 0.92 17, 15-18 (15)	15.9 ± 0.52 16, 15-17
supradigital lamellae (4th finger)	12.8 ± 0.59 13, 11-14	13.1 ± 0.93 13, 12-19	12.8 ± 0.76 13, 11-15	12.9 ± 0.90 13, 11-15 (70)	13.2 ± 0.90 14, 12-15 (15)	13.2 ± 0.97 13, 12-15
subdigital lamellae (4th toe)	18.5 ± 1.10 18, 16-21	19.2 ± 1.18 19, 16-23	17.9 ± 1.07 18, 16-20	19.7 ± 1.04 19, 17-22 (70)	20.3 ± 1.39 20, 18-23	19.5 ± 1.17 20, 17-22
supradigital lamellae (4th toe)	16.0 ± 0.88 16, 14-17	15.5 ± 1.01 15, 13-18	15.3 ± 1.01 15, 14-19	15.2 ± 0.87 15, 13-18 (70)	15.6 ± 1.15 15, 14-18 (15)	15.2 ± 0.65 15, 14-17
palmars	7.4 ± 0.93 8, 6-9	9.2 ± 0.88 9, 7-11	8.2 ± 0.74 8, 7-9	9.1 ± 0.72 9, 7-10	9.7 ± 0.86 10, 8-11 (15)	10.2 ± 0.83 10, 8-11
plantars	9.3 ± 0.74 9, 8-11	11.6 ± 1.14 12, 9-14	9.7 ± 0.91 10, 8-13	10.9 ± 0.97 11, 9-15	13.4 ± 1.32 15, 11-15	11.1 ± 1.06 12, 9-13
post-temporals	2.5 ± 0.41 2, 2-3	2.8 ± 0.36 3, 2-4 (85)	2.9 ± 0.32 3, 2-3	2.3 ± 0.42 2, 2-3 (70)	2.3 ± 0.41 2, 2-3 (15)	2.3 ± 0.43 2, 2-3
snout-vent (mm)	34.2 ± 2.26 28.0-37.3	40.4 ± 3.45 21.0-46.2	41.1 ± 3.42 28.3-49.3	37.5 ± 2.98 30.6-44.6	35.7 ± 3.85 27.7-40.8	37.1 ± 3.35 28.2-40.9
body (%svl)	50.7 ± 1.92 46.6-53.6	51.2 ± 2.69 42.2-57.6 (98)	51.0 ± 2.33 47.0-55.8	50.6 ± 2.72 42.7-58.6	49.0 ± 2.15 46.1-52.7	53.0 ± 3.33 46.8-57.9
tail (%svl)	120.4 ± 8.39 113.0-132.2 (4)	136.1 ± 8.64 116.2-155.8 (37)	133.6 ± 9.92 117.4-155.2 (18)	136.5 ± 9.32 116.5-156.5 (24)	128.6 ± 8.55 115.4-135.7 (5)	146.2 ± 9.95 131.5-161.4 (9)
forelimb (%svl)	32.2 ± 1.82 28.4-35.4	33.5 ± 1.91 28.0-37.0 (98)	34.1 ± 1.57 30.2-37.1	33.5 ± 2.26 29.0-38.4	37.8 ± 1.89 33.9-42.4	33.0 ± 1.85 29.8-36.5
hindlimb (%svl)	40.9 ± 1.73 38.4-44.0	41.1 ± 2.32 34.6-46.7	41.5 ± 2.61 35.9-45.9	42.0 ± 2.63 36.7-47.8	46.8 ± 1.42 43.7-49.3	40.7 ± 2.17 35.7-43.4
forebody (%svl)	41.7 ± 1.61 38.9-45.4	41.6 ± 1.80 37.8-48.8 (98)	42.2 ± 2.09 38.3-46.8	42.0 ± 2.09 35.8-47.4	42.9 ± 2.37 39.4-48.1	41.1 ± 2.20 36.6-44.2
head length (%svl)	20.3 ± 0.87 19.0-22.1	20.8 ± 1.04 18.7-26.1	21.2 ± 0.90 19.7-22.8	21.1 ± 1.03 18.8-24.0	21.6 ± 1.09 20.1-24.0	20.6 ± 1.15 18.5-22.2
head depth (%hl)	40.2 ± 2.86 35.7-47.8	42.3 ± 4.32 32.0-55.2	42.0 ± 2.84 36.9-48.5	43.3 ± 4.13 36.2-58.6	36.0 ± 3.37 28.4-41.8	42.8 ± 2.98 36.9-48.4
head width (%hl)	61.7 ± 2.10 58.5-65.8	62.2 ± 3.20 55.6-73.3	59.8 ± 3.15 53.6-67.4	60.3 ± 3.18 52.8-67.5	58.5 ± 2.98 54.3-62.9	60.5 ± 3.06 55.6-67.5
snout (%hl)	45.2 ± 2.07 42.2-49.8	44.9 ± 1.71 40.2-48.9 (98)	44.4 ± 1.39 41.5-47.5	46.1 ± 1.76 42.6-49.9	44.9 ± 1.70 42.1-48.5	44.1 ± 1.89 41.5-48.1
paravertebral scale (%svl)	4.2 ± 0.33 3.7-4.9	4.0 ± 0.37 3.0-4.9 (82)	3.9 ± 0.35 3.3-4.9	4.4 ± 0.51 3.4-5.7 (70)	4.3 ± 0.38 3.6-4.9 (15)	3.9 ± 0.35 3.2-4.5
dorsolateral scale (%vs)	89.9 ± 7.62 73.6-105.6	88.3 ± 8.16 69.9-104.1 (82)	89.7 ± 6.05 75.1-107.6	86.4 ± 6.55 72.1-99.4 (70)	84.1 ± 8.15 74.5-100.6 (15)	89.4 ± 5.89 77.4-101.4

Character	*C. fuhni* (14)	*C. gurrmul* (13)	*C. juno* (37)	*C. litoralis horneri* (14)	*C. litoralis litoralis* (33)	*C. megastictus* (9)
midbody scale rows	24.4 ± 1.09 24, 22-26	28.2 ± 0.73 28, 27-30	25.4 ± 1.13 26, 24-28 (36)	25.6 ± 1.22 26, 24-28	26.0 ± 1.13 26, 24-28	26.2 ± 1.20 26, 24-28
paravertebrals	46.1 ± 2.03 45, 44-50	53.5 ± 2.47 55, 49-57	48.8 ± 2.24 49, 44-54 (36)	54.5 ± 2.76 55, 50-58	56.6 ± 2.45 57, 48-62	47.2 ± 2.44 45, 44-51
nuchals	2.2 ± 0.43 2, 2-3	4.0 ± 2.12 2, 2-7	2.3 ± 0.75 2, 2-4	3.4 ± 1.40 2, 2-6	3.4 ± 1.32 2, 2-6	3.0 ± 1.12 2, 2-5
supralabials	7.1 ± 0.18 7, 7-8	6.9 ± 0.42 7, 6-8	7.0 ± 0.00 7, 7	6.9 ± 0.27 7, 6-7	7.1 ± 0.17 7, 7-8	7.0 ± 0.00 7, 7
infralabials	6.2 ± 0.38 6, 6-7	6.1 ± 0.19 6, 6-7	6.0 ± 0.17 6, 6-7	6.0 ± 0.00 6, 6	6.0 ± 0.15 6, 6-7	6.0 ± 0.00 6, 6
supraciliaries	5.2 ± 0.38 5, 5-6 (13)	5.0 ± 0.14 5, 5-6	6.0 ± 0.16 6, 6-7	5.1 ± 0.29 5, 5-6	5.1 ± 0.30 5, 5-6	6.0 ± 0.00 6, 6
ciliaries	3.2 ± 0.43 3, 3-5 (13)	3.1 ± 0.28 3, 3-4	3.1 ± 0.33 3, 2-4	3.0 ± 0.00 3, 3	3.0 ± 0.12 3, 3-4	3.0 ± 0.00 3, 3
subdigital lamellae (4th finger)	17.4 ± 1.10 18, 14-19	13.0 ± 1.17 13, 11-15	16.0 ± 1.32 16, 13-19 (36)	15.8 ± 1.32 16, 13-18	15.9 ± 0.93 16, 13-17	16.7 ± 1.41 16, 14-18
supradigital lamellae (4th finger)	14.7 ± 1.07 14, 12-16	11.6 ± 0.82 11, 10-13	13.1 ± 0.72 13, 11-14 (36)	12.8 ± 1.15 13, 11-15 (13)	13.4 ± 0.70 14, 12-14	13.1 ± 0.60 13, 12-14
subdigital lamellae (4th toe)	22.2 ± 1.82 21, 20-26	17.7 ± 0.78 18, 16-19	19.9 ± 1.72 19, 17-23	19.5 ± 1.56 20, 17-22	20.1 ± 1.11 20, 18-23	19.4 ± 0.88 19, 18-21
supradigital lamellae (4th toe)	18.3 ± 1.19 18, 16-20	15.2 ± 0.78 15, 14-17	15.9 ± 1.20 15, 13-18	15.1 ± 1.25 15, 12-17	15.7 ± 0.69 16, 14-17	15.6 ± 0.73 15, 15-17
palmars	8.8 ± 0.61 9, 8-10	7.2 ± 0.73 7, 6-9	9.1 ± 0.99 9, 7-12 (36)	9.5 ± 1.20 9, 7-11 (13)	11.0 ± 1.13 11, 9-13	8.2 ± 1.30 8, 6-10
plantars	10.6 ± 0.86 11, 9-12	7.5 ± 0.75 7, 6-9	12.1 ± 1.48 12, 10-15	10.9 ± 0.73 11, 9-12 (13)	11.8 ± 1.17 11, 10-14	10.8 ± 1.20 10, 9-13
post-temporals	3.0 3, (1)	2.6 ± 0.43 3, 2-3 (12)	2.7 ± 0.37 3, 2-3 (35)	2.2 ± 0.26 2, 2-3	2.1 ± 0.31 2, 2-3 (21)	3.0 ± 0.00 3, 3 (7)
snout-vent (mm)	41.6 ± 3.81 35.0-47.0	37.8 ± 3.61 31.9-44.3	36.7 ± 3.52 28.4-43.1	38.9 ± 7.73 26.2-51.0	41.0 ± 4.58 30.7-51.0	34.6 ± 4.73 26.4-40.5
body (%svl)	50.5 ± 2.56 46.4-54.5	52.3 ± 2.44 47.6-57.8	49.7 ± 2.66 41.5-55.5	50.3 ± 3.32 45.0-55.8	52.3 ± 2.30 48.1-56.3	48.9 ± 2.22 45.3-52.7
tail (%svl)	153.8 (1)	161.7 ± 13.87 149.5-180.2 (5)	131.3 ± 6.44 122.0-138.8 (6)	152.1 ± 15.65 135.1-171.9 (4)	142.0 ± 14.89 116.1-176.8 (12)	122.3 ± 8.33 106.2-129.6 (6)
forelimb (%svl)	40.7 ± 2.37 35.8-45.3	34.6 ± 1.67 30.9-37.5	37.7 ± 2.12 33.2-41.9	35.1 ± 2.43 31.3-39.2	35.4 ± 2.03 30.6-38.7	36.8 ± 1.48 34.7-39.2
hindlimb (%svl)	52.8 ± 2.88 47.6-57.8	44.1 ± 2.64 37.9-47.9	46.5 ± 2.96 40.9-52.2	45.1 ± 2.05 41.0-47.7	45.0 ± 2.80 38.5-48.9	44.6 ± 0.82 43.1-45.8
forebody (%svl)	42.2 ± 2.46 37.4-47.7	40.0 ± 1.76 37.0-43.7	42.8 ± 2.11 38.7-49.0	43.0 ± 2.89 37.5-47.6	41.6 ± 2.23 37.7-45.7	42.7 ± 1.15 41.1-44.7
head length (%svl)	21.2 ± 1.15 19.7-24.1	21.2 ± 0.99 19.0-22.5	21.3 ± 0.95 19.6-24.0	21.1 ± 1.28 18.9-23.2	20.6 ± 1.03 18.3-22.5	21.9 ± 0.48 21.3-22.9
head depth (%hl)	36.1 ± 3.45 32.0-41.4	43.3 ± 3.07 38.7-49.3	33.9 ± 3.72 26.3-41.1	40.1 ± 2.03 36.6-43.6	42.2 ± 3.61 37.1-53.3	32.5 ± 3.31 27.7-38.2
head width (%hl)	60.1 ± 3.37 54.3-65.1	62.4 ± 2.22 58.6-66.1	58.2 ± 3.01 53.2-65.7	59.1 ± 4.89 50.7-69.7	59.4 ± 2.47 53.1-64.4	59.9 ± 3.06 55.5-65.6
snout (%hl)	44.5 ± 1.48 42.1-47.1	45.8 ± 1.96 42.6-48.5	45.4 ± 1.84 42.0-50.1	44.4 ± 1.98 40.7-47.8	45.6 ± 1.66 42.9-49.2	44.6 ± 1.71 42.4-47.7
paravertebral scale (%svl)	4.2 ± 0.37 3.7-4.9 (8)	3.8 ± 0.21 3.5-4.2 (12)	4.3 ± 0.43 3.4-5.2 (34)	3.7 ± 0.38 2.8-4.3	3.4 ± 0.34 2.9-4.1 (21)	3.7 ± 0.30 3.4-4.2 (7)
dorsolateral scale (%vs)	95.2 ± 10.09 83.3-111.9 (8)	92.8 ± 6.40 77.6-102.1 (12)	84.3 ± 8.27 64.0-102.9 (34)	89.3 ± 6.26 80.0-103.9	98.2 ± 8.52 83.2-111.3 (21)	92.3 ± 7.13 83.3-103.6 (7)

Character	*C. mertensi* (23)	*C. metallicus* (119)	*C. ochrus* (22)	*C. pannosus* (56)	*C. plagiocephalus* (28)	*C. pulcher clarus* (31)
midbody scale rows	23.9 ± 0.45 24, 22-24	24.1 ± 0.92 24, 22-26	24.5 ± 0.80 24, 24-26	23.5 ± 1.18 24, 22-26	24.4 ± 0.98 24, 22-26	24.6 ± 0.88 24, 24-26
paravertebrals	47.4 ± 1.27 49, 45-49	49.7 ± 2.44 48, 45-56	50.7 ± 2.15 50, 47-55	47.8 ± 2.49 48, 43-56	49.2 ± 2.74 50, 45-58	49.5 ± 2.16 50, 45-55
nuchals	2.0 ± 0.00 2, 2	2.0 ± 0.18 2, 2-4	2.2 ± 0.50 2, 2-4	2.2 ± 0.56 2, 2-5	2.2 ± 0.57 2, 2-4	2.4 ± 0.92 2, 2-5
supralabials	7.0 ± 0.11 7, 6-7	7.1 ± 0.22 7, 6-8	7.0 ± 0.11 7, 7-8	7.0 ± 0.13 7, 7-8	7.0 ± 0.22 7, 6-8	6.9 ± 0.21 7, 6-7
infralabials	6.1 ± 0.31 6, 6-7	6.0 ± 0.18 6, 5-7	6.0 ± 0.00 6, 6	6.0 ± 0.00 6, 6	6.1 ± 0.22 6, 6-7	6.0 ± 0.00 6, 6
supraciliaries	5.3 ± 0.41 5, 5-6	6.0 ± 0.24 6, 5-7	5.1 ± 0.25 5, 5-6	5.1 ± 0.23 5, 5-6	5.1 ± 0.29 5, 5-6	5.0 ± 0.18 5, 5-6
ciliaries	3.0 ± 0.11 3, 3-4	3.0 ± 0.06 3, 3-4	3.2 ± 0.37 3, 3-4	3.1 ± 0.23 3, 3-4	3.2 ± 0.38 3, 3-4	3.0 ± 0.00 3, 3
subdigital lamellae (4th finger)	15.8 ± 0.88 16, 14-18	15.0 ± 1.16 14, 12-18 (118)	16.3 ± 0.98 16, 15-18	15.8 ± 1.06 16, 13-18 (55)	15.5 ± 1.17 16, 14-18 (25)	15.1 ± 0.82 15, 14-17
supradigital lamellae (4th finger)	12.7 ± 0.57 13, 12-14	12.9 ± 0.73 13, 10-14 (118)	13.0 ± 0.53 13, 12-14	12.7 ± 0.73 13, 11-14 (55)	12.9 ± 0.61 13, 11-14 (25)	12.3 ± 0.48 12, 12-13
subdigital lamellae (4th toe)	18.7 ± 1.04 18, 17-21	18.1 ± 1.35 18, 15-21 (118)	19.7 ± 0.97 20, 18-22 (21)	19.4 ± 1.25 19, 16-22 (54)	18.8 ± 1.27 20, 16-21	18.9 ± 0.98 19, 17-21
supradigital lamellae (4th toe)	15.2 ± 0.85 16, 13-16	15.2 ± 0.95 15, 13-18 (118)	16.1 ± 0.73 16, 15-18 (21)	15.2 ± 0.78 15, 14-17 (55)	15.1 ± 0.94 15, 13-17	15.6 ± 0.76 16, 14-17
palmars	9.5 ± 0.51 9, 9-10	7.7 ± 0.90 8, 6-10	9.9 ± 0.83 10, 8-11	9.1 ± 1.00 10, 7-12	9.6 ± 0.82 9, 8-12 (25)	7.6 ± 0.71 8, 6-9
plantars	10.4 ± 0.68 10, 9-12	9.6 ± 0.97 10, 7-13	11.0 ± 0.69 11, 10-12	10.4 ± 1.25 10, 8-14	10.7 ± 1.12 10, 9-13	9.8 ± 0.93 10, 8-12
post-temporals	2.0 ± 0.11 2, 2-3 (19)	2.4 ± 0.44 2, 2-3 (118)	2.9 ± 0.26 3, 2-3	2.6 ± 0.44 3, 1-3 (51)	2.4 ± 0.44 2, 2-3	2.1 ± 0.25 2, 2-3
snout-vent (mm)	34.3 ± 3.22 24.5-38.5	38.6 ± 4.18 27.9-47.9	39.0 ± 3.27 34.2-43.8	34.4 ± 2.78 29.3-41.5	33.6 ± 3.86 24.3-40.3	36.7 ± 2.38 30.7-40.6
body (%svl)	50.5 ± 2.80 44.7-54.9	50.0 ± 2.83 43.7-60.3	50.8 ± 2.46 43.1-55.1	50.6 ± 2.59 45.2-56.2	49.1 ± 3.26 40.8-55.8	50.9 ± 2.64 47.2-56.9
tail (%svl)	144.9 ± 9.73 136.9-156.8 (5)	144.2 ± 10.79 128.0-168.7 (37)	133.8 ± 10.97 126.0-141.5 (2)	133.4 ± 11.55 114.5-148.2 (15)	140.9 ± 12.05 127.8-151.5 (3)	121.8 ± 6.19 113.9-129.0 (5)
forelimb (%svl)	34.0 ± 2.50 28.4-39.8	33.6 ± 2.15 29.1-40.0	34.1 ± 2.06 29.8-37.5	33.8 ± 2.21 28.4-38.7	33.9 ± 1.94 30.7-39.6	32.3 ± 1.91 29.3-36.3
hindlimb (%svl)	42.0 ± 2.59 38.0-47.2	41.4 ± 2.56 35.8-47.7 (118)	42.5 ± 2.25 39.1-46.9 (21)	41.7 ± 2.53 36.3-46.5	42.2 ± 3.21 36.8-50.1	40.5 ± 2.12 36.1-45.0
forebody (%svl)	40.6 ± 2.69 35.0-44.4	42.4 ± 2.03 37.7-47.6	41.8 ± 2.25 36.7-45.1	42.1 ± 2.67 36.0-53.0	42.9 ± 2.59 38.0-50.1	40.9 ± 2.23 36.6-46.4
head length (%svl)	21.0 ± 1.36 19.1-23.8	21.4 ± 1.11 19.1-23.9	20.9 ± 0.92 19.2-22.4	20.7 ± 1.13 18.4-23.6	21.5 ± 1.19 19.4-24.5	20.3 ± 0.88 18.8-22.6
head depth (%hl)	43.4 ± 3.32 36.8-48.1	41.7 ± 3.70 31.6-51.9	39.2 ± 2.72 34.8-44.3	40.3 ± 3.63 33.4-49.9	39.5 ± 5.09 30.2-53.0	39.8 ± 4.68 32.9-53.4
head width (%hl)	63.2 ± 2.91 57.9-67.3	59.9 ± 2.85 52.4-70.0	62.4 ± 2.81 57.8-69.3	61.9 ± 3.78 54.2-73.3	61.8 ± 3.95 53.9-68.3	65.2 ± 3.32 58.8-71.9
snout (%hl)	45.1 ± 1.81 41.9-49.7	45.0 ± 2.03 40.2-50.5	44.9 ± 1.69 41.6-48.0	45.4 ± 2.06 41.4-52.2	45.9 ± 1.94 42.0-50.4	45.1 ± 1.26 42.1-48.4
paravertebral scale (%svl)	4.0 ± 0.48 3.3-4.9	4.0 ± 0.47 3.0-5.1 (104)	3.9 ± 0.41 3.2-4.9	4.1 ± 0.38 3.4-5.2 (51)	3.9 ± 0.34 3.2-4.8 (23)	4.0 ± 0.29 3.4-4.8 (30)
dorsolateral scale (%vs)	90.2 ± 10.58 75.2-110.7	88.3 ± 6.98 72.5-107.2 (104)	87.3 ± 7.49 72.7-103.6	90.6 ± 7.60 65.4-107.9 (51)	92.1 ± 6.75 81.8-108.3 (24)	88.2 ± 8.26 71.4-100.8 (30)

Character	*C. pulcher pulcher* (48)	*C. ruber* (31)	*C. tytthos* (34)	*C. ustulatus* (31)	*C. virgatus* (31)	*C. wulbu* (11)	*C. zoticus* (17)
midbody scale rows	23.2 ± 1.05 24, 22-26	24.5 ± 0.93 24, 23-26	23.9 ± 1.18 24, 22-26	23.0 ± 1.20 22, 21-26	21.8 ± 0.99 22, 20-24	25.4 ± 0.92 26, 24-26	24.8 ± 1.38 24, 24-28
paravertebrals	48.2 ± 2.37 47, 42-53	52.3 ± 2.48 54, 45-56	48.6 ± 2.45 48, 43-53	46.5 ± 1.61 46, 42-50	47.3 ± 2.39 47, 43-52	40.6 ± 2.16 39, 37-44	45.9 ± 1.96 45, 43-51
nuchals	2.4 ± 0.87 2, 2-6	2.2 ± 0.52 2, 2-4	2.3 ± 0.71 2, 2-5	2.3 ± 0.74 2, 2-5	2.4 ± 0.96 2, 2-6	2.6 ± 0.81 2, 2-4	2.7 ± 1.20 2, 2-6 (16)
supralabials	7.0 ± 0.31 7, 6-8	7.0 ± 0.20 7, 6-8	7.0 ± 0.09 7, 7-8	7.1 ± 0.27 7, 7-8	7.0 ± 0.18 7, 6-7	6.9 ± 0.15 7, 6-7	7.0 ± 0.00 7, 7 (16)
infralabials	6.0 ± 0.00 6, 6	6.0 ± 0.00 6, 6	6.0 ± 0.00 6, 6 (26)	6.0 ± 0.00 6, 6	6.0 ± 0.00 6, 6	6.0 ± 0.00 6, 6	6.0 ± 0.00 6, 6 (16)
supraciliaries	5.0 ± 0.19 5, 5-6	6.0 ± 0.18 6, 6-7	5.0 ± 0.17 5, 5-6	5.0 ± 0.20 5, 5-6	5.2 ± 0.33 5, 5-6	5.9 ± 0.15 6, 5-6	5.1 ± 0.25 5, 5-6 (16)
ciliaries	3.0 ± 0.16 3, 2-4	3.0 ± 0.00 3, 3	3.0 ± 0.17 3, 3-4	3.0 ± 0.09 3, 3-4	3.0 ± 0.00 3, 3	3.2 ± 0.41 3, 3-4	3.0 ± 0.00 3, 3 (16)
subdigital lamellae (4th finger)	14.6 ± 0.92 15, 12-16	15.7 ± 0.94 16, 14-18	15.1 ± 1.12 15, 13-18	14.6 ± 0.86 15, 13-16 (29)	15.7 ± 0.77 16, 14-17	16.8 ± 0.98 17, 15-18	16.0 ± 1.06 16, 14-18
supradigital lamellae (4th finger)	12.4 ± 0.79 13, 11-14	13.1 ± 0.85 13, 12-16	12.8 ± 0.83 13, 11-14	12.4 ± 0.73 12, 11-14 (29)	12.4 ± 0.67 12, 11-14	12.9 ± 0.83 13, 12-14	13.1 ± 0.60 13, 12-14
subdigital lamellae (4th toe)	18.2 ± 1.27 19, 16-22	18.8 ± 1.35 18, 17-21	18.6 ± 1.23 18, 16-21	18.0 ± 1.40 18, 15-21	19.6 ± 1.40 19, 16-22	20.4 ± 1.43 22, 18-22	18.4 ± 1.32 19, 16-21
supradigital lamellae (4th toe)	15.8 ± 0.95 16, 14-18	15.7 ± 1.35 15, 14-19	14.9 ± 0.94 15, 13-18	15.1 ± 0.94 15, 13-18 (30)	15.6 ± 0.77 15, 14-18	16.4 ± 1.37 17, 14-18	15.1 ± 0.49 15, 14-16
palmars	8.0 ± 0.77 8, 6-9	7.8 ± 0.90 8, 6-9	9.8 ± 1.23 9, 7-12	9.3 ± 0.83 9, 8-11 (30)	8.4 ± 0.88 8, 7-11	8.9 ± 1.04 8, 8-11	7.9 ± 0.66 8, 7-9
plantars	8.9 ± 0.75 9, 7-11	9.2 ± 0.88 9, 8-11	11.1 ± 1.26 11, 9-14	10.7 ± 0.75 11, 9-12	9.5 ± 1.09 10, 8-12	13.3 ± 0.65 13, 12-14	9.8 ± 1.18 10, 7-13
post-temporals	2.0 ± 0.15 2, 2-3	2.9 ± 0.21 3, 2-3	2.2 ± 0.32 2, 2-3 (26)	2.5 ± 0.40 3, 2-3	2.1 ± 0.43 2, 2-3 (26)	2.6 ± 0.45 3, 2-3	2.7 ± 0.40 3, 2-3 (16)
snout-vent (mm)	34.9 ± 2.75 28.0-41.7	40.9 ± 3.51 31.5-47.2	31.3 ± 3.26 23.7-38.6	35.2 ± 3.10 30.1-41.6	34.8 ± 3.23 24.6-39.7	35.8 ± 1.62 33.3-39.0	33.4 ± 3.32 25.4-38.7
body (%svl)	51.2 ± 2.66 44.5-55.9	51.4 ± 2.93 39.8-58.3	50.9 ± 3.03 44.6-57.0 (26)	50.0 ± 2.34 44.6-56.1	50.4 ± 2.60 45.8-55.4	50.1 ± 2.09 47.7-53.8	48.6 ± 2.31 43.9-52.0
tail (%svl)	128.9 ± 9.38 114.4-142.3(12)	132.6 ± 12.37 114.4-168.3 (21)	133.8 ± 7.66 122.6-147.0 (8)	144.4 ± 7.66 136.5-161.9 (8)	128.6 ± 7.53 113.9-137.0 (7)	134.5 (1)	127.1 ± 17.11 108.0-146.0 (4)
forelimb (%svl)	32.1 ± 1.66 28.7-36.6	33.5 ± 2.32 27.1-39.8	32.2 ± 2.57 27.0-39.7 (26)	34.7 ± 2.05 31.0-38.9	33.1 ± 2.01 28.6-38.3	38.4 ± 2.04 35.1-41.2	35.0 ± 2.58 29.6-39.0
hindlimb (%svl)	40.4 ± 2.56 35.6-47.0	40.9 ± 2.45 34.0-44.8	41.4 ± 2.31 33.9-48.8	44.3 ± 3.05 38.5-50.0	41.0 ± 2.88 32.3-45.8	47.3 ± 2.34 43.3-51.1	42.2 ± 2.47 38.4-46.0
forebody (%svl)	41.3 ± 1.84 36.7-44.5	42.1 ± 2.29 36.4-47.2	42.3 ± 2.31 38.5-49.0 (26)	42.2 ± 2.00 37.9-46.5	42.8 ± 2.88 32.3-45.8	42.9 ± 1.67 40.7-45.8	42.8 ± 1.77 38.7-46.3
head length (%svl)	19.7 ± 1.06 17.8-21.8	20.8 ± 0.98 18.7-22.9	21.3 ± 1.10 19.1-23.6	20.9 ± 1.02 19.3-23.5	20.7 ± 0.95 18.8-22.3	19.9 ± 0.61 19.0-20.8	21.1 ± 0.89 19.8-22.8 (16)
head depth (%hl)	38.9 ± 3.39 29.2-45.1	41.1 ± 3.27 34.0-49.3	40.6 ± 3.64 34.3-48.5	34.7 ± 4.16 26.0-43.0 (30)	38.2 ± 3.65 32.0-44.9	34.9 ± 2.18 31.1-38.2	32.5 ± 2.13 28.6-36.0 (16)
head width (%hl)	61.9 ± 3.74 55.0-70.5	61.5 ± 2.52 55.3-68.4	61.6 ± 3.69 55.8-70.3	59.2 ± 3.25 54.1-67.6 (30)	57.6 ± 3.38 50.9-65.4	65.4 ± 3.29 61.1-70.4	60.5 ± 2.17 56.3-63.8 (16)
snout (%hl)	44.9 ± 2.10 41.9-49.7	44.7 ± 1.46 41.1-48.0	46.0 ± 1.57 43.3-49.5 (26)	44.1 ± 1.86 40.6-48.5	44.9 ± 1.99 42.0-51.0	44.6 ± 2.27 40.7-48.4	45.6 ± 2.27 41.5-50.1 (16)
paravertebral scale (%svl)	4.0 ± 0.35 3.2-5.1 (43)	4.0 ± 0.39 3.1-4.6 (35)	4.0 ± 0.38 3.3-4.7 (26)	4.0 ± 0.43 3.2-4.8	4.5 ± 0.49 3.7-5.7 (27)	4.3 ± 0.26 3.8-4.6	4.2 ± 0.39 3.6-4.9
dorsolateral scale (%vs)	92.9 ± 6.87 79.7-107.3 (43)	90.7 ± 6.74 78.5-105.5 (35)	88.4 ± 6.69 76.5-104.2 (26)	89.1 ± 6.60 76.8-104.5	80.9 ± 8.65 64.3-103.4 (27)	94.1 ± 5.09 88.2-103.1	91.1 ± 7.88 75.2-110.9

(B). Summary of variation in qualitative characters for *Cryptoblepharus* taxa from the Australian region. Character states presented as percentages of total sampled. Sample sizes are in parentheses.

Character	*C. adamsi* (24)	*C. australis* (105)	*C. buchananii* (44)	*C. cygnatus* (71)	*C. daedalos* (16)	*C. exochus* (29)
plantars (condition)	rounded 100%	rounded 3% acute 97%	rounded 100%	rounded 100%	rounded 100%	acute 100%
subdigital lamellae (condition)	smooth 100%	smooth 100%	smooth 100%	smooth 10% callused 90%	smooth 100%	smooth 100%
loreals (largest)	subequal 54% posterior 25% anterior 21%	subequal 54% posterior 37% anterior 9%	subequal 2% posterior 98%	subequal 21% posterior 79%	posterior 100%	subequal 81% posterior 12% anterior 8%
subocular (supralabial)	5th labial 77% 6th labial 23%	5th labial 98% 6th labial 2%	5th labial 100%	5th labial 90% 6th labial 10%	5th labial 100%	5th labial 100%
postnasal (presence)	absent 100%	absent 100%	absent 100%	absent 100%	absent 100%	absent 100%
prefrontal (contact point)	broad 100%	broad 93% narrow 3% separated 4%	broad 95% narrow 5%	broad 74% narrow 13% separated 13%	broad 86% narrow 7% separated 7%	broad 100%
body pattern (type)	longitudinal 100%	longitudinal 100%	obscure 6% longitudinal 94%	obscure 1% longitudinal 99%	flecked 100%	longitudinal 100%
pale stripes (condition)	narrow 37% broad 63%	broad 100%	absent 5% narrow 8% broad 87%	absent 2% broad 98%	absent 100%	very narrow 100%
plantars (pigmentation)	pale 100%	pale 100%	pale 100%	pale 100%	pale 100%	pale 100%

Character	*C. fuhni* (14)	*C. gurrmul* (13)	*C. juno* (37)	*C. litoralis horneri* (14)	*C. litoralis litoralis* (33)	*C. megastictus* (9)
plantars (condition)	rounded 100%	rounded 100%	rounded 100%	rounded 100%	rounded 100%	rounded 100%
subdigital lamellae (condition)	callused 100%	smooth 100%	smooth 100%	smooth 50% callused 50%	callused 100%	smooth 100%
loreals (largest)	subequal 14% posterior 72% anterior 14%	subequal 69% posterior 31%	subequal 8% posterior 92%	subequal 57% anterior 43%	subequal 18% posterior 3% anterior 79%	posterior 100%
subocular (supralabial)	5th labial 100%	4th labial 11% 5th labial 89%	5th labial 100%	4th labial 7% 5th labial 93%	5th labial 100%	5th labial 100%
postnasal (presence)	absent 100%	present 100%	absent 100%	absent 93% present 7%	absent 100%	absent 100%
prefrontal (contact point)	broad 79% narrow 7% separated 14%	broad 100%	broad 82% narrow 5% separated 13%	broad 90% separated 10%	broad 100%	broad 100%
body pattern (type)	longitudinal 100%	flecked 8% longitudinal 92%	obscure 11% flecked 54% blotched 30% longitudinal 5%	flecked 8% longitudinal 92%	flecked 21% longitudinal 79%	flecked 11% blotched 89%
pale stripes (condition)	narrow, broken 100%	absent 7% narrow 7% broad 86%	absent 96% broad 4%	absent 8% broad 92%	absent 27% broad 73%	absent 100%
plantars (pigmentation)	dark 100%	pale 61% dark 39%	pale 100%	dark 100%	dark 100%	pale 100%

Character	*C. mertensi* (23)	*C. metallicus* (119)	*C. ochrus* (22)	*C. pannosus* (64)	*C. plagiocephalus* (28)	*C. pulcher clarus* (31)
plantars (condition)	acute 100%	rounded 100%	acute 100%	acute 100%	acute 100%	rounded 100%
subdigital lamellae (condition)	smooth 30% weakly keeled 65% strongly keeled 5%	smooth 99% callused 1%	smooth 36% weakly keeled 64%	smooth 2% weakly keeled 32% strongly keeled 66%	weakly keeled 85% strongly keeled 15%	smooth 100%
loreals (largest)	subequal 85% anterior 15%	subequal 16% posterior 84%	subequal 57% anterior 43%	subequal 73% posterior 5% anterior 22%	subequal 65% posterior 35%	subequal 65% posterior 32% anterior 3%
subocular (supralabial)	5th labial 100%	5th labial 98% 6th labial 2%	5th labial 100%	5th labial 98% 6th labial 2%	5th labial 100%	4th labial 3% 5th labial 97%
postnasal (presence)	absent 100%	absent 100%	absent 100%	absent 100%	absent 100%	absent 100%
prefrontal (contact point)	broad 100%	broad 97% narrow 2% separated 1%	broad 95% separated 5%	broad 96% narrow 2% separated 2%	broad 100%	broad 97% narrow 3%
body pattern (type)	longitudinal 100%	obscure 3% longitudinal 97%	longitudinal 100%	longitudinal 100%	flecked 24% longitudinal 76%	longitudinal 100%
pale stripes (condition)	absent 95% narrow 5%	absent 3% narrow 1% broad 96%	narrow 100%	absent 25% narrow 9% broad 66%	absent 21% broad 79%	narrow 74% broad 26%
plantars (pigmentation)	pale 100%	pale 100%	pale 100%	pale 100%	pale 100%	pale 6% dark 94%

Character	*C. pulcher pulcher* (48)	*C. ruber* (31)	*C. tytthos* (34)	*C. ustulatus* (31)	*C. virgatus* (31)	*C. wulbu* (11)	*C. zoticus* (17)
plantars (condition)	rounded 100%	rounded 100%	acute 100%	rounded 100%	rounded 100%	rounded 100%	rounded 100%
subdigital lamellae (condition)	smooth 100%	smooth 100%	weakly keeled 9% strongly keeled 91%	smooth 100%	smooth 100%	smooth 100%	smooth 100%
loreals (largest)	subequal 65% posterior 6% anterior 29%	subequal 16% posterior 84%	subequal 73% posterior 6% anterior 21%	subequal 77% posterior 10% anterior 13%	subequal 32% posterior 58% anterior 10%	subequal 9% posterior 82% anterior 9%	subequal 50% posterior 3% anterior 47%
subocular (supralabial)	4th labial 4% 5th labial 89% 6th labial 7%	4th labial 3% 5th labial 95% 6th labial 2%	5th labial 99% 6th labial 1%	5th labial 93% 6th labial 7%	4th labial 3% 5th labial 97%	5th labial 100%	5th labial 100%
postnasal (presence)	absent 100%	absent 100%	absent 100%	absent 100%	absent 100%	absent 100%	absent 100%
prefrontal (contact point)	broad 98% narrow 2%	broad 97% narrow 3%	broad 96% separated 4%	broad 100%	broad 97% narrow 3%	broad 100%	broad 88% narrow 6% separated 6%
body pattern (type)	longitudinal 100%	obscure 10% flecked 26% longitudinal 64%	longitudinal 100%	obscure 3% longitudinal 97%	obscure 3% longitudinal 97%	blotched 100%	obscure 6% flecked 76% blotched 12% longitudinal 6%
pale stripes (condition)	narrow 100%	absent 39% narrow 3% broad 58%	narrow 94% broad 6%	absent 3% narrow 97%	narrow 100%	absent 100%	absent 100%
plantars (pigmentation)	pale 17% dark 83%	pale 100%	pale 100%	pale 100%	pale 100%	pale 100%	pale 100%

(C). Summary of morphometric and meristic characters for *Cryptoblepharus* taxa from the south-west Indian Ocean region. Sample sizes are in parenthesis.

Character	*C. africanus* (10)	*C. ahli* (7)	*C. aldabrae* (10)	*C. ater* (10)	*C. bitaeniatus* (10)	*C. boutoni* (12)	*C. caudatus* (8)
midbody scale rows	22.2 ± 0.79 22, 21-24	24.0 ± 0.00 24, 24	23.4 ± 0.97 24, 22-24	24.2 ± 0.63 24, 24-26	28.2 ± 0.63 28, 28-30	25.7 ± 0.65 26, 24-26	26.1 ± 1.36 26, 24-28
paravertebrals	50.2 ± 1.93 50, 48-54	53.4 ± 2.15 56, 50-56	49.7 ± 3.02 47, 46-56	51.8 ± 2.74 50, 47-56	55.8 ± 2.62 53, 53-60	50.0 ± 2.13 49, 48-54	56.9 ± 2.10 55, 55-60
nuchals	3.1 ± 0.99 4, 2-4	2.1 ± 0.38 2, 2-3	2.9 ± 0.99 3, 2-5	2.4 ± 0.84 2, 2-4	3.7 ± 0.82 4, 2-5	3.3 ± 0.89 4, 2-4	2.2 ± 0.46 2, 2-3
supralabials	7.2 ± 0.48 7, 6-8	7.1 ± 0.38 7, 7-8	6.8 ± 0.42 7, 6-7	7.2 ± 0.35 7, 7-8	7.2 ± 0.35 7, 7-8	7.2 ± 0.40 7, 7-8	7.0 ± 0.00 7, 7
infralabials	6.4 ± 0.46 6, 6-7	6.9 ± 0.38 7, 6-7	6.5 ± 0.53 7, 5-7	6.6 ± 0.46 7, 6-7	6.6 ± 0.52 7, 6-7	6.5 ± 0.45 6, 6-7	6.2 ± 0.26 6, 6-7
supraciliaries	5.2 ± 0.42 5, 4-6	5.1 ± 0.38 5, 5-6	5.0 ± 0.00 5, 5	5.0 ± 0.00 5, 5	5.0 ± 0.00 5, 5	5.1 ± 0.31 5, 5-6	4.9 ± 0.18 5, 4-5
ciliaries	3.0 ± 0.16 3, 3-4	3.0 ± 0.00 3, 3	3.1 ± 0.21 3, 3-4	3.0 ± 0.00 3, 3	3.0 ± 0.00 3, 3	3.1 ± 0.29 3, 3-4	3.0 ± 0.00 3, 3
subdigital lamellae (4th finger)	15.7 ± 0.67 16, 14-16	16.1 ± 1.21 15, 15-18	15.0 ± 0.47 15, 14-16	16.1 ± 1.10 16, 14-18	15.0 ± 1.05 16, 13-16	15.1 ± 0.54 15, 14-16 (11)	14.6 ± 1.13 15, 13-16 (7)
supradigital lamellae (4th finger)	13.3 ± 0.48 13, 13-14	13.6 ± 0.79 13, 13-15	12.6 ± 0.52 13, 12-13	13.5 ± 0.97 13, 12-15	13.4 ± 0.52 13, 13-14	12.9 ± 0.54 13, 12-14 (11)	12.4 ± 0.53 12, 12-13 (7)
subdigital lamellae (4th toe)	20.3 ± 1.06 20, 18-22	20.3 ± 1.11 20, 19-22	19.5 ± 0.97 20, 18-21	20.2 ± 0.92 21, 19-21	19.8 ± 0.92 19, 19-21	20.0 ± 0.89 20, 19-22 (11)	18.4 ± 1.13 19, 17-20 (7)
supradigital lamellae (4th toe)	17.5 ± 1.08 18, 16-19	16.7 ± 0.49 17, 16-17	15.7 ± 1.16 16, 14-18	16.8 ± 0.63 17, 16-18	16.9 ± 0.88 17, 15-18	15.9 ± 0.83 15, 15-17 (11)	16.1 ± 0.90 17, 15-17 (7)
palmars	9.8 ± 0.92 10, 8-11	11.6 ± 1.13 11, 10-13	12.1 ± 1.29 13, 10-14	10.3 ± 0.95 10, 9-12	10.1 ± 0.74 10, 9-11	11.4 ± 0.69 11, 11-13 (11)	11.4 ± 0.92 11, 10-13
plantars	10.5 ± 0.71 11, 9-11	12.6 ± 1.13 12, 11-14	13.3 ± 1.57 12, 12-17	11.3 ± 1.16 12, 9-13	12.2 ± 0.42 12, 12-13	13.7 ± 1.07 14, 12-15	12.2 ± 1.16 13, 10-13
snout-vent (mm)	43.9 ± 3.54 36.3-47.6	47.7 ± 2.02 45.6-50.7	36.9 ± 4.60 31.1-45.6	43.9 ± 2.00 40.8-48.2	40.3 ± 1.52 38.2-42.4	37.0 ± 3.25 30.4-42.0	43.9 ± 2.62 40.4-48.7
body (%svl)	54.0 ± 3.72 48.4-59.6	55.0 ± 1.42 53.2-57.3	54.5 ± 2.74 50.6-58.3	53.0 ± 2.63 48.9-58.1	50.3 ± 2.30 47.8-54.4	50.9 ± 2.37 45.5-54.3	54.4 ± 2.89 51.3-58.5
tail (%svl)	152.4 ± 3.73 147.0-156.1 (5)	159.9 ± 0.00 159.9 (1)	142.9 ± 3.72 140.3-145.5 (2)	-	127.4 ± 0.07 127.3-127.4 (2)	136.4 ± 16.44 124.8-148.0 (2)	144.9 ± 4.13 138.8-150.8 (6)
forelimb (%svl)	34.7 ± 1.75 31.7-37.3	32.7 ± 2.22 30.4-36.8	33.7 ± 1.61 31.1-35.6	34.3 ± 1.92 30.3-36.7	32.3 ± 1.62 29.5-35.1	35.9 ± 2.15 33.3-39.5	30.9 ± 1.75 27.5-31.1 (7)
hindlimb (%svl)	44.2 ± 2.28 40.2-47.2	42.5 ± 2.90 39.3-47.1	42.5 ± 1.91 39.5-45.5	43.3 ± 2.02 40.4-45.4	41.7 ± 2.39 37.3-44.5	45.0 ± 3.19 41.2-50.3	39.4 ± 2.36 35.7-42.6(7)
forebody (%svl)	40.1 ± 1.43 38.5-43.0	39.6 ± 2.10 36.6-42.1	41.4 ± 2.53 36.5-44.0	40.9 ± 1.98 37.0-43.9	41.6 ± 1.33 39.7-43.6	41.3 ± 1.39 38.7-43.7	40.2 ± 1.48 38.3-42.3
head length (%svl)	19.3 ± 0.82 18.4-20.8	18.8 ± 0.76 18.0-19.8	20.5 ± 1.08 18.1-21.8	20.6 ± 0.84 19.5-21.8	20.4 ± 0.71 19.5-22.0	20.7 ± 0.83 19.7-22.8	19.1 ± 0.82 17.6-20.3
head depth (%hl)	46.9 ± 3.27 41.9-52.3	46.1 ± 3.46 40.2-50.6	49.4 ± 2.85 43.4-52.5	45.4 ± 2.63 41.3-50.2	47.0 ± 3.16 42.2-51.2	45.0 ± 1.94 41.8-47.8	50.5 ± 1.81 49.1-54.5
head width (%hl)	63.0 ± 3.07 59.4-67.4	63.5 ± 3.61 56.7-66.6	65.6 ± 1.78 63.5-69.4	62.2 ± 2.58 55.8-64.9	62.8 ± 2.48 59.5-67.7	61.6 ± 2.75 54.1-65.0	68.4 ± 3.65 60.5-72.6
snout (%hl)	44.5 ± 1.50 42.6-47.9	44.9 ± 1.52 42.1-46.7	45.0 ± 1.82 43.1-48.8	45.0 ± 1.88 43.1-49.3	46.7 ± 2.32 43.6-51.2	45.4 ± 2.73 41.0-50.8	46.2 ± 2.00 42.2-49.1
paravertebral scale (%svl)	4.3 ± 0.30 4.0-4.7 (5)	3.4 ± 0.19 3.2-3.7 (5)	3.9 ± 0.51 3.4-4.7 (5)	4.5 ± 0.15 4.3-4.7 (5)	3.7 ± 0.18 3.4-3.9 (5)	3.0 ± 0.21 2.6-3.2 (5)	4.5 ± 0.29 4.0-4.8 (5)
dorsolateral scale (%vs)	78.8 ± 4.11 74.1-84.0 (5)	94.8 ± 6.64 86.0-100.8 (5)	87.1 ± 6.14 82.0-96.7 (5)	79.3 ± 6.30 72.9-86.5 (5)	95.8 ± 7.20 84.3-103.5 (5)	89.0 ± 4.95 81.3-94.5 (5)	87.4 ± 3.73 82.9-92.8 (5)

Character	*C. cognatus* (4)	*C. gloriosus gloriosus* (5)	*C. gloriosus mayottensis* (11)	*C. gloriosus mohelicus* (5)	*C. quinquetaeniatus* (12)	*C. voeltzkowi* (2)
midbody scale rows	22.0 ± 0.00 22, 22	21.0 ± 1.00 22, 20-22	23.4 ± 0.92 24, 22-24	22.8 ± 1.10 22, 22-24	22.5 ± 0.80 22, 22-24	24.0 ± 0.00 24, 24
paravertebrals	50.0 ± 0.82 50, 49-51	50.6 ± 2.51 51, 47-54	51.7 ± 1.74 52, 48-55	47.0 ± 0.71 47, 46-48	52.0 ± 2.22 50, 49-56	49.5 ± 3.54 n/a, 47-52
nuchals	5.0 ± 1.73 4, 4-7 (3)	2.6 ± 1.34 2, 2-5	2.8 ± 0.98 2, 2-4	2.4 ± 0.55 2, 2-3	3.5 ± 1.68 2, 2-6	4.0 ± 2.83 n/a, 2-6
supralabials	6.6 ± 0.48 7, 6-7	7.0 ± 0.00 7, 7	7.0 ± 0.00 7, 7	7.0 ± 0.00 7, 7	7.0 ± 0.00 7, 7	6.7 ± 0.35 n/a, 6-7
infralabials	6.2 ± 0.50 6, 6-7	6.2 ± 0.45 6, 6-7	6.9 ± 0.30 7, 6-7	6.6 ± 0.55 7, 6-7	6.7 ± 0.47 7, 6-7	6.0 ± 0.00 6, 6
supraciliaries	5.0 ± 0.00 5, 5	5.3 ± 0.45 5, 5-6	5.3 ± 0.40 5, 5-6	5.0 ± 0.00 5, 5	5.0 ± 0.00 5, 5	5.0 ± 0.00 5, 5
ciliaries	3.0 ± 0.00 3, 3	2.9 ± 0.55 3, 2-4	3.0 ± 0.00 3, 3	3.0 ± 0.00 3, 3	3.0 ± 0.00 3, 3	3.0 ± 0.00 3, 3
subdigital lamellae (4th finger)	14.0 ± 0.82 14, 13-15	15.6 ± 0.55 16, 15-16	14.6 ± 0.81 15, 13-16	15.7 ± 0.50 16, 15-16 (4)	15.9 ± 1.08 16, 14-18	15.5 ± 0.71 n/a, 15-16
supradigital lamellae (4th finger)	13.0 ± 0.82 13, 12-14	12.2 ± 0.45 12, 12-13	12.9 ± 0.70 13, 12-14	13.0 ± 0.00 13, 13 (4)	13.0 ± 0.60 13, 12-14	13.0 ± 0.00 13, 13
subdigital lamellae (4th toe)	17.7 ± 0.50 18, 17-18	19.0 ± 1.87 19, 16-21	18.7 ± 0.79 18, 18-20	19.7 ± 0.58 20, 19-20 (3)	21.1 ± 1.00 21, 20-23	21.0 ± 1.41 n/a, 20-22
supradigital lamellae (4th toe)	16.0 ± 0.00 16, 16	15.6 ± 2.07 16, 12-17	16.2 ± 0.75 16, 15-17	16.7 ± 0.58 17, 16-17 (3)	16.7 ± 0.75 17, 15-18	16.5 ± 0.71 n/a, 16-17
palmars	8.7 ± 1.26 9, 7-10	12.0 ± 1.58 n/a, 10-14	10.4 ± 0.93 10, 9-12	10.2 ± 0.96 11, 9-11	11.3 ± 0.78 12, 10-12	8.5 ± 0.71 n/a, 8-9
plantars	10.2 ± 1.71 n/a, 8-12	13.8 ± 1.92 13, 12-17	12.3 ± 1.12 13, 10-14	11.0 ± 1.00 n/a, 10-12 (3)	12.5 ± 0.67 12, 12-14	10.0 ± 0.00 10, 10
snout-vent (mm)	41.1 ± 2.96 37.0-43.8	39.8 ± 2.31 38.0-43.7	36.5 ± 2.24 33.0-39.9	38.8 ± 1.18 37.4-39.7	39.0 ± 3.80 32.4-43.5	39.9 ± 3.24 37.6-42.2
body (%svl)	54.0 ± 0.25 53.6-54.2	54.7 ± 4.13 49.7-59.6	51.5 ± 2.20 48.6-56.5	49.6 ± 2.49 47.7-52.4	52.1 ± 2.15 49.2-55.6	50.3 ± 0.86 49.7-50.9
tail (%svl)	131.4 ± 0.00 131.4 (1)	-	157.6 ± 6.76 152.8-162.4 (2)	146.9 ± 0.00 146.9 (1)	127.8 ± 3.48 124.6-129.5 (2)	143.5 ± 0.00 143.5 (1)
forelimb (%svl)	33.7 ± 3.28 31.0-37.7	30.1 ± 2.35 27.7-33.0	35.7 ± 1.48 32.0-37.7	35.4 ± 0.92 34.4-36.1	34.1 ± 1.29 31.1-36.0	35.2 ± 1.03 34.5-36.0
hindlimb (%svl)	42.8 ± 3.54 40.1-48.0	39.0 ± 1.56 37.0-40.8	44.4 ± 2.50 39.8-47.3	41.9 ± 2.72 39.3-44.7	43.2 ± 1.84 40.4-46.7	47.0 ± 1.14 46.2-47.8
forebody (%svl)	39.4 ± 1.13 38.3-40.6	39.2 ± 1.37 37.7-41.3	40.8 ± 1.68 37.6-43.1	42.7 ± 1.55 41.5-44.5	40.5 ± 2.52 37.2-44.5	41.0 ± 1.80 39.7-42.2
head length (%svl)	19.7 ± 0.60 19.0-20.5	19.0 ± 0.96 18.2-20.1	20.5 ± 0.60 19.3-21.2	21.0 ± 0.83 20.1-21.8	20.2 ± 1.12 18.8-21.7 (11)	20.5 ± 0.55 20.2-20.9
head depth (%hl)	42.6 ± 2.26 39.6-44.9	42.5 ± 4.32 36.9-46.8	46.6 ± 2.93 43.6-50.9	44.1 ± 6.23 38.5-50.8	43.3 ± 4.24 37.9-54.1 (11)	48.7 ± 2.39 47.0-50.4
head width (%hl)	59.8 ± 2.50 57.8-62.9	60.6 ± 3.38 58.0-66.4	61.1 ± 2.54 57.1-66.5	58.4 ± 1.44 57.2-60.0	57.8 ± 2.68 53.9-62.6 (11)	63.7 ± 0.94 63.1-64.4
snout (%hl)	45.3 ± 1.72 43.5-47.3	43.6 ± 1.85 40.6-45.2	44.9 ± 2.11 40.9-48.0	47.3 ± 1.99 45.7-49.5	45.4 ± 1.59 42.8-47.6 (11)	43.0 ± 0.44 42.7-43.3
paravertebral scale (%svl)	4.5 ± 0.36 4.2-5.0	4.5 ± 0.66 3.7-5.1 (4)	3.6 ± 0.16 3.4-3.8 (5)	4.0 ± 0.35 3.6-4.3	4.1 ± 0.23 3.9-4.5 (5)	3.6 ± 0.15 3.5-3.7
dorsolateral scale (%vs)	80.6 ± 4.88 73.9-85.6	80.7 ± 8.32 70.6-87.9 (4)	80.3 ± 5.78 73.3-87.3 (5)	85.0 ± 9.94 77.4-96.3	78.0 ± 6.06 73.3-88.5 (5)	87.9 ± 1.14 87.1-88.7

(D). Summary of morphometric and meristic characters for *Cryptoblepharus* taxa from the Indo-Pacific region. Sample sizes are in parenthesis.

Character	*C. baliensis baliensis* (10)	*C. baliensis sumbawanus* (10)	*C. burdeni* (5)	*C. cursor cursor* (1)	*C. cursor larsonae* (4)	*C. egeriae* (10)
midbody scale rows	26.0 ± 1.33 26, 24-28	25.9 ± 1.20 26, 24-28	30.8 ± 1.10 30, 30-32	24	25.7 ± 0.50 26, 25-26	27.3 ± 1.06 28, 26-29
paravertebrals	49.4 ± 2.55 48, 46-53	48.8 ± 3.08 50, 45-55	53.4 ± 2.88 51, 51-58	50	52.5 ± 3.51 n/a, 49-56	59.4 ± 1.43 61, 57-61
nuchals	2.1 ± 0.32 2, 2-3	3.1 ± 1.37 2, 2-6	2.2 ± 0.50 2, 2-3 (4)	4	3.2 ± 0.96 4, 2-4	3.4 ± 1.71 2, 2-7
supralabials	7.0 ± 0.00 7, 7	7.3 ± 0.41 7, 7-8	7.0 ± 0.00 7, 7	7	7.0 ± 0.00 7, 7	8.0 ± 0.00 8, 8
infralabials	6.1 ± 0.39 6, 5-7	6.0 ± 0.16 6, 6-7	6.1 ± 0.22 6, 6-7	5	6.0 ± 0.00 6, 6	6.7 ± 0.42 7, 6-7
supraciliaries	6.0 ± 0.47 6, 5-7	6.0 ± 0.00 6, 6	5.1 ± 0.22 5, 5-6	5	5.0 ± 0.00 5, 5	5.9 ± 0.16 6, 5-6
ciliaries	3.3 ± 0.47 3, 3-4	3.0 ± 0.16 3, 3-4	3.0 ± 0.00 3, 3	3	3 ± 0.00 3, 3	3.8 ± 0.85 3, 3-6
subdigital lamellae (4th finger)	17.1 ± 1.10 17, 16-19	17.4 ± 0.88 17, 16-19 (9)	15.8 ± 1.30 15, 15-18	15	14.8 ± 0.29 15, 14-15 (3)	19.0 ± 0.88 18, 18-21
supradigital lamellae (4th finger)	12.5 ± 0.71 13, 11-13	13.0 ± 0.50 13, 12-14 (9)	12.8 ± 0.84 13, 12-14	11	11.3 ± 0.58 11, 11-12 (3)	14.7 ± 0.63 15, 14-16
subdigital lamellae (4th toe)	21.8 ± 1.48 22, 19-24	21.4 ± 0.73 22, 20-22 (9)	18.8 ± 1.79 17, 17-21	18	18.9 ± 0.63 19, 18-19	22.7 ± 0.89 23, 21-24
supradigital lamellae (4th toe)	16.5 ± 0.71 16, 16-18	16.1 ± 1.27 17, 14-18 (9)	15.6 ± 0.89 15, 15-17	14	14.6 ± 0.48 15, 14-15	18.5 ± 1.32 18, 17-22
palmars	10.9 ± 0.88 11, 9-12	10.0 ± 1.12 10, 8-12 (9)	8.4 ± 1.14 8, 7-10	11	11.0 ± 0.82 11, 10-12	10.0 ± 1.03 9, 9-12
plantars	11.2 ± 0.92 11, 10-13	11.0 ± 0.71 11, 10-12 (9)	9.8 ± 0.84 9, 9-11	12	13.6 ± 1.80 n/a, 11-15	10.4 ± 0.81 10, 9-12
snout-vent (mm)	38.6 ± 1.77 35.4-41.7	38.5 ± 1.29 36.4-41.1	43.9 ± 1.13 42.9-45.6	36.9	36.8 ± 3.41 31.9-39.5	45.7 ± 1.63 43.2-47.7
body (%svl)	49.1 ± 1.92 46.1-52.4	50.4 ± 2.03 46.4-52.9	53.2 ± 1.01 52.3-54.8	50.9	51.9 ± 4.44 47.8-58.2	51.4 ± 1.94 48.4-54.1
tail (%svl)	139.7 (1)	136.4 ± 1.53 135.3-137.4 (2)	134.9 ± 2.89 132.9-136.9 (2)	159.0	155.0 (1)	161.7 ± 4.89 156.0-167.8 (4)
forelimb (%svl)	35.5 ± 2.29 31.0-39.5	33.0 ± 2.17 28.1-35.5	34.0 ± 0.86 33.1-35.1	35.0	34.8 ± 1.65 32.8-36.2	35.6 ± 1.46 33.0-37.9
hindlimb (%svl)	44.2 ± 2.59 38.7-47.4	41.3 ± 1.88 37.4-43.2	44.4 ± 0.98 43.1-45.5	44.9	44.2 ± 1.68 42.7-45.8	43.0 ± 2.52 34.0-48.1
forebody (%svl)	43.0 ± 2.25 38.4-45.4	43.2 ± 1.31 40.3-44.7	41.4 ± 2.10 39.2-44.3	41.8	38.1 ± 2.08 35.8-39.9	42.8 ± 1.97 40.5-46.3
head length (%svl)	21.8 ± 1.12 19.1-22.9	21.9 ± 0.96 20.1-23.3	21.3 ± 0.60 20.6-22.0	20.8	20.2 ± 0.26 20.0-20.5	21.5 ± 0.81 19.8-22.6
head depth (%hl)	47.2 ± 2.97 43.1-51.9	47.3 ± 1.98 44.9-51.7	37.4 ± 2.08 35.4-40.6	55.7	49.1 ± 2.04 47.3-51.9	43.9 ± 3.75 37.2-49.6
head width (%hl)	60.6 ± 4.06 52.3-66.0	60.6 ± 2.07 57.4-63.1	57.6 ± 2.16 55.2-59.9	59.7	65.7 ± 3.01 62.2-68.2	57.6 ± 2.53 54.0-63.0
snout (%hl)	44.7 ± 1.37 42.7-47.3	45.8 ± 1.62 42.5-47.6	44.5 ± 0.79 43.7-45.6	43.1	44.3 ± 2.82 40.5-47.1	43.8 ± 1.83 41.3-46.5
paravertebral scale (%svl)	4.5 ± 0.34 4.0-5.1 (7)	4.5 ± 0.24 4.3-4.9 (6)	3.2 ± 0.20 3.0-3.4 (3)	4.0	4.8 ± 0.30 4.5-5.0 (3)	4.1 ± 0.16 3.9-4.3 (4)
dorsolateral scale (%vs)	73.2 ± 5.78 63.0-80.7 (7)	78.7 ± 4.17 73.8-86.3 (6)	96.1 ± 3.92 91.7-99.3 (3)	89.3	83.7 ± 0.42 83.2-84.0 (3)	87.0 ± 5.00 80.0-91.4 (4)

Character	*C. eximius* (8)	*C. furvus* (16)	*C. intermedius* (2)	*C. keiensis* (7)	*C. leschenault* (15)	*C. litoralis vicinus* (6)
midbody scale rows	25.0 ± 1.07 26, 24-26	26.0 ± 0.00 26, 26	25.5 ± 0.71 n/a, 25-26	22.3 ± 0.76 22, 22-24	25.6 ± 1.12 26, 24-28	26.3 ± 0.82 26, 26-28
paravertebrals	53.6 ± 1.60 54, 50-55	57.7 ± 2.68 60, 53-62	46.0 ± 2.83 n/a, 44-48	49.9 ± 1.07 50, 48-51	49.2 ± 2.86 50, 44-54	50.8 ± 3.06 n/a, 47-55
nuchals	2.9 ± 1.46 2, 2-6	3.9 ± 1.63 4, 2-8	2.0 ± 0.00 2, 2	3.9 ± 0.38 4, 3-4	2.3 ± 1.03 2, 2-6	2.0 ± 0.00 2, 2
supralabials	6.9 ± 0.35 7, 6-7	7.1 ± 0.31 7, 6-8	7.0 ± 0.00 7, 7	7.0 ± 0.00 7, 7	7.0 ± 0.00 7, 7	7.3 ± 0.41 7, 7-8
infralabials	6.9 ± 0.64 7, 6-8	6.1 ± 0.27 6, 6-7	7.0 ± 0.00 7, 7	6.0 ± 0.00 6, 6	6.2 ± 0.36 6, 6-7	6.0 ± 0.00 6, 6
supraciliaries	4.9 ± 0.18 5, 4-5	5.1 ± 0.27 5, 5-6	6.0 ± 0.00 6, 6	5.9 ± 0.19 6, 5-6	6.1 ± 0.34 6, 5-7	5.0 ± 0.00 5, 5
ciliaries	3.0 ± 0.00 3, 3	3.1 ± 0.29 3, 3-4	3.0 ± 0.00 3, 3	3.0 ± 0.00 3, 3	3.0 ± 0.00 3, 3	3.1 ± 0.66 3, 2-4
subdigital lamellae (4th finger)	17.4 ± 1.81 19, 15-19 (7)	18.8 ± 1.28 19, 17-22	19.5 ± 0.71 n/a, 19-20	18.0 ± 1.10 18, 16-19 (6)	17.4 ± 1.39 16, 15-19	17.3 ± 1.21 16, 16-19
supradigital lamellae (4th finger)	12.7 ± 0.95 13, 11-14 (7)	13.2 ± 0.77 13, 12-15	13.5 ± 0.71 n/a, 13-14	12.3 ± 0.52 12, 12-13 (6)	12.9 ± 0.74 13, 11-14	13.5 ± 1.22 13, 13-16
subdigital lamellae (4th toe)	20.9 ± 1.57 22, 19-23 (7)	22.5 ± 1.55 23, 20-25 (15)	23.0 ± 0.00 23, 23	23.0 ± 1.15 24, 21-24	22.0 ± 1.63 22, 18-25	22.2 ± 1.33 22, 20-24
supradigital lamellae (4th toe)	16.3 ± 1.60 17, 14-18 (7)	17.0 ± 1.20 16, 15-19 (15)	18.5 ± 0.71 n/a, 18-19	15.6 ± 1.13 15, 14-17	16.1 ± 1.61 16, 13-19	16.3 ± 1.03 16, 15-18
palmars	11.2 ± 1.16 11, 10-13	12.3 ± 1.30 12, 10-15	9.5 ± 0.71 n/a, 9-10	9.6 ± 0.53 10, 9-10	9.5 ± 0.83 10, 8-11	12.0 ± 1.26 11, 11-14
plantars	13.1 ± 1.64 13, 11-16	13.4 ± 1.50 15, 10-15	10.5 ± 0.71 n/a, 10-11	9.3 ± 0.76 9, 8-10	10.8 ± 1.18 11, 9-13	15.5 ± 0.55 16, 15-16
snout-vent (mm)	34.9 ± 1.20 33.2-36.4	42.4 ± 2.49 37.8-47.0	42.4 ± 0.39 42.1-42.7	38.4 ± 1.08 37.1-39.5	38.9 ± 3.20 33.3-43.9	41.3 ± 3.15 37.0-45.7
body (%svl)	51.3 ± 3.01 47.9-58.2	53.6 ± 2.78 49.1-58.0	50.9 ± 5.10 47.3-54.5	53.0 ± 0.87 51.3-53.7	50.2 ± 2.14 45.0-53.1	54.3 ± 2.33 51.2-57.1
tail (%svl)	141.7 (1)	143.5 (1)	-	-	154.0 ± 3.04 151.8-156.1 (2)	-
forelimb (%svl)	35.8 ± 1.99 32.4-39.3	34.2 ± 1.90 31.7-37.9	34.8 ± 0.30 34.6-35.0	33.5 ± 2.43 30.0-37.1	33.1 ± 1.79 29.9-36.0	35.3 ± 3.21 30.3-40.3
hindlimb (%svl)	45.1 ± 2.92 40.6-51.3	42.4 ± 2.93 37.5-48.5	42.5 ± 0.81 41.9-43.1	41.8 ± 2.23 38.4-44.7	41.0 ± 2.88 34.8-44.6	45.2 ± 4.08 39.9-51.0
forebody (%svl)	42.8 ± 0.95 41.0-43.8	40.6 ± 1.78 37.4-44.0	42.7 ± 1.39 41.7-43.7	41.5 ± 1.00 40.0-42.8	42.1 ± 1.95 39.7-45.0	39.3 ± 1.63 37.9-42.5
head length (%svl)	21.5 ± 0.40 20.8-22.0	20.2 ± 0.93 18.8-21.5	20.1 ± 0.60 19.7-20.5	20.5 ± 1.03 19.1-21.8	21.0 ± 1.24 18.9-23.2	20.5 ± 1.02 19.3-22.0
head depth (%hl)	45.2 ± 2.80 39.1-48.0	42.9 ± 2.46 38.1-48.0	47.0 ± 3.57 44.5-49.5	43.3 ± 2.35 40.2-47.6	44.0 ± 5.61 33.7-52.4	47.1 ± 4.26 42.8-51.3
head width (%hl)	62.2 ± 2.32 56.3-66.7	56.7 ± 1.53 53.8-58.5	64.3 ± 3.17 62.0-66.5	61.3 ± 5.31 53.1-70.6	61.4 ± 2.61 58.2-66.5	62.6 ± 2.89 58.2-66.1
snout (%hl)	45.8 ± 2.17 43.2-48.8	45.5 ± 1.71 42.7-49.1	47.1 ± 0.24 47.0-47.3	45.5 ± 1.56 43.1-47.1	45.6 ± 1.49 42.2-48.3	45.8 ± 1.73 44.1-48.6
paravertebral scale (%svl)	3.6 ± 0.21 3.3-3.8 (6)	4.2 ± 0.33 3.7-4.7	4.5 ± 0.28 4.3-4.7	3.6 ± 0.09 3.5-3.7 (6)	4.0 ± 0.69 3.3-5.0 (10)	-
dorsolateral scale (%vs)	82.7 ± 9.60 67.3-95.2 (6)	79.3 ± 6.23 72.4-93.9	95.5 ± 9.07 78.2-104.0 (6)	86.3 ± 8.16 72.8-97.2 (6)	84.1 ± 7.18 73.3-96.5 (10)	-

Character	*C. nigropunctatus* (2)	*C. novaeguineae* (6)	*C. novocaledonicus* (9)	*C. novohebridicus* (4)	*C. poecilopleurus paschalis* (8)	*C. poecilopleurus poecilopleurus* (16)
midbody scale rows	24.0 ± 0.00 24, 24	22.0 ± 0.00 22, 22	24.7 ± 1.00 24, 24-26	23.5 ± 1.00 24, 22-24	28.2 ± 1.36 28, 27-30	28.3 ± 1.01 28, 26-30
paravertebrals	57.0 ± 1.41 n/a, 56-58	47.0 ± 2.75 47, 44-53	54.6 ± 3.61 53, 48-59	51.5 ± 1.29 n/a, 50-53	57.9 ± 1.38 57, 56-60	54.4 ± 2.96 54, 49-59
nuchals	2.0 ± 0.00 2, 2	2.0 ± 0.00 2, 2	3.1 ± 1.54 2, 2-6	6.2 ± 1.26 6, 5-8	2.9 ± 0.83 2, 2-4	2.9 ± 1.02 2, 2-5
supralabials	7.0 ± 0.00 7, 7	7.0 ± 0.00 7, 7	7.0 ± 0.00 7, 7	6.9 ± 0.25 7, 6-7	7.6 ± 0.50 8, 7-8	7.2 ± 0.36 7, 7-8
infralabials	6.2 ± 0.35 n/a, 6-7	6.4 ± 0.51 6, 6-7	6.8 ± 0.45 7, 6-7 (5)	6.7 ± 0.50 7, 6-7	6.5 ± 0.53 6, 6-7	6.2 ± 0.44 6, 5-7
supraciliaries	5.0 ± 0.00 5, 5	5.7 ± 0.47 6, 5-7	4.9 ± 0.17 5, 4-5	4.7 ± 0.50 5, 4-5	5.5 ± 0.46 6, 5-6	5.1 ± 0.17 5, 5-6
ciliaries	3.0 ± 0.00 3, 3	3.0 ± 0.13 3, 3-4	3.0 ± 0.00 3, 3	3.0 ± 0.00 3, 3	3.0 ± 0.00 3, 3	3.0 ± 0.37 3, 2-4
subdigital lamellae (4th finger)	18.5 ± 0.71 n/a, 18-19	17.4 ± 1.22 18, 15-19	17.7 ± 0.87 18, 16-19	15.7 ± 0.50 16, 15-16	18.1 ± 0.64 18, 17-19	16.9 ± 1.29 17, 15-20
supradigital lamellae (4th finger)	13.0 ± 0.00 13, 13	13.0 ± 1.21 12, 11-15	12.9 ± 0.78 13, 12-14	13.0 ± 0.82 13, 12-14	13.1 ± 0.35 13, 13-14	13.2 ± 0.75 13, 12-15
subdigital lamellae (4th toe)	24.0 ± 1.41 n/a, 23-25	22.0 ± 1.69 23, 19-24	21.1 ± 1.45 21, 19-24	20.2 ± 0.96 21, 19-21	23.9 ± 1.25 24, 22-26	21.9 ± 1.65 22, 19-25
supradigital lamellae (4th toe)	16.0 ± 1.41 n/a, 15-17	15.7 ± 0.61 16, 15-17	16.0 ± 1.12 15, 15-18	16.2 ± 0.50 16, 16-17	16.4 ± 0.74 17, 15-17	16.2 ± 0.98 16, 14-18
palmars	14.5 ± 0.71 n/a, 14-15	10.4 ± 1.45 10, 8-13	11.8 ± 1.09 12, 10-13	9.5 ± 1.00 10, 8-10	13.5 ± 0.93 13, 12-15	11.3 ± 0.95 12, 10-13
plantars	16.5 ± 0.71 n/a, 16-17	10.9 ± 1.23 11, 8-12	12.9 ± 1.17 13, 11-15	12.2 ± 1.50 11, 11-14	14.9 ± 1.13 16, 13-16	12.7 ± 1.06 13, 11-15
snout-vent (mm)	47.3 ± 5.35 43.5-51.1	35.6 ± 2.17 31.8-39.2	37.6 ± 2.08 34.1-41.2	35.3 ± 1.49 33.5-37.0	43.1 ± 5.42 35.6-50.6	44.1 ± 3.50 36.0-49.3
body (%svl)	54.9 ± 2.56 53.1-56.7	51.8 ± 3.11 45.4-56.1	50.8 ± 3.68 47.2-56.1 (5)	52.0 ± 3.08 47.6-54.7	55.2 ± 3.68 48.7-60.2	53.9 ± 2.24 49.2-57.6
tail (%svl)	160.9 (1)	129.2 ± 3.71 124.3-133.1 (4)	145.6 (1)	133.5 ± 9.95 126.5-140.6 (2)	143.9 ± 5.61 137.5-148.1 (3)	144.0 (1)
forelimb (%svl)	33.1 ± 3.03 31.0-35.3	35.6 ± 2.25 31.9-40.0	35.7 ± 2.21 32.8-38.7 (5)	33.2 ± 1.41 31.2-34.3	32.9 ± 1.65 31.2-35.9	33.1 ± 2.00 29.8-36.5
hindlimb (%svl)	41.6 ± 0.27 41.4-41.8	42.6 ± 2.21 37.7-45.2	45.3 ± 1.55 42.5-47.3	41.3 ± 1.87 39.4-43.1	41.1 ± 2.50 38.1-44.9	40.6 ± 1.99 37.5-45.4
forebody (%svl)	41.2 ± 3.36 38.8-43.6	41.3 ± 1.46 39.0-43.9	42.7 ± 1.17 40.9-43.7 (5)	42.2 ± 0.90 41.4-43.5	40.9 ± 2.41 36.9-45.2	40.5 ± 1.91 36.0-43.6
head length (%svl)	20.1 ± 1.12 19.3-20.9	20.8 ± 0.95 18.8-22.6	21.2 ± 0.64 20.2-22.3	21.0 ± 0.53 20.3-21.5	20.2 ± 1.28 18.6-22.5	19.9 ± 0.80 17.6-20.9
head depth (%hl)	50.5 ± 4.93 47.0-54.0	41.8 ± 3.29 35.8-48.4	46.7 ± 2.84 43.1-51.6	48.0 ± 0.96 46.8-49.1	46.6 ± 4.05 40.0-52.2	46.9 ± 2.33 43.2-52.5
head width (%hl)	65.7 ± 2.57 63.8-67.5	60.8 ± 2.42 54.7-64.2	62.1 ± 2.41 58.4-65.1	60.4 ± 0.90 59.1-61.0	61.9 ± 2.68 58.0-66.3	62.9 ± 2.14 59.3-65.8
snout (%hl)	42.6 ± 1.92 41.2-44.0	45.0 ± 1.58 42.4-48.0	45.7 ± 1.40 43.9-47.8 (5)	47.5 ± 2.83 43.7-50.3	45.6 ± 1.80 42.7-48.3	44.7 ± 1.98 41.7-48.3
paravertebral scale (%svl)	4.6 ± 0.55 4.2-5.0	4.7 ± 0.57 3.8-5.7 (13)	3.8 ± 0.22 3.5-4.1 (6)	4.4 ± 0.52 4.0-5.1	4.0 ± 0.38 3.4-4.6	3.3 ± 0.48 3.0-4.1 (5)
dorsolateral scale (%vs)	81.6 ± 9.82 68.0-96.5 (6)	78.0 ± 8.91 68.0-99.4 (13)	86.7 ± 3.83 81.8-92.2 (6)	76.5 ± 7.66 64.1-85.5 (6)	83.0 ± 3.32 77.9-87.3	87.2 ± 6.47 78.2-94.1 (5)

Character	*C. renschi* (6)	*C. richardsi* (11)	*C. rutilus* (1)	*C. schlegelianus* (1)	*C. xenikos* (5)	*C. yulensis* (14)
midbody scale rows	24.3 ± 1.51 24, 22-26	25.5 ± 1.21 26, 24-28	20	26	22.0 ± 0.00 22, 22	23.9 ± 0.95 24, 22-26
paravertebrals	49.5 ± 3.94 52, 44-53	54.5 ± 1.86 53, 52-58	47	46	49.8 ± 2.49 50, 46-53	51.0 ± 2.25 53, 47-55
nuchals	2.0 ± 0.00 2, 2	4.2 ± 1.47 4, 2-6	4	4	3.0 ± 1.00 2, 2-4	2.0 ± 0.00 2, 2
supralabials	7.0 ± 0.00 7, 7	7.1 ± 0.30 7, 7-8	7	7	7.1 ± 0.22 7, 7-8	7.0 ± 0.00 7, 7
infralabials	6.0 ± 0.00 6, 6	6.0 ± 0.00 6, 6	6	7	6.0 ± 0.00 6, 6	6.6 ± 0.51 7, 6-7
supraciliaries	5.7 ± 0.52 6, 5-6	5.0 ± 0.15 5, 4-5	5	5	5.0 ± 0.00 5, 5	5.8 ± 0.54 6, 4-6
ciliaries	3.2 ± 0.42 3, 3-4	3.2 ± 0.40 3, 3-4	3	3	3.0 ± 0.00 3, 3	3.0 ± 0.20 3, 2-4
subdigital lamellae (4th finger)	16.5 ± 1.22 17, 14-17	17.5 ± 1.44 17, 15-20	18	13	15.8 ± 1.10 16, 14-17	15.6 ± 1.28 15, 14-18
supradigital lamellae (4th finger)	12.2 ± 0.41 12, 12-13	13.3 ± 0.47 13, 13-14	14	11	12.2 ± 0.45 12, 12-13	12.5 ± 0.52 13, 12-13
subdigital lamellae (4th toe)	20.7 ± 1.97 20, 18-24	21.8 ± 1.47 21, 20-25	23	16	19.2 ± 1.48 19, 17-21	20.1 ± 1.10 20, 19-23
supradigital lamellae (4th toe)	15.2 ± 0.75 15, 14-16	16.4 ± 0.92 16, 15-18	15	13	14.6 ± 0.55 15, 14-15	15.6 ± 0.63 16, 15-17
palmars	9.5 ± 0.84 9, 9-11	12.0 ± 1.26 12, 10-14	11	8	9.0 ± 0.71 9, 8-10	9.2 ± 0.70 9, 8-10
plantars	10.3 ± 1.03 10, 9-12	12.7 ± 1.49 14, 10-15	10	11	9.0 ± 0.71 9, 8-10	9.9 ± 1.00 9, 9-12
snout-vent (mm)	35.8 ± 2.96 30.6-39.5	38.6 ± 3.58 32.0-43.1	35.4	40.3	35.3 ± 2.59 32.2-38.0	37.2 ± 3.44 29.9-41.9
body (%svl)	51.3 ± 3.21 48.1-56.7	49.0 ± 2.91 42.2-53.0	54.2	50.2	50.6 ± 1.64 48.4-52.8	50.6 ± 2.32 47.5-54.5
tail (%svl)	153.5 (1)	166.5 ± 11.70 158.2-174.7 (2)	129.1	-	-	141.8 ± 5.63 135.5-145.2 (3)
forelimb (%svl)	33.0 ± 2.26 30.5-35.7	34.4 ± 1.75 32.2-38.0	36.5	28.6	30.9 ± 2.72 27.0-34.4	32.9 ± 1.64 30.0-35.0
hindlimb (%svl)	42.2 ± 2.80 38.8-45.6	46.1 ± 1.69 43.5-49.1	44.1	38.8	39.8 ± 2.21 36.3-42.4	39.5 ± 1.79 35.1-42.4
forebody (%svl)	41.4 ± 2.19 38.6-44.3	42.0 ± 2.47 39.8-47.6	41.4	36.5	41.9 ± 1.08 40.7-43.7	42.1 ± 2.24 38.7-45.9
head length (%svl)	21.0 ± 0.84 20.2-22.3	21.2 ± 0.88 20.2-23.1	20.3	19.4	20.2 ± 0.79 19.3-21.2	21.3 ± 0.88 19.6-22.2
head depth (%hl)	46.9 ± 3.58 41.0-50.1	40.2 ± 2.42 36.3-44.0	46.7	39.5	40.1 ± 2.89 37.3-44.7	42.4 ± 3.49 37.1-48.6
head width (%hl)	62.3 ± 2.64 58.4-65.4	57.8 ± 2.31 54.5-61.9	58.6	59.8	57.7 ± 2.62 54.5-60.5	61.1 ± 2.31 56.2-66.2
snout (%hl)	44.9 ± 1.00 44.0-46.8	46.6 ± 1.71 43.7-48.8	44.0	43.4	50.3 ± 1.22 48.6-51.7	46.0 ± 1.31 43.6-48.4
paravertebral scale (%svl)	5.3 ± 0.55 4.8-6.4	4.4 ± 0.30 3.9-5.0	4.6	3.5	4.5 ± 0.32 4.0-4.8	-
dorsolateral scale (%vs)	74.8 ± 5.68 66.7-84.0	77.0 ± 10.04 61.3-91.5	73.4	81.1	79.5 ± 9.03 69.6-90.8	-

APPENDIX 4

Non-type material examined:

Cryptoblepharus australis (104 specimens). NEW SOUTH WALES: ANWC R911, 15 km west of Booligal, 33°54'S 144°37'E; ANWC R1651, Macquarie Marshes, 30°47'S 147°33'E, 10 Aug 1977; ANWC R2767, Macquarie River, Macquarie Marshes, 30°47'S 147°30'E, 18 Jul 1979; ANWC R2837, Sandy Camp Station, Macquarie Marshes, 30°52'S 147°45'E, 18 Sep 1979; ANWC R3198, Clear Lake, Walgett, 29°48'S 147°18'E, 07 May 1981. NTM R529-530, Alice Springs Hills, 23°42'S 133°51'E, 02 Aug 1974; NTM R765, R767, Alice Springs, 23°42'S 133°52'E, 28-29 May 1975; BMNH 1910.52822, Hermannsburg, 23°57'S 132°46'E; BMNH 1975.1065, Kintore Range, summit of Mount Leisler, 23°21'S 129°23'E, Mar 1967; BMNH 1975.1066, The Olgas, 25°18'S 130°44'E, 16 Mar 1967; NTM R7070, Aileron, 22°39'S 133°21'E, 1979; NTM R8469, Frewena, 19°26'S 135°24'E, 27 Feb 1980; NTM R11065, Reedy Rockhole, George Gill Ranges, 24°18'S 131°36'E, 25 Jan 1983; NTM R12711, Alice Springs, 23°42'S 133°52'E, 13 Sep 1984; NTM R12717, Finke River, near Glen Helen, 23°42'S 132°40'E, 16 Sep 1984; NTM R13365, Harts Range Store, Chitabine Lodge, 22°59'S 134°56'E, 09 Sep 1985; NTM R14309, Rockhole Gorge, Loves Creek Station, 23°32'S 134°52'E, 21 Sep 1989; NTM R14384, Hale River, Loves Creek Station, 23°33'S 134°58'E, 19 Oct 1989; NTM R14485, Arapunya Station, Dulcie Range, 22°30'S 135°35'E, 27 Aug 1987; NTM R15257, Loves Creek Station, Hale River, 23°33'S 134°58'E, 19 Oct 1989; NTM R15395, Chewings Ranges, Giles Yard Spring, 23°39'S 132°59'E, 26 Feb 1990; NTM R15519, Owen Springs, Ryans Gap., 23°48'S 132°14'E, 22 Oct 1990; NTM R15553, Chalet Camp, Owen Springs Station, 23°44'S 132°55'E, 16 Oct 1990; NTM R15918, Trephina Gorge Nature Park, 23°32'S 134°24'E, 09 Oct 1991; NTM R15940, 1 km southeast of Boggyhole Bore, MacDonnell Ranges, 23°48'S 133°21'E, 22 Oct 1991; NTM R18212, Harts Range, 23°03'S 135°10'E, 24 Nov 1994; NTM R18244-245, Arltunga, old police station, 23°26'S 134°41'E, 28 Feb 1997, *ABTC* BH1-BH2; NTM R18248, R18250, Arltunga visitors centre, 23°27'S 134°41'E, 28 Feb 1997, *ABTC* BH5, BH7; NTM R18264, Trephina Gorge National Park, rangers residence, 23°32'S 134°22'E, 01 Mar 1997, *ABTC* BJ1; NTM R20686, Finke Gorge National Park, 24°04'S 132°45'E, 06 Sep 1992; NTM R21671, Alice Springs, 23°42'S 133°52'E, 17 Aug 1995, *ABTC* V19; NTM R21683, 21695-699, Alice Springs, 23°42'S 133°52'E, 12 Jun 1995; NTM R22422, Alice Springs, 23°42'S 133°52'E, 30 Mar 1996, *ABTC* Y85; NTM R22948-949, Alice Springs, 23°42'S 133°52'E, 28 Oct 1996, *ABTC* BC8-BC9; NTM R23347, Talipata Gorge, 23°23'S 131°24'E, 06 Mar 1996; NTM R23478, Barkly Homestead (Roadhouse), Barkly Highway, 19°43'S 135°49'E, 23 Jan 1998, *ABTC* CO8; NTM R25629-630, Tennant Creek, 19°39'S 134°11'E, 20 Dec 1999, *ABTC* DZ3-DZ4; NTM R25729-730, Barkly Homestead Roadhouse, Barkly Highway, 19°43'S 135°49'E, 11 May 2000, *ABTC* ED7-ED8; NTM R31836, Alice Springs, 23°42'S 133°53'E, 22 Aug 1963; SMF 58587-588, Todd River bed, Alice Springs, 23°42'S 133°52'E, 1-16 Mar 1957; SMF 58641-642, Ayers Rock, 25°21'S 131°02'E, 19 Mar 1957; SMF 58644-645, 58651, Alice Springs, 23°42'S 133°52'E, 09 Apr 1957. QUEENSLAND: NTM R23440, Roma, 26°34'S 148°47'E, 20 Jan 1998, *ABTC* CK7; NTM R23442-443, Augathella, 25°48'S 146°35'E, 20 Jan 1998, *ABTC* CK9, CL1; NTM R23447-449, R23452, Blackall, 24°26'S 145°28'E, 20 Jan 1998, *ABTC* CL4-CL6, CL9; NTM R23454-455, Barcaldine, 23°33'S 145°17'E, 20 Jan 1998, *ABTC* CM2-CM3; NTM R23458, R23460, R23462-464, Winton, 22°23'S 143°02'E, 21 Jan 1998, *ABTC* CM6, CM8, CN1-CN3; NTM R23465-467, Mckinlay, 21°16'S 141°17'E, 22 Jan 1998, *ABTC* CN4-CN6; NTM R23468-471, Mount Isa, 20°41'S 139°29'E, 22 Jan 1998, *ABTC* CN7-CN9, CO1; NTM R23472-474, R23476, Camooweal, caravan park, 19°55'S 138°07'E, 23 Jan 1998, *ABTC* CO2-CO4, CO6; NTM R25745-746, Georgina River, Camooweal, 19°52'S 138°06'E, 12 May 2000, *ABTC* EF1-EF2; QM J26307, J26400-404, 25 km southwest of Coongoola, 27°49'S 145°43, 23 Aug 1975; SAM R54567-568, Mitchell Highway, 8 Km north of NSW/Qld border, 28°57'S 145.33'E, 26 May 2000. SOUTH AUSTRALIA: NTM R6988, Kingston, 28°02'S 135.53'E; NTM R9247, Middleback Ranges, Eyre Peninsula, 33°11'S 137°06'E, 1900; NTM R22029-031, 11 km north of Copley, 30°25'S 138°24'E, 18 Dec 1995, *ABTC* Y10-Y12; NTM R22032-03, Leigh Creek, 30°29'S 138°24'E, 18 Dec 1995, *ABTC* Y13-Y14; NTM R22035, Breakfast Time Creek, 44 km south of Leigh Creek., 30°48'S 138°24'E, 18 Dec 1995, *ABTC* Y16; SAM R42849, Noonbah Station, 24°06'S 143°11'E, 15 Oct 1993. WESTERN AUSTRALIA: WAM R65821, Comet Vale, 29°57'S 121°07'E; WAM R65832, 3.5 km northeast of Comet Vale, 29°56'S 121°08'E; WAM R103862, Comet Vale, 29°56'S 121°07'E, *ABTC* R103862; WAM R126585, between Carbine Homestead and Rowles Lagoon, 30°27'S 120°41'E, *ABTC* R126585.

Cryptoblepharus buchananii (44 specimens). WESTERN AUSTRALIA: WAM R132631, Burrup Peninsula, 20°34'S 116°48'E, *ABTC* R132631; WAM R70734, King Bay, Burrup Peninsula, 20°38'S 116°45'E, 12 May 1980; WAM R70102, Dampier, 20°40'S 116°42'E, 19 May 1980; WAM R68380, Dampier, 20°40'S 116°42'E, 06 Feb 1980; WAM R34735, Millstream, 21°35'S 117°04'E, 25 Sep 1969; WAM R94625, Millstream, 21°35'S 117°04'E, 09 May 1986; WAM R117013, Nanjilgardy Pool, Turee Creek, 23°23'S 117°52'E, *ABTC* R117013; WAM R42294, Nyianihya Roadhouse, 19 km southeast of Jiggalong, 23°30'S 120°54'E, 18 Sep 1972; WAM R83755, Durba Gorge, 23°45'S 122°31'E, 18 July 1983; WAM R84097-098, Coondil Pool, Mt. Clere Station, 25°03'S 117°34'E, 02 May 1983; WAM R51923, Carnarvon Range, 25°17'S 120°42'E, 23 Nov 1975; ANWC R1699, Millibillillie Station, Wiluna, 26°36'S 120°21'E; WAM R123513, Zu3, 27°15'S 114°04'E, *ABTC* R123513; NTM R22067-069, Kalbarri, 27°42'S 114°09'E, 15 Jan 1996; WAM R113692, 15 km southeast of Port Gregory, 28°19'S 114°22'E, *ABTC* R113692; NTM R22064-066, Northampton, 28°21'S 114°37'E, 14 Jan 1996; WAM R85732, 39 km east of Laverton, 28°28'S 122°50'E, 24 Aug 1978; WAM R114610, Spalding Park, Geraldton, 28°46'S 114°37'E, *ABTC* R114610; SMF R58561, New Norcia, 30°58'S 116°12'E; WAM R26521, Zanthus, 31°02'S 123°34'E, Mar 1966; WAM R117369-370, 28 km southsoutheast of Woolgangie, 31°24'S 120°39'E, *ABTC* R117369-370; WAM R72554, Buningonia Spring, 31°25'S 123°33'E, 19 Aug 1980; WAM R126094, R126097, R127636, Neerabup National Park, 31°41'S 115°45'E, *ABTC* R126094, R126097, R127636; WAM R65409, 22 km north of Heartbreak Ridge, 31°51'S 122°24'E, 12 Nov 1978; SMF R58562, City Beach, Perth, 31°56'S 115°45'E; SMF R58643, Forrest Park, Darling Ranges, 31°56'S 115°52'E, 19 Jan 1957; NTM R21686-687, South Perth, 31°57'S 115°51'E, 01 Jul 1995; WAM R66141, 1.1 km southeast of Mcdermid Rock, 32°01'S 120°44'E, 12 Jul 1979; WAM R119234, Bungendore, Perth, 32°11'S 116°02'E, *ABTC* R119234; WAM R68030, 4 km southwest of Lake Cronin, 32°24'S 119°45'E, 29 Nov 1979; WAM R114714, 3 km north of Mandurah, 32°30'S 115°43'E, *ABTC* R114714; WAM

R103741, North Dandalup Proposed Dam, 32°31'S 116°02'E, *ABTC* R103741; NTM R22061-063, Donnybrook, 33°34'S 115°49'E, 08 Jan 1996, *ABTC* Y39-Y41.

Cryptoblepharus cygnatus (32 specimens, paratypes of nomen nudum *C. swansoni*). NORTHERN TERRITORY: NTM R3008-009, R3013-014, R3016-039, R3041-044, Smith Street, Darwin, 12°27'S 130°50'E, collected by D. Metcalfe, 01-02 Feb 1977.

Cryptoblepharus fuhni (12 specimens). QUEENSLAND: QM J20515-516, J20567-571 (paratypes), Melville Range, 14°16'S, 144°30'E, 30 Nov 1970; QM J37853-855, Cape Melville, 14°10'S, 144°30'E; QM J58845-846, Cape Melville, 14°11'S, 144°31'E, ABTC J58845-846; QM J58849, Cape Melville, 14°11'S, 144°31'E.

Cryptoblepharus litoralis horneri (13 specimens). NORTHERN TERRITORY: NTM R7761, Rimbija Island, Cape Wessel, 11°01'S 136°45'E, P. Horner and G. Gow, 16 Oct 1979; NTM R17063, Truant Island, 11°41'S 136°46'E, H. Larson, 19 Nov 1990, *ABTC* R53; NTM R17065-066, Murgenella, 11°22'S 132°57'E, P. Horner, 28 Aug 1987; NTM R18548, Bromby Islands, 11°50'S 136°40'E, R. Chatto, 12 Jul 1996; NTM R19039, Emu Island, Wessel Islands, 11°01'S 136°44'E, P. Horner and survey team, 23 Jul 1993, *ABTC* W26; NTM R19040, Jensen Island, Jensen Bay, Marchinbar Island, 11°09'S 136°42'E, P. Horner and survey team, 18 Jul 1993, *ABTC* W27; NTM R19128-129, Wessel Islands (island L), 11°33'S 136°20'E, P. Horner and survey team, 09 Aug 1993, *ABTC* X11-X12; NTM R22828-829, island 14, Bromby Islands, English Company Islands, 11°49'S 136°43'E, survey team, 06 Oct 1996; NTM R22832, island 10a, Bromby Islands, English Company Islands, 11°50'S 136°38'E, survey team, 06 Oct 1996.

Cryptoblepharus litoralis litoralis (32 specimens). QUEENSLAND: SMF 53230 (paratype), Etty Bay, Innisfail, 17°33'S 146°05'E, R. Mertens and H. Felten, 21 Apr 1957; SMF 53242 (paratype), Bramston Beach, 20 miles north of Innisfail, 17°20'S 146°01'E, R. Mertens and H. Felten, 01 May 1957; SMF 53244-246 (paratypes), Palm Beach, 15 miles north of Cairns, 16°51'S 145°55'E, R. Mertens and H. Felten, 18 May 1957; QM J11962, Palm Cove, 16 km north of Cairns, 16°45'S 145°40'E; QM J17520, Quarantine Bay, near Cooktown, 15°29'S 145°17'E, 21 Aug 1969; QM J17841, Quarantine Bay, ca.6.4 km south of Cooktown, 15°29'S 145°17'E, 06 Oct 1969; QM J25446, J25448-449, Flying Fish Point, 17°30'S 146°05'E, 23 Jan 1975; NTM R18865-867, R18884, Cooktown wharf, 15°28'S 145°15'E, P. and R. Horner, 22 Dec 1997, *ABTC* BX5-BX7, BZ6; NTM R18893-898, Flying Fish Point, 17°30'S 146°05'E, P. and R. Horner, 31 Dec 1997, *ABTC* BZ7-BZ9, CA1-CA3; NTM R18901-904, Flying Fish Point, 17°30'S 146°05'E, P. and R. Horner, 01 Jan 1998, *ABTC* CA6-CA9; NTM R18905-906, harbour area, Mourilyan, 17°36'S 146°07'E, P. and R. Horner, 01 Jan 1998, *ABTC* CB1-CB2; NTM R18929, Dingo Beach, 20°05'S 148°30'E, P. and R. Horner, 06 Jan 1998, *ABTC* CD7; NTM R18945-948, Airlie Beach, 20°16'S 148°43'E, P. and R. Horner, 07 Jan 1998, *ABTC* CE9, CF1-CF3.

Cryptoblepharus megastictus (8 specimens). WESTERN AUSTRALIA: AM R140117-120, 1 km south of Mcgowens Beach, Kalumburu, 14°09'S 126°38'E; NTM R22788-789, Kalumburu, 14°13'S 126°38'E. 06 Sep 1996, *ABTC* Z96-Z97; WAM R131656, Kalumburu, on road to Honeymoon Beach, 14°13'S 126°38'E, 18 Jun 1997; WAM R131668, Solea Falls, Drysdale National Park, 14°40'S 127°00'E, 22 Jun 1997.

Cryptoblepharus metallicus (119 specimens). NORTHERN TERRITORY: NTM R16127-128, Cadell River crossing, Arnhem Land, 12°15'S 134°26'E, 12 Jul 1989, *ABTC* K08-KO9; NTM R16353, Nathan River Station, 15°32'S 135°25'E, 23 Jun 1990, *ABTC* M23; NTM R16459, Bing Bong Station, 15°37'S 136°21'E, 16 Jul 1990, *ABTC* N67; NTM R18051, Alyawarre Desert Area, Poison Creek, 20°42'S 135°36'E, 29 Oct 1992; NTM R18054, Alyawarre Desert Area, 20°42'S 135°36'E, 28 Oct 1992; NTM R18653-655, Homestead, Bradshaw Station, 15°21'S 130°17'E, 26 Aug 1997, *ABTC* BP7-BP9; NTM R18662, Lobby Creek, Bradshaw Station, 15°20'S 130°06'E, 30 Sep 1997, *ABTC* BQ9; NTM R18798, R18802, Elsey National Park, 14°56'S 133°08'E, Dec 1996, *ABTC* BE7, BE6; NTM R18838, Hi-Way Inn Roadhouse, Daly Waters, 16°16'S 133°22'E, 13 Dec 1997, *ABTC* BU8; NTM R18840-842, Homestead, Woologorang Station, 17°14'S 137°57'E, 14 Dec 1997, *ABTC* BV1-BV3; NTM R19056, Guluwuru Island, 11°31'5'S 136°25'E, 29 Jul 1993, *ABTC* W47; NTM R19094, Jirgari Island, 11°48'S 136°08'E, Aug 1993, *ABTC* W75; NTM R19095, Jirgari Island, 11°48'S 136°08'E, Aug 1993, *ABTC* W76; NTM R19125, Raragala Island (North), 11°34'S 136°20'E, 08 Aug 1993, *ABTC* X10; NTM R21175, Jabiluka Project Area, 12°33'5'S 132°55'E, 06 Jun 1994, *ABTC* S20; NTM R21848, R21850, R21855-856, Wadamunga Lagoon, Roper River,, 14°49'S 134°57'E, 27 Oct 1995; NTM R21864, Long Billabong, Wulunurrayi Creek,, 15°18'S 135°21'E, 02 Nov 1995; NTM R21874, R21878, R21887, Sherwin Creek / Roper River junction, 14°40'S 134°22'E, 04-11 Jun 1995; NTM R22017, Bularriny, Napier Peninsula, 12°02'S 135°44'E, 24 Oct 1995, *ABTC* Y02; NTM R22096-097, Timber Creek, 15°39'S 130°29'E, 25 Jan 1996, *ABTC* Y65-Y66; NTM R22633, Long Billabong, Roper River, 15°18'S 135°20'E, 19 May 1996, *ABTC* Z41; NTM R22637, R22639, Wadamunga Lagoon, Roper River, 14°48'S 134°56'E, 21 May 1996, *ABTC* Z50, Z49; NTM R22727-728, Gayngaru Walk, Nhulunbuy, 12°10'S 136°47'E, 25 Aug 1996, *ABTC* AA4-AA5; NTM R22732, R22746, English Company Isles, Pobasso Island, 11°54'S 136°27'E, 27 Aug 1996, *ABTC* AA9, AC5; NTM R22759, R22777, English Company Isles, Astell Island, 11°52'S 136°25'E, 30 Aug 1996, *ABTC* AD9, AF9; NTM R22906, Spirit Hills, Keep River, 15°23'S 129°05'E, 08 Oct 1996, *ABTC* AY6; NTM R23479-480, Town Area, Elliot, 17°33'S 133°33'E, 23 Jan 1998, *ABTC* CO9, CP1; NTM R23483, Longreach Waterhole, Elliot, 17°37'S 133°28'E, 23 Jan 1998, *ABTC* CP4; NTM R23666-667, Limestone Gorge area, Gregory National Park, 16°03'S 130°23'E, 03 Apr 1998, *ABTC* CP5-CP6; NTM R23668, Timber Creek, 15°39'S 130°29'E, 03 Apr 1998, *ABTC* CP7; NTM R23770, R23797, Wickham River, Gregory National Park, 16°51'S 130°11'E, 03 Jun 1998, *ABTC* CT1, CV5; NTM R23919, R23926, Djapididjapin Creek, near Ramingining, Arafura Swamp, 12°22'S 134°55'E, 24 Jul 1998, *ABTC* DB7. DC5; NTM R24031-032, Mount Lambell, Nitmiluk National Park, 14°01'S 132°44'E, 05 Jul 1998, *ABTC* CZ2-CZ3; NTM R24770-771, North Angalarri Valley, Bradshaw Station, 14°58'S 130°50'E, 31 Aug 1999, *ABTC* DL7, DM2; NTM R24776, Mount Golla Golla, Bradshaw Station, 15°19'S 130°28'E, 02 Sep 1999, *ABTC* DM7; NTM R24785, R24790, R24796, Lobby Creek, Bradshaw Station, 15°22'S 130°06'E, 04-09 Jun 1999, *ABTC* DQ9, DS4, DU8; NTM R25734-736, Brunette Downs Racecourse, Barkly Tablelands, 18°36'S 136°05'E, 11 May 2000, *ABTC* EE3-EE5; NTM R25878, Borroloola, 16°05'S 136°19'E, 19 May 2000, *ABTC* ET6; NTM R25880, Carpentaria Highway, 35 km east of Cape Crawford, 16°32'S 135°60'E, 19 May 2000, *ABTC* ET8; NTM R3874, Jabiru, 12°40'S 132°53'E, 30 Jul 1977; NTM R4087-4089, 6.5 km northwest of Daly River (Elizabeth Downs Rd), 13°43'S 130°30'E, 20 Aug 1977; NTM R8570-571, Brunette Downs,, 18°38'S 135°57'E, 06 Mar 1980. QUEENSLAND: NTM R18843-845, Leichhardt Falls, Leichhardt River, 18°13'S 139°53'E, 15 Dec

1997, *ABTC* BV4-BV6; NTM R18848-849, Burke & Wills Roadhouse, Matilda Hwy, 19°14'S 140°21'E, 17 Dec 1997, *ABTC* BV9, BW1; NTM R18856, Mount Surprise, 18°09'S 144°19'E, 18 Dec 1997, *ABTC* BW8; NTM R18891, Hells Gate Roadhouse, 17°28'S 138°22'E, 14 Dec 1997; NTM R18908, Ayr, 19°35'S 147°24'E, 04 Jan 1998, *ABTC* CB4; NTM R18939, 5.4 km west of Dingo Beach, 20°08'S 148°30'E, 06 Jan 1998, *ABTC* CE8; NTM R18965, 10 km north of Townsville, 19°15'S 146°40'E, 04 Jan 1998; NTM R18975, Clairview, 22°07'S 149°32'E, 11 Jan 1998, *ABTC* CG8; NTM R21333-335, Musselbrook Reserve, Mining Camp, 18°35'S 138°07'E, 14 Apr 1995, *ABTC* U67, U89; NTM R23488, Doomadgee, 17°54'S 139°17'E, 15 Dec 1997; NTM R25782, Chillagoe Rd (11 km east of Karumba Rd), Normanton, 17°26'S 141°17'E, 15 May 2000, *ABTC* EJ2; NTM R25786, Walkers Creek (Karumba Road), Normanton, 17°28'S 141°11'E, 15 May 2000, *ABTC* EJ6; NTM R25825, Brannigan Creek, Normanton, 17°25'S 141°09'E, 16 May 2000, *ABTC* EN8; NTM R25830, Flinders River, Normanton, 17°53'S 140°47'E, 16 May 2000, *ABTC* EO4; NTM R25846, 10 km southeast of Hells Gate roadhouse, 17°32'S 138°24'E, 18 May 2000, *ABTC* EQ2; NTM R25865, Beames Brook, Burketown, 17°53'S 139°21'E, 18 May 2000, *ABTC* ES2; NTM R25869, 50 km northwest of Doomadgee, 17°43'S 138°28'E, 18 May 2000, *ABTC* ES6; NTM R25872, Hells Gate roadhouse, 17°27'S 138°21'E, 18 May 2000, *ABTC* ES9; SAM R5399 A and B, Mornington Island, 16°36'S 139°21'E, 5 1960; SAM R9773, Strathgordon Homestead, 14°41S 142°10'E, 27 6 1968; ANWC R273, Warren Point, 8 km southsoutheast of Mitchell, 26°33'S 148°01'E, 17 05 1968; ANWC R1599, Bolwarra Station, near Chillagoe. 17°25'S 143°56'E, 22 06 1977. WESTERN AUSTRALIA: NTM R22092-093, Kununurra, 15°46'S 128°44'E, 25 Jan 1996, *ABTC* Y61-Y62; NTM R22094-095, Lake Argyle, 16°07'S 128°44'E, 25 Jan 1996, *ABTC* Y63-Y64; NTM R22514-515, Wyndham, 15°29'S 128°06'E, 02 Jul 1996, *ABTC* Z75-Z76; NTM R22519, Ellenbrae Station, 15°58'S 127°03'E, 05 Jul 1996, *ABTC* Z80; NTM R22520-521, Drysdale River Station, 15°42'S 126°22'E, 06 Jul 1996, *ABTC* Z81-Z82; NTM R22525-526, Mt Elizabeth Homestead, 16°25'S 126°06'E, 10 Jul 1996, *ABTC* Z86-Z87; WAM R94837, Osmond Yard, Ord River, 17°14'S 128°38'E, 14 04 1986; WAM R99651, Lake Argyle, 16°18'S 124°48'E; WAM R126000, 12 km southwest of Carlton Hill Homestead, 15°33'S 128°28'E, *ABTC* R126000; WAM R126009, 30 km east of Wyndham, 15°28'S 128°25'E, *ABTC* R126009; WAM R126019, 7 km southwest of Point Spring Yard, 15°27'S 128°49'E, *ABTC* R126019; WAM R126048, 5 km south of Carlton Hill Homestead, 15°32'S 128°31'E, *ABTC* R126048; WAM R132760, Carlton Hill Station, 15°27'S 128°44'E, *ABTC* R132760; WAM R132769, Ivanhoe Station, 15°38'S 128°41'E, *ABTC* R132769; WAM R132777, Carlton Hill, 15°13'S 128°41'E, *ABTC* R132777.

Cryptoblepharus plagiocephalus (27 specimens). WESTERN AUSTRALIA: NTM R22070-071, R22073, Denham, 25°55'S 113°32'E, 16 Jan 1996, *ABTC* Y42-Y43; NTM R22074-078, Carnavon, 24°53'S 113°40'E, 18 Jan 1996, *ABTC* Y44-Y48; WAM R45828, R45841, Dirk Hartog Island, Shark Bay, 25°45'S 113°03'E; WAM R47667-668, Barrow Island, 20°46'S 115°24'E; MNHP R3088, Van Diemen's Land, 1801-1803; WAM R113603, Dirk Hartog Island, 25°50'S 113°05'E, *ABTC* R113603; WAM R115229, Eurardy Station, 27°34'S 114°40'E, *ABTC* R115229; WAM R120633, Mr1, 24°30'S 114°38'E, *ABTC* R120633; WAM R123920, Bulong, 30°45'S 121°48'E, *ABTC* R123920; WAM R123935-936, Bulong, 30°45'S 121°48'E, *ABTC* R123935-936; WAM R131780, 12 km west north west of Wandida Homestead, 27°56'S 115°32'E, *ABTC* R131780; WAM R131789, Hamelin Homestead, 26°26'S 114°12'E, *ABTC* R131789; WAM R135134, Rosemont, 27°56'S 122°19'E, *ABTC* R135134; WAM R137970, Yardie Creek, Cape Range, 22°22'S 113°51'E, *ABTC* R137970: QM J30924-925, Hamelin Pool, 26°12'S 114°04'E, 19 Feb 1962; QM J30926, Bellefin Prong, east coast of Carrang Station. 26°06'S 113°18'E, 24 Aug 1970; QM J30927, Dirk Hartog Island, 25°45'S 113°03'E.

Cryptoblepharus pulcher clarus (31 specimens). SOUTH AUSTRALIA: NTM R22040-041, 5 km southeast of Smokey Bay, 32° 23'S 133° 59'E, 30 Dec 1995, *ABTC* Y19-Y20; SAM R31454, Wardang Island, 34° 30'S, 137° 22'E, *ABTC* R31454; SAM R36544, 7 km north of Courtabie, 33° 08'S. 134° 51'E, *ABTC* R36544. WESTERN AUSTRALIA: NTM R22042-043, Eyre Hwy. 40 km east of Cocklebiddy, 31° 59'S 126° 34'E, 01 Jan 1996, *ABTC* Y21-Y22; NTM R22044-049, Deralinya Ruins, 89 km south of Balladonia, 33° 03'S 123° 22'E, 02 Jan 1996, *ABTC* Y23-Y28; NTM R22050-060, Dalyup River, South Coast Highway bridge, 33° 42'S 121° 35'E, 03 Jan 1996, *ABTC* Y29-Y38; QM J30920, Esperance, Pink Lake, 33° 51'S, 121° 50'E, 03 Feb 1960; QM J30921, 22.4 km east of Esperance, 33° 45'S, 122° 02'E, 09 Dec 1959; SMF 58563, Hopetown, 33° 57'S, 120° 07'E; WAM R119432, near Carracarrup Pool, 33° 44'S, 119° 59'E, *ABTC* R119432; WAM R77856-858, Burnabbie, 32° 08'S, 126° 20'E, *ABTC* R77856-858; WAM R77930, 41km southwest of Eucla Motel, 31° 53'S, 128° 31'E, *ABTC* R77930.

Cryptoblepharus pulcher pulcher (49 specimens). NEW SOUTH WALES: NTM R21808-809, Uralla, 30° 39'S 151° 30'E, 26 Sep 1995; NTM R23690-691, Earlwood, Sydney, 33° 53'S 151° 22'E, Apr 1998, *ABTC* CQ1-CQ2; NTM R23692, Caringbah, Sydney, 34° 02'S 151° 08'E, Apr 1998, *ABTC* CQ3; NTM R23746-747, R23749, Earlwood, Sydney, 33° 53'S 151° 22'E, Apr 1998, *ABTC* CQ4-CQ5; NTM R23751-753, Yalwal, 34° 56'S 150° 23'E, Jun 1998, *ABTC* CX4-CX6. QUEENSLAND: NTM R18927-928, Airlie Beach, 20° 16'S 148° 43'E, 05 Jan 1998, *ABTC* CD5-CD6; NTM R18951-952, R18954, R18967, Far Beach, Mackay, 21° 10'S 149° 12'E, 09 Jan 1998, *ABTC* CF6-CF7, CF9; NTM R18969, R18973, Clairview, 22° 07'S 149° 32'E, 11 Jan 1998, *ABTC* CG2, CG6; NTM R18980-981, Tannum Sands, 23° 57'S 151° 22'E, 11 Jan 1998, *ABTC* CH3-CH4; NTM R18984-985, R18987, caravan park, Gin Gin, 24° 59'S 151° 57'E, 12 Jan 1998, *ABTC* CH7-CH8, CI1; NTM R18989-992, Gympie, 26° 10'S 152° 38'E, 12 Jan 1998, *ABTC* CI3-CI6; NTM R18993-994, R18996, Tewantin, 26° 24'S 153° 00'E, 13 Jan 1998, *ABTC* CI7-CI8, CJ1; NTM R18997-999, Chappel Hill, Brisbane, 27° 30'S 152° 57'E, 14 Jan 1998, *ABTC* CJ2-CJ4; NTM R23429-430, R23432, Chappel Hill, Brisbane, 27° 30'S 152° 57'E, 14 Jan 1998, *ABTC* CJ6-CJ7, CJ9; NTM R23433-435, Dalby, 27° 12'S 151° 16'E, 19 Jan 1998, *ABTC* CK1-CK3; NTM R23436, Miles, 26° 39'S 150° 11'E, 19 Jan 1998, *ABTC* CK4; NTM R8915, 5 miles south of Gympie, 26° 13'S 152° 42'E, Sep 1980; QM J11933-937, Brisbane, St. Lucia, 27° 30'S, 153° 01'E, 30 Jul 1961.

OTU virgA1x3 (taxon of *C. pulcher* x *C. adamsi* sp. nov. hybrid origin). QUEENSLAND: NTM R18931-933, Dingo Beach, 20°05'S 148°30'E, 06 Jan 1998, *ABTC* CD9, CE1-CE2; NTM R18949, Airlie Beach, 20°16'S 148°43'E, 07 Jan 1998, *ABTC* CF4.

Cryptoblepharus ruber (31 specimens). NORTHERN TERRITORY: NTM R22638, Roper River, 14°48'S 134°56'E, 23 May 1996, *ABTC* Z55; NTM R23669-670, Brandy Bottle Creek, Victoria Hwy, 15°18'S 131°33'E, 04 Apr 1998, *ABTC* CP8-CP9; NTM R24773-775, R24777, Mount Golla Golla, Bradshaw Station, 15°19'S 130°28'E, 02 Sep 1999, *ABTC* DM5-DM6, DM8; NTM R24786, Mosquito Flat, Bradshaw Station, 15°22'S 130°06'E, 04 Sep 1999, *ABTC* DR2; NTM R18663-664, R18684, Mosquito

Flat, Bradshaw Station, 15°23'S 130°08'E, 28 Sep 1997, *ABTC* BR1-BR2, BS4; WAM R137944, R137948, Spirit Hills Homestead, 15°26'S 129°01'E, *ABTC* R137944, R137948; NTM R13616-617, Victoria River, 7 km south of Hwy bridge, 15°35'S 131°05'E, 20 May 1986, *ABTC* D05-DO6; NTM R20841, Keep River, 15°41'S 129°02'E, 13 May 1987, *ABTC* G58; NTM R22352, R22358, Cockatoo Lagoon, Keep River Nat. Pk, 15°58'S 129°02'E, 23 Apr 1995, *ABTC* Y86, Y92; NTM R16387, Wave Hill Station, Flora Bore, 17°50'S 130°55'E. 01 Jul 1990. *ABTC* M68. WESTERN AUSTRALIA: WAM R60795, Mitchell Plateau, 14°40'S 125°50'E, 01 Nov 1978; NTM R22522, Mitchell Falls, 14°41'S 125°39'E, 07 Jul 1996, *ABTC* Z83; WAM R53722, Mitchell Plateau, 14°52'S 125°50'E, 17 Jun 1976; WAM R132727, 5 km east of Point Springs Yard, 15°24'S 128°53'S, *ABTC* R132727; NTM R22518, Jack's Hole, Durack River Station, 15°50'S 128°24'E, 04 Jul 1996, *ABTC* Z79; NTM R22528-529, Mt Elizabeth Station, 16°13'S 125°59'E, 10 Jul 1996, *ABTC* Z89-Z90; WAM R108750, Bream Gorge, Osmond Valley, 17°15'S 128°18'E, *ABTC* R108750; WAM R40264, Coulomb Point, 17°21'S 122°09'E, Jul 1971; NTM R22083-084, Cable Beach, Broome, 17°55'S 122°12'E, 23 Jan 1996, *ABTC* Y53-Y54; WAM R14065, Broome, 17°58'S 122°14'E, Jan 1962.

Cryptoblepharus virgatus (30 specimens). QUEENSLAND: ANWC R5235, R5244, R5270, eastern Meilwraith Range lowlands, Cape York Peninsula, 13°30'S 143°18'E, 08-13 Aug 1990; NTM R18868-877, Cooktown, town area, 15°28'S 145°15'E, 22 Dec 1997, *ABTC* BX8-BX9, BY1-BY8; NTM R18878-883, Lions Den Hotel, Bloomfield Track, 15°42'S 145°13'E, 23 Dec 1997, ABTC BY9, BZ1-BZ5; NTM R18885-886, Cooktown, town area, 15°28'S 145°15'E, 22 Dec 1997; NTM R18899-900, Flying Fish Point, Innisfail, 17°30'S 146°05'E, 31 Dec 1997, ABTC CA4-CA5; SAM R2957, East Innisfail, 17°32'S 146°10'E, 09 Jan 1944; SAM R5520, Thursday Island, 10°35'S 142°13'E, 17 Mar 1960; SAM R21131, Cairns, 16°55'S 145°46'E, ABTC R21131; SMF 53250, Flying Fish Point, Innisfail, 17°29'S 146°05'E, 28 Apr 1957: SMF 58558-559, Cairns, 16°55'S 145°46'E, 18 May 1957; SMF 58589, Green Island, 16°46'S 145°58'E, 15 May 1957.

Cryptoblepharus africanus (3 specimens). BMNH 96.9.24.28, Brara, south Somaliland, Capt. V.B. Bottego; BMNH 98.1.28.9, Lugh, south Somaliland, Capt. Ferrandi; BMNH 1902.11.8.1, Shimoni, east coast of Africa, A.B. Percival.

Cryptoblepharus aldabrae (1 specimen). BMNH 1978.1308-10, Aldabra, Indian Ocean, P. Niedzwiedzki, 1977.

Cryptoblepharus boutonii (12 specimens). ZMB 8722, Fouquets Island, Mauritius. K. Möbius; SMF 22126, Mauritius, ex BMNH; BMNH 55.12.26.327A-D, Mauritius; BMNH 1994.77-86, Ile de la Passe, Mauritius, C. Jones, 16 September 1993.

Cryptoblepharus cognatus (2 specimens). SMF 67220-21, Nosy Bé Island, Madagascar. H. Fricke, September 1969.

Cryptoblepharus gloriosus gloriosus (1 specimen). BMNH 1953.1.12.23, Gloriosa Island, west Madagascar. E.Brown, 1952.

Cryptoblepharus balieusis bulieusis (9 specimens). INDONESIA: SMF 22123, SMF 22201-03, Sangsit, Bali. R. Mertens, 1927; SMF 22205-06, Selong, Lombok. R. Mertens, 1927; SMF 22207, 22122, Narmada, Lombok. R. Mertens, 1927; SMF 51818, Parang Island, Karimundjawa island group. A. Hoogerwerf, 1955.

Cryptoblepharus egeriae (7 specimens). SMF 22127; SAM 32510, QM J37902-905, QM J37907, Christmas Island, Indian Ocean.

Cryptoblepharus exiuiius (8 specimens). BMNH 1947.3.1.88-92, Thithia (Cicia) Island, Lau group, Fiji. R. Lever, 1945; SMF 15605, Viti Levu, Fiji. Poehl, 1887; SMF 68161, Viti Levu Bay, Fiji. H. Grossmann, 1974; SMF 69705, bridge over Nandi River, Nandi, Viti Levu, Fiji. K. Klemmer, 1978.

Cryptoblepharus leschenault (10 specimens). INDONESIA: BMNH 1969.1530, Wetar Island, Kepulauan Barat Daya. Burden-Dunn Expedition, 1926; SMF 22121, 22186, 22193-98, Endeh, Flores. R. Mertens, 1927; SMF22174, Wolo Waro, central Flores. R. Mertens, 1927.

Cryptoblepharus nigropunctatus (2 specimens). SMF 22124-25, Haha shima, Bonin Islands (Ogasawara-gunto), Kanto region, Japan.

Cryptoblepharus novaeguineae (4 specimens). NEW GUINEA: SMF 15606, Simbang. L. Méhely, 1898; SMF 58716-17, Vogelkop, Ajamaroe, L. Brongersma, 1952; BMNH 1987.416, Ela Beach, Port Moresby. M. O'Shea, 1986.

Cryptoblepharus poecilopleurus paschalis (1 specimen). BMNH 1972.2038, Isla de Pascua (Easter Island), Valparaiso province. J. Ortiz, 10 October 1968.

Cryptoblepharus poecilopleurus poecilopleurus (13 specimens). BMNH 1976.2289, near Coyhaique, Chili. S. Jacquemart, 1975; SMF 15614-15, Pinipel, Nissan Atoll. E. Wolf, 1909; SMF 15629-31, Eua, Tonga Islands. E. Wolf, 1909; SMF 15654, 15656-57, Mui, Cook Islands. E. Wolf, 1909; SMF 15669-71. Makatea, Paumotu. E. Wolf, 1909; SMF 68154, Malden, Central Line Islands. H. Grossmann, 1975.

Cryptoblepharus renschi (2 specimens). INDONESIA: SMF 58714, Padar Island. I. Dareversusky, 1959; SMF 58718, Komodo Island, I. Dareversusky, 1962.

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Crowley, L.M. 1949. Working class conditions in Australia, 1788-1851. Unpublished PhD thesis. University of Melbourne.

Sadlier, R.A. 1990. A new species of scincid lizard from western Arnhem Land, Northern Territory. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 7(2): 29-33.

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