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Elevation of Divergent Color Polymorphic and Monomorphic Lizard Lineages (Squamata: Agamidae) to Species Level

Caroline M. Dong^{1,2,3}, Greg R. Johnston⁴, Devi Stuart-Fox¹, Adnan Moussalli², Katrina J. Rankin¹, and Claire A. McLean^{1,2}

The Australian Tawny Dragon lizard (*Ctenophorus decresii*), as currently recognized, comprises two genetically divergent lineages, northern and southern, that differ notably in male coloration. A narrow contact zone exists between the lineages with asymmetric and limited hybridization, indicating incompatibility and highlighting the need for further taxonomic assessment. Here, we evaluate morphological variation in *C. decresii* and elevate the lineages to separate species. The southern lineage retains the name *C. decresii* (Duméril and Bibron, 1837), and we formally reinstate *C. modestus* for the northern lineage, which was previously a synonym of *C. decresii* (*Amphibolurus modestus*, Ahl, 1926). We redescribe *C. modestus* and *C. decresii* and highlight important considerations for reevaluation of their conservation statuses. Recognition of *C. modestus* represents another species that may have differentiated in relatively mesic mountainous refugia during Pleistocene glacial-interglacial cycles, and underscores the importance of divergence in male coloration as a driver of speciation in the rock dragon species group.

CTENOPHORUS is the largest genus of Australian agamid lizards, comprising a radiation of 33 currently recognized species (Melville and Wilson, 2019; Sadlier et al., 2019). Within the genus, there is a monophyletic group of six saxicolous species: *C. decresii*, *C. fionni*, *C. mirrityana*, *C. rufescens*, *C. tjantjalka*, and *C. vadrappa*. All are found in South Australia, with the exception of *C. mirrityana* which is endemic to an adjacent area of western New South Wales. Additionally, all of these species are sexually dimorphic with slightly larger, more brightly colored and patterned males and cryptically colored females and juveniles (Houston, 1974; Johnston, 1992; McLean et al., 2013). Male throat and dorsolateral coloration are distinguishing characteristics between species and function as important sexual signals (Stuart-Fox and Johnston, 2005; Osborne et al., 2012). These traits are emphasized during territorial and courtship displays involving dorsolateral compression of the body and extension of the throat, alongside head-bobbing and hindlimb push-ups (Gibbons, 1979; Ramos and Peters, 2016).

The Tawny Dragon (*C. decresii*) comprises two largely allopatric lineages which differ notably in male throat and dorsolateral color and pattern (Houston, 1974; McLean et al., 2014a). The northern lineage occurs in the Flinders and Olary Ranges, while the southern lineage occurs in the Mount Lofty Ranges, on the Fleurieu Peninsula, and on Kangaroo Island. Divergence between the two lineages is consistent with range contraction to allopatric refugia during glacial-interglacial Pleistocene cycles (Byrne, 2008; McLean et al., 2014a), and a secondary contact zone exists near the Barossa Valley, between the Olary and Mount Lofty Ranges (McLean et al., 2014a; Dong et al., 2019a: bioRxiv 840678). Differing refugium-specific selective pressures may have led to the evolution of divergent phenotypes between lineages

(e.g., McLean et al., 2014b). Males of the southern lineage are monomorphic with blue throat coloration with an ultraviolet (UV) reflectance peak, and some yellow reticulation in the Kangaroo Island population (McLean et al., 2014a; Fig. 1A, B). The northern lineage is color polymorphic with four discrete male throat color morphs: orange, yellow, orange-yellow (yellow with an orange central patch), and gray (Teasdale et al., 2013; Fig. 1D–G).

McLean et al. (2013, 2014a) characterized phenotypic and genetic divergence among *C. decresii* (northern and southern), *C. fionni*, *C. mirrityana*, and *C. vadrappa*, and highlighted the need to further investigate the taxonomic statuses of the *C. decresii* lineages. McLean et al. (2014a) found phylogeographic discordance: mitochondrial and nuclear sequence data suggested that populations in the northern Flinders Ranges (northern-most range) were more closely related to the southern lineage than the geographically proximate northern lineage, while this was not supported by microsatellite data. Since then, comprehensive genomic data (1,333 single nucleotide polymorphism loci; SNPs) for populations across the range of *C. decresii* have shown that the northern Flinders Ranges populations clearly group with the northern lineage (Fig. 2). Furthermore, an in-depth study of the contact zone indicates that intrinsic genetic incompatibilities and sexual signal divergence restrict gene flow between the lineages (Dong et al., 2019a: bioRxiv 840678). Hybridization is asymmetric and limited; hybrids backcross almost exclusively to the northern lineage and predominantly have northern lineage mtDNA haplotypes and northern throat phenotypes (in terms of coloration and UV reflectance; Dong et al., 2019a: bioRxiv 840678). Together, these patterns indicate reproductive incompatibility between

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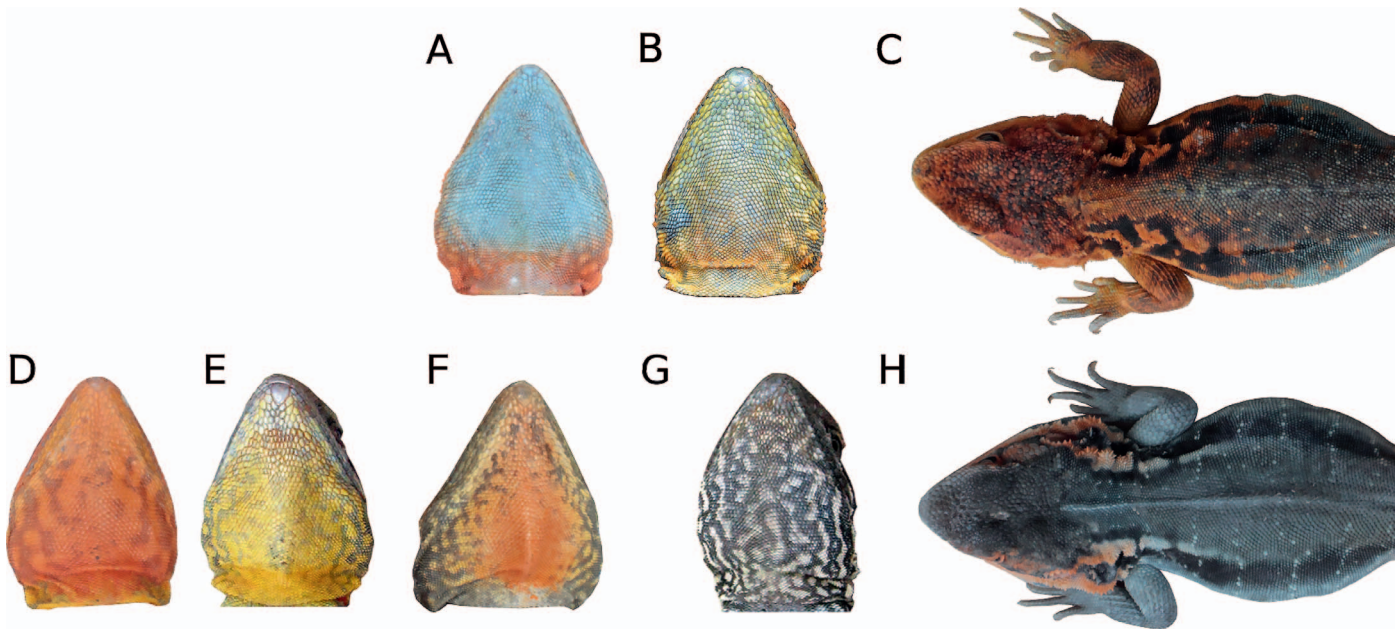


Fig. 1. (A) The blue mainland male throat of *C. decresii sensu stricto* and (B) the blue reticulated with yellow throat found on Kangaroo Island. The four male throat morphs of *Ctenophorus modestus*: (D) orange, (E) yellow, (F) orange-yellow (yellow with an orange central patch), and (G) gray. Male dorsolateral patterning and coloration differ where (C) *C. decresii sensu stricto* has a more “pinched” or broken lateral stripe with a greater extent of bordering orange or yellow coloration, and (H) *C. modestus* has a relatively straight edged lateral stripe with cream and orange coloration terminating at the shoulder.

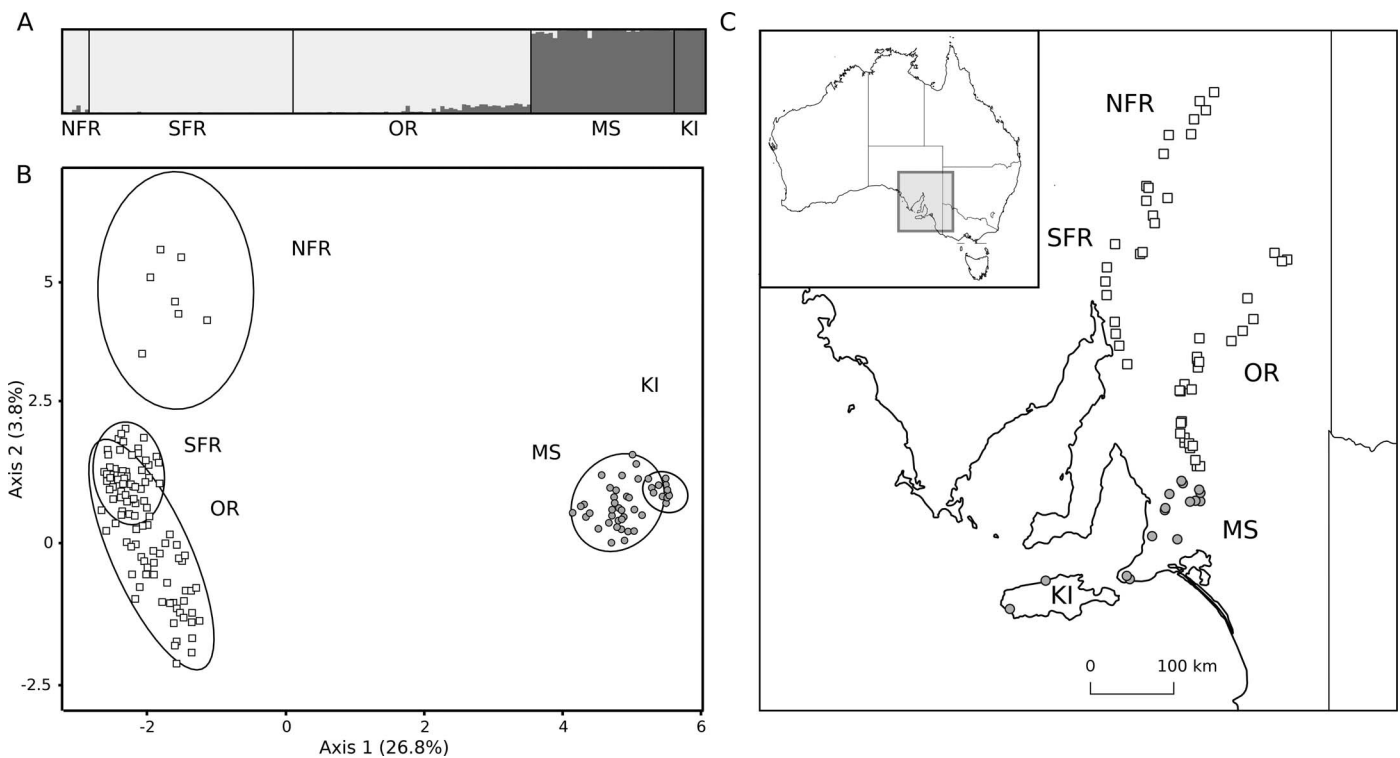


Fig. 2. Genetic divergence between *Ctenophorus modestus* (northern Flinders Ranges [NFR], southern Flinders Ranges [SFR], Olary Ranges [OR]) and *C. decresii* (mainland south [MS] which encompasses the Mount Lofty Ranges and Fleurieu Peninsula, and Kangaroo Island [KI]) and specimens examined for morphological analyses. (A) Results of a Bayesian analysis of ancestry in the program STRUCTURE ($K = 2$). Each vertical bar represents an individual and individuals are ordered by population and latitude (from north to south). The proportion of white and gray represents the proportion of *C. modestus* and *C. decresii* ancestry in each individual, respectively. (B) Two-dimensional principal coordinate plot (PCoA) showing pairwise genetic distances between individuals: *Ctenophorus modestus* (squares), *C. decresii* (circles). 95% confidence ellipses of each population are shown. Both A and B were constructed from a genomic SNP dataset of 1333 SNPs ($n = 148$). (C) Map showing geographic locations of samples of *C. modestus* and *C. decresii* shown in A and B.

Table 1. Morphometric measurements and meristic characters used in linear discriminant analyses, including abbreviations and definitions of characters.

Abbreviation	Character
SVL	Snout–vent length, from tip of rostral scale to cloaca
TL	Tail length, from cloaca to tip of tail
AGL	Axilla–groin length, from base of forelimb to base of hindlimb
HL	Head length, from tip of rostral scale to posterior of jaw bone
HW	Head width, at widest point
HD	Head depth, at center of tympanum
EYE	Eye diameter, from anterior to posterior
SL	Snout length, from tip of rostral scale to anterior of eye
JL	Jaw length, from posterior of eye to posterior of jaw bone
NW	Width between nostrils
HUML	Humerus length
RADL	Radius length
HANL	Hand length, from wrist to tip of fourth finger
FINL	Fourth finger length
FEML	Femur length
TIBL	Tibia length
FOOT	Foot length, from ankle to tip of fourth toe
TOE	Fourth toe length
SUPRA	Number of supralabial scales
INFRA	Number of infralabial scales
ROSNAS	Number of scales between rostral and nasal
SUPRANAS	Number of scales between supralabial and nasal
INTERNAS	Number of internasal scales across the top of the snout
SDL	Number of subdigital lamellae on fourth toe
FP	Number of femoral pores (males only)

the two lineages, which restricts the direction and extent of hybridization.

Here, we formally recognize and redescribe the northern and southern lineages of *C. decresii* as separate species based on notable morphological, phenotypic, and genetic differentiation and evidence of reproductive incompatibilities between the lineages. The type specimens of *C. decresii* originate from Kangaroo Island and refer to the southern lineage; *decresii* gives reference to the French name for Kangaroo Island, L'Île de Decrès. The northern lineage is referred to as *Amphibolurus modestus* (Ahl, 1926), previously regarded as a synonym of *C. decresii* by Cogger et al. (1983).

MATERIALS AND METHODS

We compared morphometric measurements and meristic characters (Table 1) of northern ($n = 70$; male = 45, female = 25) and southern ($n = 40$; male = 21, female = 19) *C. decresii*, as well as *C. fionni* ($n = 15$; male = 10, female = 5) and *C. vadrappa* ($n = 15$; male = 10, female = 5; Fig. 3A; Table S1; see Data Accessibility), as they are the most closely related and morphologically similar species within the rock dragon group (McLean et al., 2013). Data are from McLean et al. (2013) and were collected from adult (SVL ≥ 65 mm for males and ≥ 60 mm for females) preserved specimens held in collections at the Australian Museum, Sydney, South

Australian Museum (SAM), and Museums Victoria (NMV). Full details of data collection and additional univariate data analyses are given in McLean et al. (2013). To assess whether *A. modestus* applied to the northern or southern lineage of *C. decresii*, we obtained photographs, measurements, and meristics of the two syntypes of *A. modestus* (ZMB 30092) held in the Museum für Naturkunde in Berlin, Germany. The syntypes included a subadult male which was re-registered as ZMB54516 in 1995 and a female which retained the original registration number (ZMB30092; Frank Tillack, in lit., 12 December 2019). To confirm that the type specimens of *C. decresii* represent the southern lineage, we obtained photographs, measurements, and meristics of the two syntypes, an adult male (MNHN 6545) and adult female (MNHN 6545A) held in the Muséum national d'Histoire naturelle in Paris, France. Institutional abbreviations follow Sabaj (2020).

Linear discriminant analyses (LDA) were used to test whether individuals could be reliably assigned to the four *a priori* taxa. Males and females were analyzed separately to account for sexual dimorphism, using 23 variables for both (Table 1). Morphometric measurements were expressed as a percentage of snout–vent length (SVL). Tail length (TL) was excluded from both analyses because many individuals had damaged tails (due to predation or intraspecific aggression). Femoral pore count was excluded for females because they could only be counted reliably for males, and SVL was excluded for males because ZMB54516 is a subadult (SVL = 52.9 mm). An additional LDA was conducted on males without the specimen of *A. modestus* in order to include SVL as a variable (24 variables used). For all analyses, species was used as a dependent variable (i.e., northern *C. decresii*, southern *C. decresii*, *C. fionni*, *C. vadrappa*) with morphological data as independent variables. Data were centered and scaled, and analyses were conducted using the R package MASS (v7.3.50; Venables and Ripley, 2002) in R v 3.5.1 (R Core Team, 2018).

RESULTS

Discrimination among males of the four taxa (northern *C. decresii*, southern *C. decresii*, *C. fionni*, and *C. vadrappa*) was highly significant (males: Wilks' $\lambda = 0.095$, $F_{69,180} = 3.13$, $P < 0.0001$). Linear discriminant analysis (LDA) on male morphological variables indicated that the male type specimens of *A. modestus* and *C. decresii* fell within the 95% confidence ellipses of the northern and southern lineages of *C. decresii*, respectively (Fig. 3B). Differentiation along the first axis (LD1; variance explained = 52.4%) is driven primarily by number of femoral pores, number of infralabial scales, tibia length, and head length (Table 2). The second axis (LD2) showed differentiation (variance explained = 28.5%) among northern *C. decresii*, *C. fionni*, and *C. vadrappa*, driven primarily by tibia length and foot length (Table 2; Fig. 3B). Similarly, discrimination of the four taxa including SVL as a variable (excluding the type specimen of *A. modestus*) for males was highly significant (Wilks' $\lambda = 0.071$, $F_{72,174} = 3.44$, $P < 0.0001$). Differentiation along LD1 (variance explained = 60.7%) is driven primarily by SVL, number of femoral pores, and hand length (Table S2; see Data Accessibility). LD2 showed differentiation (variance explained = 23.7%) among northern *C. decresii*, *C. fionni*, and *C. vadrappa*, driven primarily by foot length and tibia length (Table S2; Fig. S1; see Data Accessibility). In both analyses of males, northern *C.*

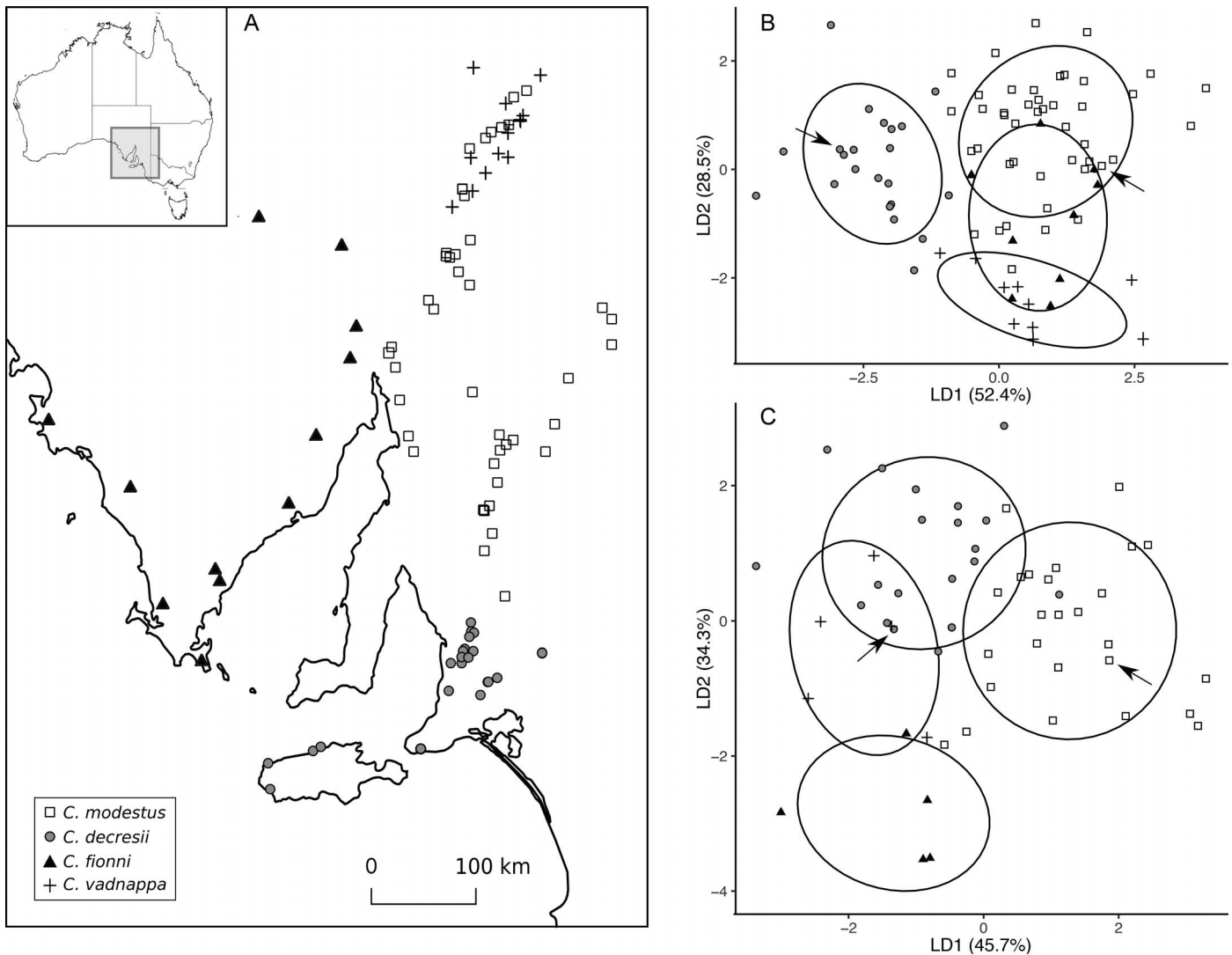


Fig. 3. (A) Map showing localities of examined museum specimens: *Ctenophorus modestus* (squares); *C. decresii sensu stricto* (circles); *C. fionni* (triangles); and *C. vadrappa* (plus [+]). Specimens without GPS coordinates are excluded. (B–C) Linear discriminant analyses of (A) males and (B) females based on 23 variables: *Ctenophorus modestus* (squares); *C. decresii* (circles); *C. fionni* (triangles); and *C. vadrappa* (plus [+]). 95% confidence ellipses are shown. The lectotypes (males) and paralectotypes (females) of *C. modestus* and *C. decresii* are indicated with arrows.

decresii and southern *C. decresii* were strongly differentiated along LD1 with 95% confidence ellipses that do not overlap (Fig. 3B; Fig. S1; see Data Accessibility). The 95% confidence ellipse of northern *C. decresii* partially overlaps with that of *C. fionni* but not that of *C. vadrappa*; the ellipses of *C. fionni* and *C. vadrappa* partially overlap with each other; the ellipse of southern *C. decresii* does not overlap with any other taxon (Fig. 3B; Fig. S1; see Data Accessibility).

For females, discrimination among the four taxa was also significant (Wilks' $\lambda = 0.104$, $F_{69,90} = 1.48$, $P = 0.039$). LDA on morphological variables showed differentiation along LD1 (variance explained = 45.7%) driven by tibia length, number of scales between rostral and nasal, and humerus length (Table 2; Fig. 3C). Differentiation along LD2 (variance explained = 34.4%) was driven by SVL, the number of infralabial scales, and hand length (Table 2; Fig. 3C). LDA indicated that the female type specimen of *A. modestus* fell within the 95% confidence ellipse of northern *C. decresii* (Fig. 3C). The female type specimen of *C. decresii* falls in the overlap between ellipses of southern *C. decresii* and *C.*

vadrappa (Fig. 3C). However, the collection locality of the specimen (i.e., Kangaroo Island) precludes the possibility of the specimen being *C. vadrappa*. The 95% confidence ellipse of southern *C. decresii* partially overlaps with that of both northern *C. decresii* and *C. vadrappa*; however, the ellipses of northern *C. decresii* and *C. vadrappa* do not overlap with each other. The 95% confidence ellipse of *C. fionni* very marginally overlaps with that of *C. vadrappa* only.

***Ctenophorus decresii* (Duméril and Bibron, 1837)**

Tawny Rock Dragon
Figures 1A–C, 4A–B, 5A

Grammatophora decresii (Duméril and Bibron, 1837: 472–474).

Amphibolurus decresii 'southern race' (Houston, 1974: 51).
Ctenophorus decresii 'southern lineage' (McLean et al., 2013: 52).

Types.—The original description was based on two syntypes, a male and a female, from L'Île de Decrès (Kangaroo Island)

Table 2. Standardized linear discriminant coefficients for the first two canonical variables for males and females. Characters strongly correlated with canonical variables (large absolute values) are bolded and italicized.

Character	Males		Females	
	LD1	LD2	LD1	LD2
SVL	NA	NA	0.426	-1.026
AGL_SVL	0.278	-0.051	-0.313	-0.015
HL_SVL	-0.532	0.497	0.058	-0.704
HW_SVL	0.017	-0.366	-0.229	0.033
HD_SVL	0.185	0.312	0.661	0.619
EYE_SVL	-0.062	0.028	-0.426	-0.001
SL_SVL	-0.143	-0.227	0.367	0.354
JL_SVL	0.461	-0.442	0.294	0.204
NW_SVL	0.339	0.331	0.352	0.129
HUML_SVL	-0.158	0.139	0.753	0.276
RADL_SVL	-0.405	0.050	-0.679	-0.254
HANL_SVL	0.412	0.284	0.164	0.825
FINL_SVL	-0.457	0.311	0.284	-0.411
FEML_SVL	0.487	-0.304	0.684	-0.285
TIBL_SVL	0.654	-0.736	-1.024	-0.612
FOOT_SVL	-0.155	-0.595	-0.705	-0.306
TOE_SVL	-0.211	0.058	0.220	-0.110
SUPRA	0.377	-0.208	0.379	0.867
INFRA	0.665	0.503	0.484	-0.981
ROSNAS	-0.232	0.259	-0.755	0.029
SUPRANAS	0.408	-0.241	-0.478	-0.653
INTERNAS	-0.114	0.325	0.106	0.542
SDL	-0.181	-0.082	0.059	0.592
FP	-0.766	-0.100	NA	NA
Proportion of variance	0.524	0.285	0.457	0.343

and registered as MNHN 6545 (Duméril and Bibron, 1837). We designate the male as lectotype (MNHN 6545; Fig. 5A) and the female as paralectotype (MNHN 6545A; Fig. S2; see Data Accessibility) because only the male exhibits the diagnostic coloration.

Diagnosis.—*Ctenophorus decresii* is a member of the *C. decresii* species group (Houston, 1974; Houston and Hutchinson, 1998). Within the *C. decresii* species group, *C. decresii* is distinguishable by the following combination of characters: snout scales smooth to longitudinally keeled; vertebral scales flat; presence of a broad dark undulating lateral stripe, often constricted into blotches and interrupted to form two separate blotches posterior to the tympanum; and in males, the throat is blue or blue and yellow with yellow to orange margins.

Description.—A moderately sized lizard reaching a maximum SVL of approximately 88 mm and total length of 230 mm. Head and body depressed. Tail long and tapered to a fine tip. Forelimbs moderately long, almost reaching groin when adpressed. Hindlimbs long and reaching or almost reaching snout when adpressed. Finger lengths: 4 > 3 > 5 > 2 > 1; toe lengths: 4 > 3 > 5 > 2 > 1. Characteristic of the genus, a distinct row of enlarged keeled scales extending from the nostril, below the eye to above the tympanum (Houston and Hutchinson, 1998). Ear membranes exposed and scale-free. Scales on snout are smooth to longitudinally keeled. 12–18 supralabial scales; 11–16 infralabial scales; 4–6 scales between

rostral and nasal; 4–6 scales between supralabial and nasal; 10–13 internasal scales; 21–29 subdigital lamellae on the fourth toe (McLean et al., 2013). Dorsal crest is small, no more than a series of keeled scales, becoming smaller posteriorly and not reaching base of tail. Nuchal crest low or absent. Scales on the dorsal surfaces of the limbs and tail are keeled. The gular fold is strongly developed and extends across the shoulders. 40–46 femoral and precloacal pores are arranged in a straight line along the thighs. Pores are present but smaller in females.

Adult male base color varies from gray-blue to brown, with pale blue flanks (Figs. 1C, 4A). The dorsolateral surface of the head is orange to yellow, extending past the shoulders. The extent of this coloration varies among individuals and depends on location but does not extend further than the mid-point of the axilla-groin length. A broad black lateral stripe begins posterior to the tympanum and terminates at the groin (Figs. 1C, 4A). The lateral stripe forms two separate blotches on the shoulder, one circular and enclosed entirely by orange to yellow coloration, while the other is elongated and wraps partly around the other. The remaining length of the lateral stripe is wavy edged or broken. On the ventral surface, males are cream with orange flushes on the belly, hindlimbs, and the length of the tail during the breeding season. A dark chest patch tapers to a point midbody and sometimes extends along the undersides of the forelimbs. This dark patch may vary in intensity, from black to gray. Male throat coloration in mainland populations is ultraviolet-blue with yellow to orange coloration along the gular fold (Fig. 1A); in Kangaroo Island populations, the base blue color is overlain with yellow reticulations (McLean et al., 2014a; Fig. 1B).

Adult females are cryptically colored, predominantly gray-brown to orange-brown, densely patterned with darker and lighter speckling (Fig. 4B) and sometimes a thin, pale vertebral line. Similar to males, a black lateral stripe runs along the flanks, similar in shape to that of males but sometimes less prominent. White to cream on the ventral surface. Varying degrees of gray reticulations on the throat, sometimes with a blue tinge. Orange to yellow flushes on the belly and gular region during the breeding season. Juveniles resemble adult females in coloration and pattern. Color patterning remains visible in fresh spirit-preserved specimens but fades with time.

Measurements (mm) and meristic characters of lectotype.—(Bilateral meristics as left [L] and right [R]) SVL, 80; TL, 146.5; AGL, 37; HL, 25; HW, 19.5; HD, 11.5; EYE, 4.7; SL, 9.3; JL, 13.5; NW, 6.5; HUML, 14; RADL, 11.5; HANL, 14; FINL, 10.5; FEML, 17.6; TIBL, 21.3; FOOT, 30.1; TOE, 16.5; SUPRA, 15R/14L; INFRA, 18R/17L; ROSNAS, 5R/5L; SUPRANAS, 5R/5L; INTERNAS, 11; SDL, 30R/NA-L; FP, 24R/21L.

Distribution and natural history.—*Ctenophorus decresii* inhabits rocky areas and outcrops, sheltering in rock crevices. The species occurs in the Mount Lofty Ranges, on the Fleurieu Peninsula, and on Kangaroo Island in South Australia, Australia (Figs. 2C, 3A, 6). These lizards occupy temperate habitats with varying levels of vegetation. Adults occur almost exclusively on rocks, perching conspicuously on elevated sites to bask and/or perform territorial and courtship displays. They are active in hot weather and, if disturbed, will run into a crevice or beneath a rock slab.

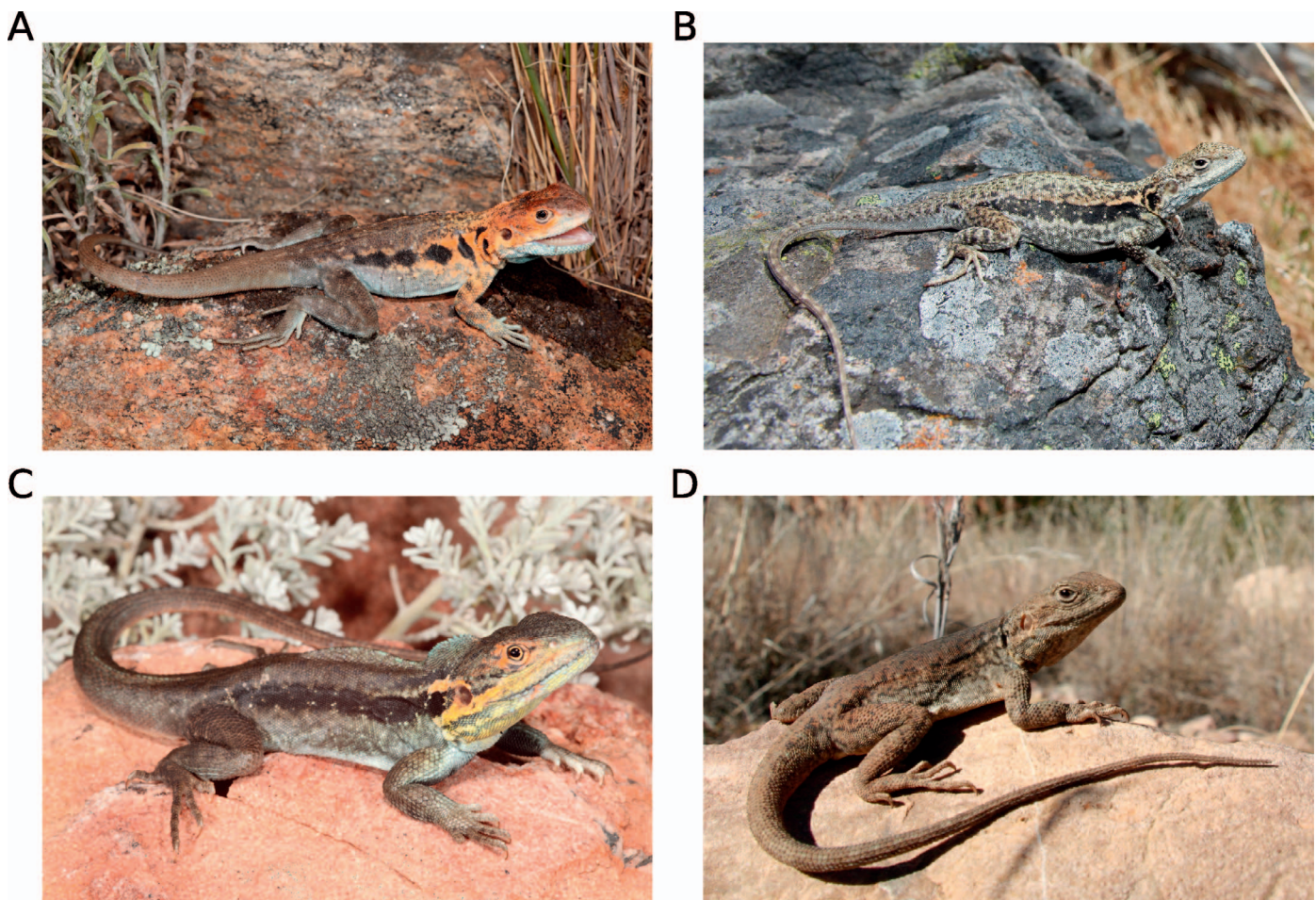


Fig. 4. Males (A, C) and females (B, D) of *Ctenophorus decresii* (A, B) from Palmer and Mengler's Hill Lookout, respectively, and *C. modestus* (C, D) from Telowie Gorge, all from South Australia, Australia (photos: copyright Adam Elliott).

***Ctenophorus modestus* (Ahl, 1926)**

Swift Rock Dragon

Figures 1D–H, 4C–D, 5B

Amphibolurus modestus (Ahl, 1926: 187–188).

Amphibolurus decresii 'northern race' (Houston, 1974: 52).

Ctenophorus decresii 'northern lineage' (McLean et al., 2013: 52).

Types.—The original description was based on two syntypes, both from 'Australien' and registered as ZMB30092 (Ahl, 1926). We designate the subadult male as lectotype (now registered as ZMB 54516; Fig. 5B) and the adult female as paralectotype (ZMB 30092; Fig. S3; see Data Accessibility) because only the male exhibits the diagnostic coloration. No exact locality is available for these specimens.

Diagnosis.—*Ctenophorus modestus* is a member of the *C. decresii* species group (Houston, 1974; Houston and Hutchinson, 1998). Within the *C. decresii* species group, *C. modestus* is distinguishable by the following combination of characters: snout scales smooth to longitudinally keeled; vertebral scales flat; a smooth-edged dark lateral stripe, sometimes interrupted to form a separate blotch posterior to the tympanum; and in males, throat coloration is polymorphic (orange, yellow, orange-yellow, or gray) with or without an overlay of gray reticulations and a small central black patch.

Description.—A moderately sized lizard reaching a maximum SVL of approximately 85 mm and total length of 255 mm. Head and body depressed. Tail long and tapered to a fine tip. Forelimbs moderately long, almost reaching groin when adpressed. Hindlimbs long and reaching or almost reaching snout when adpressed. Finger lengths: 4 > 3 > 5 > 2 > 1; toe lengths: 4 > 3 > 5 > 2 > 1. Characteristic of the genus, a distinct row of enlarged keeled scales extending from the nostril, below the eye to above the tympanum (Houston and Hutchinson, 1998). Ear membranes exposed and scale-free. Scales on snout are smooth to longitudinally keeled. 13–18 supralabial scales; 13–18 infralabial scales; 4–6 scales between rostral and nasal; 4–6 scales between supralabial and nasal; 9–13 internasal scales; 19–27 subdigital lamellae on the fourth toe (McLean et al., 2013). Small clustered pale yellow to orange spines anterior to tympanum. Dorsal crest is small, no more than a series of keeled scales, becoming smaller posteriorly and not reaching base of tail. Nuchal crest low or absent. Scales on the dorsal surfaces of the limbs and tail are keeled. The gular fold is strongly developed and extends across the shoulders. 34–45 femoral and precloacal pores are arranged in a straight line along the thighs. Pores are present but smaller in females.

Adult male base color varies from gray-blue to brown, with pale blue flanks (Figs. 1H, 4C). The dorsolateral surface of the head is brown, with orange around the eyes, nostrils, and

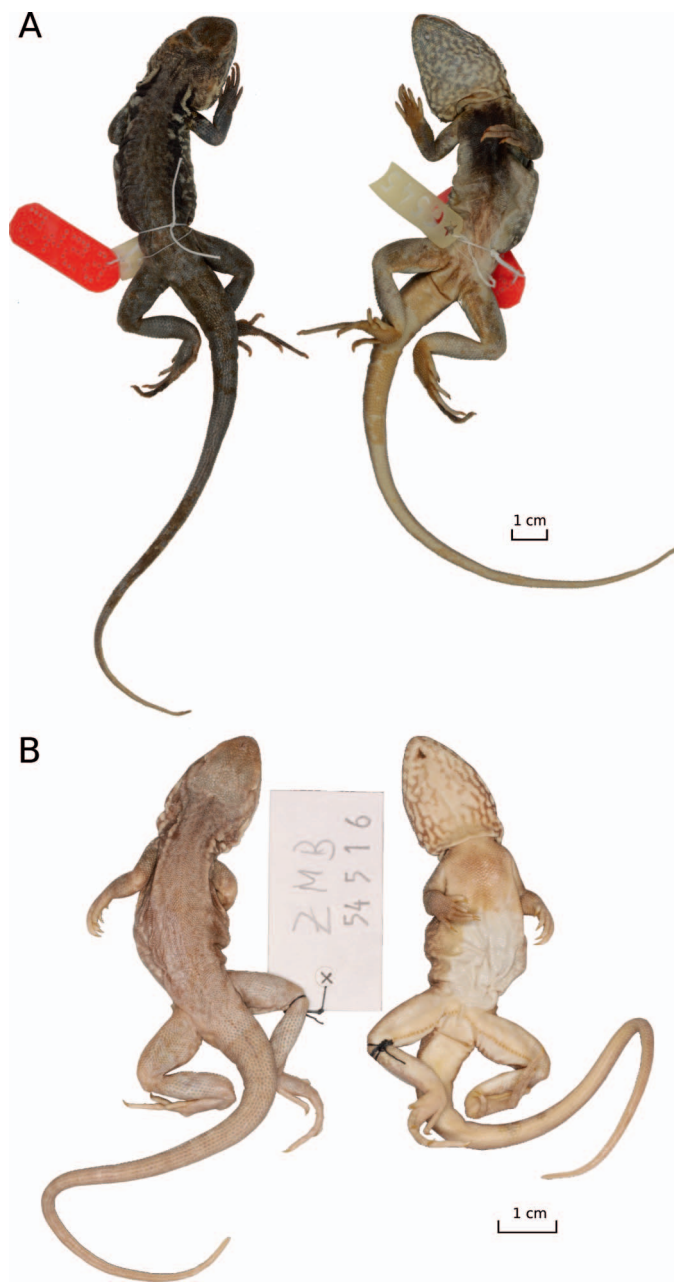


Fig. 5. (A) Dorsal (left) and ventral (right) photographs of the lectotype of *Ctenophorus decresii* (Duméril and Bibron, 1837; MNHN 6545). This specimen is an adult male collected from Kangaroo Island, South Australia, in January 1803 (photos: Nicolas Vidal, Muséum national d'Histoire naturelle Paris). (B) Dorsal (left) and ventral (right) photographs of the lectotype of *Ctenophorus modestus* (Ahl, 1926; ZMB 54516). This specimen is a subadult male from "Australien" without an exact locality or reference to a collector or donor (photos: Frank Tillack, Museum für Naturkunde Berlin).

along the upper jaw, and beneath the tympanum terminating at the neck. The extent of this coloration varies among individuals and depends on location. A broad black lateral stripe begins posterior to the eye, becoming thicker posterior to the tympanum and terminating at the groin. A thin cream, yellow, or orange stripe begins at the tympanum and terminates just posterior to the shoulder (Figs. 1H, 4C). On the ventral surface, males are cream with orange flushes on the belly, hindlimbs, and the length of the tail during the

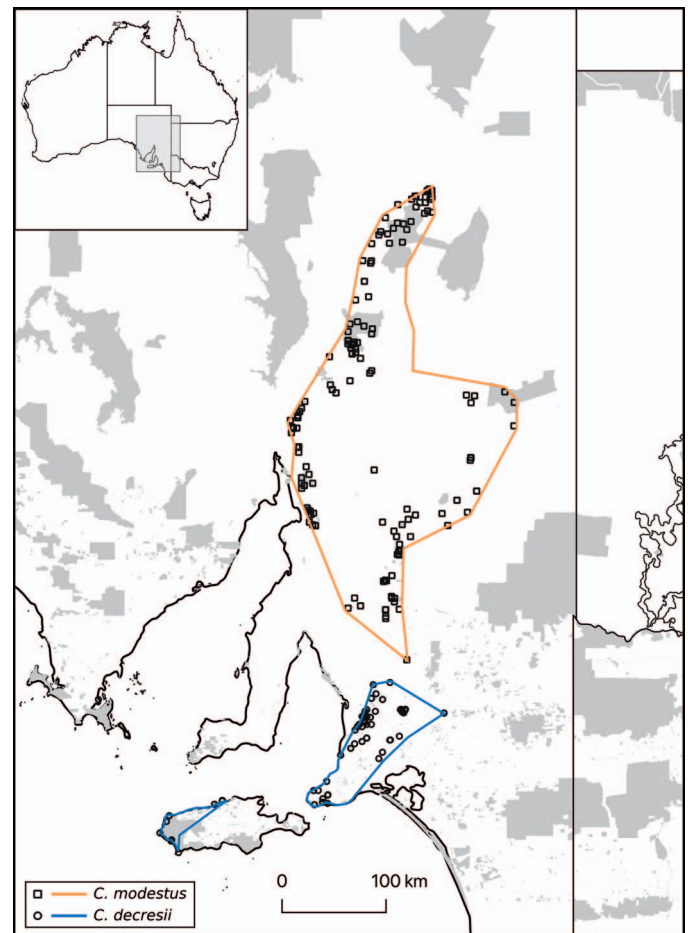


Fig. 6. Geographic distribution of *Ctenophorus modestus* (squares) and *C. decresii* (circles) based on specimens in Australian Museums from the Atlas of Living Australia (data: <https://doi.org/10.26197/5d91626857226>); coordinates which were likely inaccurate (e.g., unsuitable habitat) were removed. Protected areas described in the Collaborative Australian Protected Areas Database (CAPAD, 2018) are shown as gray areas. The extent of occurrence is shown for *C. modestus* (49,102 km²; orange lines) and *C. decresii* (6,604 km² total [mainland: 5,772 km²; Kangaroo Island: 832 km²], blue lines).

breeding season. A dark chest patch tapers to a point midbody and sometimes extends along the undersides of the forelimbs. This dark patch may vary in intensity, from black to gray. Male throat coloration varies among individuals with distinct gray, orange, yellow, and orange-yellow morphs (Teasdale et al., 2013; Fig. 1D–G). Base throat color sometimes overlain with gray reticulations or with a distinct black mark in the center of the throat.

Adult females are cryptically colored, predominantly gray-brown to orange-brown, densely patterned with darker and lighter speckling (Fig. 4D) and sometimes a thin, pale vertebral line. Similar to males, a black lateral stripe runs along the flanks, but sometimes less prominently than in males. White to cream on the ventral surface, with varying degrees of gray reticulations on the throat. Orange to yellow flushes on the belly and gular region during the breeding season. Juveniles resemble adult females in coloration and pattern. Color patterning remains visible in fresh spirit-preserved specimens but fades with time.

Measurements (mm) and meristic characters of lectotype.—(Bilateral meristics as left [L] and right [R]) SVL, 52.9; TL, 95.6; AGL, 24.3; HL, 18.1; HW, 14.0; HD, 7.8; EYE, 3.8; SL, 6.6; JL, 8.3; NW, 5.3; HUML, 7.7; RADL, 8.5; HANL, 11.7; FINL, 5.6; FEML, 14.5; TIBL, 17.4; FOOT, 21.3; TOE, 11.5; SUPRA, 15L/16R; INFRA, 18L/19R; ROSNAS, 4–5L,5R; SUPRANAS, 4L/3–4R; INTERNAS, 12; SDL, 25L/25R; FP, 22L/20R.

Distribution and natural history.—*Ctenophorus modestus* inhabits rocky areas and outcrops, sheltering in rock crevices, similar to other members of the *C. decresii* group (Gibbons, 1979). The species occurs throughout the Flinders and Olary Ranges in South Australia, Australia (Figs. 2C, 3A, 6). These lizards occupy habitats ranging from well-watered to semi-arid, with sparse vegetation and are active in hot weather (Houston, 1974; Gibbons, 1979). Adults occur almost exclusively on rocks, but juveniles may be found among surrounding vegetation up to 100 meters away (Houston, 1974; Gibbons and Lillywhite, 1981). Adults perch conspicuously on elevated sites to bask and/or perform territorial and courtship displays (Gibbons, 1979). If disturbed, they will run into a crevice or beneath a rock slab. Predators are predominantly birds but likely also include elapid snakes (Gibbons and Lillywhite, 1981; Stuart-Fox et al., 2004).

Comparisons among species in the *C. decresii* complex

Similar species.—Members of the *C. decresii* species group differ most markedly in male coloration and geographic distribution. The distribution of *C. modestus* does not overlap with four other species in the *C. decresii* species group (*C. decresii*, *C. mirrityana*, *C. rufescens*, *C. tjantjalka*). The dorsal color pattern of *C. modestus* is very similar to that of *C. mirrityana* which occurs in the Barrier Ranges of western New South Wales, but can be distinguished by the absence of a thinner non-continuous orange stripe within the black lateral stripe, absence of a dark median throat stripe in males, and a larger head relative to SVL (McLean et al., 2013). *Ctenophorus tjantjalka* occurs in the low stony hills and eroded creek lines of the Lake Eyre Basin in northern South Australia and has a shorter, deeper head relative to *C. modestus*. Male *C. tjantjalka* are uniform light blue above with salmon flanks and lack the dark lateral stripe of *C. modestus*. *Ctenophorus rufescens* occurs primarily in the granitic ranges of north-western South Australia. Both sexes of *C. rufescens* are rusty to medium brown, lacking both the bright yellow, orange, or blue coloring on the head of male *C. modestus* and the dark lateral stripe in juvenile and female *C. modestus*. It is most likely that *C. modestus* may be confused with *C. fionni*, which occurs west of Spencer Gulf and Lake Torrens in South Australia. Male *C. fionni* exhibit extensive geographic variation in coloration (Houston, 1974) and do not differ consistently in any morphological trait from *C. modestus*. Available keys (e.g., Cogger, 2018) differentiate between *C. modestus* and *C. fionni* based on the presence of scattered pale tubercles on the flanks on the former; however, this is primarily diagnostic of *C. decresii sensu stricto*. Additional diagnostic traits are needed to allow *C. fionni* to be distinguished from most other members of the *C. decresii* group independent of a collection locality.

In the northern-most part of its geographic range, *C. modestus* occurs in sympatry with *C. vahnappa*. These species can be distinguished by adult male coloration, juvenile and female coloration, and morphology of the snout and

vertebral scales. Adult male *C. vahnappa* have red variegations on the sides of the body that tend to align in vertical bars and no dark lateral stripe, whereas adult male *C. modestus* lack red reticulations and have a dark lateral stripe. Juvenile and adult female *C. vahnappa* also lack the dark lateral stripe, which is present in *C. modestus*. *Ctenophorus vahnappa* have wrinkled snout scales, whereas the snout scales are keeled in *C. modestus*. In *C. vahnappa*, the vertebral scales are keeled, whereas they are smooth in *C. modestus*.

There are notable differences in male throat coloration between *C. modestus* and *C. decresii sensu stricto*. Male *C. modestus* have orange, yellow, orange-yellow, or gray throats (Fig. 1D–G), whereas male *C. decresii* have blue throats (Fig. 1A–B). The black lateral stripe is relatively straight-edged in *C. modestus* compared with the irregular edge in *C. decresii* (Fig. 1C, H). *Ctenophorus modestus* and *C. decresii* also differ significantly in six morphological characters, with both sexes of *C. modestus* having higher SVLs (*C. modestus* male: 66.3–84.6 mm, female: 65.1–82.9 mm; *C. decresii* male: 65.2–77.5, mm female: 61.9–74.13 mm), greater numbers of supralabial (*C. modestus* male: 13–18, female: 13–17; *C. decresii* male: 12–16, female: 12–18) and infralabial scales (*C. modestus* male: 13–18, female: 14–18; *C. decresii* male: 12–16, female: 11–16), and males of *C. modestus* having longer jaws (*C. modestus* male: 0.16–0.21 mm; *C. decresii* male: 0.15–0.2 mm; values adjusted for SVL), deeper heads (*C. modestus* male: 0.13–0.18 mm, *C. decresii* male: 0.13–0.17 mm; values adjusted for SVL), and fewer femoral pores (*C. modestus* male: 34–45; *C. decresii* male: 40–46; McLean et al., 2013).

Conservation status.—*Ctenophorus decresii* (including *C. modestus*) is currently classified as Least Concern by the International Union for Conservation of Nature Red List of Threatened Species (IUCN, 2012; Melville et al., 2018). The taxonomic separation of the northern and southern lineages into *C. modestus* and *C. decresii*, respectively, warrants a reevaluation of each species' conservation status. Both have distributions that are more restricted than the original distribution of *C. decresii sensu lato*. To measure the extent of occurrence (km²) for *C. modestus* and *C. decresii sensu stricto*, we drew minimum convex polygons encompassing occurrences based on all specimens in Australian Museums, downloaded from the Atlas of Living Australia. The extent of occurrence for *C. modestus* is 49,102 km² (Fig. 6) and falls almost entirely within the Flinders Lofty Block (FLB) bioregion as delineated by the Interim Biogeographic Regionalisation for Australia (IBRA version 7; Department of the Environment, 2012). The extent of occurrence for *C. decresii* is 6,604 km² (mainland: 5,772 km²; Kangaroo Island: 832 km²; Fig. 6), distributed within both the FLB and Kanmantoo (KAN) bioregions. The FLB and KAN bioregions consist of 8.9% and 20.3% protected areas (CAPAD, 2018; Table 3). However, the distributions of *C. modestus* and *C. decresii* overlap minimally with protected areas, except in the northern Flinders Ranges and on Kangaroo Island (Fig. 6).

The species is locally abundant in suitable habitat in the southern Flinders Ranges and Olary Ranges (Gibbons and Lillywhite, 1981); however, suitable rocky habitat is fragmented and most vegetation has been cleared in the southern part of their range. Further, the population of *C. modestus* north of Blinman (31°05'37.1"S, 138°40'41"E) in the northern Flinders Ranges is predicted to decline under future climate scenarios (Walker et al., 2014). The IUCN

Table 3. Amounts and types of protected areas relevant to the distribution of *Ctenophorus decresii sensu lato*. For the Flinders Lofty Block (FLB) and Kanmantoo (KAN) IBRA bioregions: total area (ha) of the region, total protected area (ha) within the region, percentage of area protected of total area, and percentage of total protected area within each IUCN Protected Area Category: Ia ('Strict Nature Reserve'), Ib ('Wilderness Area'), II ('National Park'), III ('National Monument or Feature'), IV ('Habitat/Species Management Area'), V ('Protected Landscape/Seascape'), VI ('Protected area with sustainable use of natural resources'). Data from CAPAD (2018).

Bioregion	Total area (ha)	Protected area (ha)	% protected	% Protected area per IUCN category						
				Ia	Ib	II	III	IV	V	VI
FLB	6,615,765	591,396	8.9	39.1	0.0	34.6	3.4	0.9	0.0	22.0
KAN	812,414	164,881	20.3	7.0	42.2	23.6	21.9	0.6	0.0	4.4

assessment acknowledges a decreasing population trend due to this range contraction (Melville et al., 2018). A better understanding of temporal variation in population density is needed to assess population trends in the northern part of the geographic distribution of both species.

Ctenophorus decresii may merit conservation management due to its more restricted and fragmented distribution. The total extent of occurrence for the species is less than 20,000 km² (i.e., 6,604 km²). Further, the habitat is fragmented, given that the species occurs only in rocky areas with low to moderate vegetation cover (criteria B1-a). *Ctenophorus decresii* is particularly vulnerable to habitat loss due to human development and bush rock removal (Michael et al., 2010). Although the FLB and KAN bioregions have both experienced grazing pressure from sheep, cattle, and feral goats leading to habitat degradation and clearing, it has occurred more severely in the KAN bioregion (Environment Australia, 2000; Bastin, 2008). Therefore, *C. decresii* likely has a higher risk conservation status than *C. modestus*. Land clearing has had detrimental impacts on genetic variation in ecologically similar species (Driscoll, 2004; Driscoll and Hardy, 2005; Levy et al., 2010), and vegetation clearance around rock outcrops reduces dispersal between patches of suitable habitat in saxicolous species (Stow et al., 2001; Levy et al., 2010).

Bush rock removal has been implicated in the decline of several threatened reptile species (Michael et al., 2010; Fitzsimons and Michael, 2017; Michael and Lindenmayer, 2018). Additionally, habitat loss and fragmentation resulting from agriculture creates remnant edge habitats where reptiles experience significantly higher predation risk (Hansen et al., 2019). Furthermore, the degree to which populations of *C. decresii* have been impacted by recent extensive bushfires on Kangaroo Island and in Cudlee Creek on the mainland (ca. December 2019–January 2020) are still unknown. Although continued monitoring is necessary, the bushfires are likely to negatively impact many subcriteria of B1-b (i–ii: geographic range, iii: area, extent, and/or quality of habitat, iv: number of locations or subpopulations, v: number of mature individuals).

Throat polymorphism.—The throat color polymorphism in *C. modestus* is well characterized by a large body of literature. Throat coloration is a sexual signal, develops before sexual maturity, is fixed for life, and does not vary with body size (Gibbons and Lillywhite, 1981; Stuart-Fox, 2002), and may function in rival recognition (Osborne et al., 2012). Four discrete male throat morphs (i.e., orange, yellow, orange-yellow, gray) are present in all surveyed populations (Teasdale et al., 2013) with morph frequencies influenced by local environmental conditions (mean annual aridity index and vegetation cover; McLean et al., 2015). The four morphs

employ different behavioral strategies, with the gray and orange morphs being the least and most aggressive and bold, respectively, and the yellow morph's behavior dependent on the competitor's morph (Yewers et al., 2016). These alternative behavioral strategies also correspond to different hormone profiles (Yewers et al., 2017). Throat morphs are associated with MHC supertypes with gray morphs twice as likely to possess supertype four (Hacking et al., 2018).

The genetic and biochemical basis of throat coloration in *C. modestus* has been characterized. Throat morphs are autosomally inherited and controlled by at least two loci. The extent of orange or yellow within morphs behaves as a quantitative (polygenic) trait (Rankin et al., 2016). Orange and yellow skin coloration are produced from a combination of pteridine pigments (self-synthesized) and carotenoid pigments (acquired through the diet), whereas gray skin is produced from melanin pigments (McLean et al., 2017).

Ctenophorus modestus and *C. decresii* share tetrachromatic visual systems with well-developed color vision and no significant differences in spectral sensitivity or opsin expression (Yewers et al., 2015; Dong et al., 2019b). Throat morphs of *C. modestus* vary in conspicuousness, as perceived by agamid lizards (Teasdale et al., 2013). Gray morphs are the least chromatically conspicuous and orange and orange-yellow morphs are the most conspicuous against rock and lichen backgrounds. The throat colors of *C. decresii* and *C. modestus* are locally adapted to be more conspicuous against native lichen than non-native lichen as perceived by agamid lizards (McLean et al., 2014b).

Biology.—The mating season of *C. modestus* is from September to December. Females produce clutches of between 3–7 eggs, commonly laying two clutches in one breeding season (maximum of three clutches; Dong, Rankin, McLean, Stuart-Fox, unpubl.). At oviposition, eggs have a mass of 1.16±0.19 g (mean±SE) and offspring hatch in 52–65 days when incubated at 28–28.5°C (Rankin et al., 2016; Dong et al., unpubl.). There are low rates of multiple paternity within clutches: a 4.3% rate (1 in 23 clutches) in a wild population (Hacking et al., 2017), and rates of 3.7% (1 in 27 clutches; Dong et al., unpubl.) and 0% (0 in 25 clutches; Rankin et al., 2016) in captive populations. An incubation temperature of 28.5°C yielded a sex ratio of 1:0.72 (males:females; *n* = 58, 3 unsexed; Rankin et al., 2016) and 28°C yielded a sex ratio of 1:0.57 (males:females; *n* = 58, 11 unsexed; Dong et al., unpubl.). It is not definitively known whether the species exhibits genetic sex determination (GSD) or temperature-dependent sex determination (TSD). Previous studies on the reproductive biology of *C. decresii sensu lato* demonstrating TSD in the species were conducted on individuals from New South Wales (Harlow, 2000; McFadden and Harlow, 2007),

which have since been re-classified as *C. mirrityana* (McLean et al., 2013). Dragon lizards in the family Agamidae include both GSD and TSD species, with both occurring within the same genera (see references in Ezaz et al., 2009). Further empirical studies are needed to establish the sex-determining mechanisms of both *C. modestus* and *C. decresii*.

Few published studies have focused solely on *C. decresii sensu stricto*. The species has a similar breeding season of September–December. Females produce one clutch per breeding season (rarely a second clutch) of between 3–6 eggs (Dong et al., unpubl.). At oviposition, eggs have a mass of 1.51 ± 0.21 g and will hatch in 57–61 days when incubated at $28 \pm 0.12^\circ\text{C}$ (mean \pm SE; Dong et al., unpubl.). There was no evidence for multiple paternity from 14 clutches in a captive population (Dong et al., unpubl.), and an incubation temperature of 28°C yielded a sex ratio of 1:0.71 (males:females; $n = 58$, 11 unsexed; Dong et al., unpubl.).

DISCUSSION

Wells and Wellington (1985) previously resurrected *C. modestus* (Ahl, 1926) from synonymy with *C. decresii* and nominated the larger of the two syntypes as a lectotype. However, they provided no rationale or evidence to support this decision. We regard Wells and Wellington's (1985) recognition of *C. modestus* as unavailable for application for the following reasons: (1) they did not provide a "... definition that states in words characters that are purported to differentiate the taxon" as required under Article 13(a)(i–ii) of the third edition of the Code of Zoological Nomenclature applicable at that time; (2) Ahl's (1926) description of *C. modestus* also did not meet this criterion, so Wells and Wellington (1985) also did not provide a "... bibliographic reference to such a published statement..." as required by the same article of the Code. Suggesting that the larger female syntype be regarded as the lectotype suggests Wells and Wellington may not have viewed the syntypes of *C. modestus* because it was well understood at the time that adult male coloration is a key character used to differentiate species in the *C. decresii* group (Houston, 1974; Gibbons and Lillywhite, 1981). The importance of male coloration in species diagnosis in this group has become even clearer since then (Johnston, 1992; McLean et al., 2013) and is the reason we have nominated the smaller male syntype as the lectotype. While Ahl's (1926) description of *C. modestus* does not provide a clear means of "... differentiating the taxon" required of publications in 1985, it does conform to the requirements of the Code for species descriptions prior to 1931. Therefore, the name *Amphibolurus modestus* Ahl (1926; now *Ctenophorus modestus*) is available for application. Furthermore, Ahl's male syntype of *C. modestus* is clearly conspecific with the taxon referred to previously as the "northern race" (Houston, 1974) or "northern lineage" (McLean et al., 2013, 2014a) of *C. decresii sensu lato* based on morphology (Fig. 3B) and dorsal patterning (Fig. 5B). The female syntype is consistent with the "northern race/lineage" of *C. decresii sensu lato* based on morphology, although it is not objectively determinable based on phenotype.

We have resurrected *C. modestus* from synonymy with *C. decresii* on the basis of genetic distinctiveness and diagnostic differences in male coloration, mensural, and meristic characters. Historical changes in the distribution of suitable habitat appear to have had an influence on the evolution of

the *C. decresii* species group. Extensive rock in the past presumably allowed ancestors of the *C. decresii* group to disperse widely in southern Australia with subsequent isolation leading to the evolution of different species (Houston, 1974). Further, the combination of sexual selection and local adaptation to environmental differences in climate, vegetation, and native rock and lichen coloration have likely contributed to divergence in male coloration between species (McLean et al., 2014b).

DATA ACCESSIBILITY

Supplemental material is available at <https://www.ichthyologyandherpetology.org/h2020064>. Unless otherwise indicated in the figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source in accordance with the Creative Commons Attribution CC BY License.

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