

## A NEW SPECIES OF *CTENOPHORUS* (LACERTILIA: AGAMIDAE) FROM LAKE DISAPPOINTMENT, WESTERN AUSTRALIA

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**ABSTRACT:** *Ctenophorus* is the largest genus of Australian agamid lizards, with an extensive radiation in the arid zone. Here we describe a distinctive new dragon species—*Ctenophorus nguyarna*—from the isolated Lake Disappointment in Western Australia. The new species is characterised by heterogeneous dorsal scales tending to form vertical rows on the flanks, a reticulated orange and black background color, and black bars on the dorsum and black vertical bars on the tail. To provide a molecular context as to the distinctiveness and placement of the new species we analysed five sequences of *Ctenophorus* sp. nov., two new sequences of *C. salinarum* and 11 previously published sequences of *Ctenophorus* species, representing ~1573 bases of the mitochondrial genome. Our phylogeny strongly supports at least two independent origins of salt lake specialization in both the western and eastern arid zone. Based on molecular data the sister taxon is *C. salinarum*, which is also associated with salt lakes in Western Australia. The other specialist is the Lake Eyre Dragon (*C. maculosus*) from South Australia that lives on and under the salt crust itself, and has a number of unique derived characters for *Ctenophorus*. There are likely to be other new species of agamid lizards in Australia's vast and little-explored arid zone.

**Key words:** Agamidae; Arid zone; *Ctenophorus*; Molecular phylogeny; Salt lakes; Western Australia

*CTENOPHORUS* (Fitzinger, 1843) is the most diverse genus of dragon lizards in Australia and is comprised of 24 species (Melville et al., 2001) that are almost all distributed throughout the arid areas of the continent. They are a prominent element of the Australian arid zone herpetofauna owing to their abundance, conspicuous social behavior, fleetness, and brilliant coloration. *Ctenophorus* dragon species exhibit a variety of different forms and lifestyles including dorsoventrally flattened rock-dwelling dragons (e.g., *C. ornatus*), extremely swift sand-dwelling dragons (e.g., *C. isolepis*), robust dragons that excavate burrows (e.g., *C. nuchalis*), and large dragons that inhabit open ground (e.g., *C. cristatus*).

This diverse genus also includes species that have exploited the barren, salt-encrusted surfaces of saline lakes with halophytic vegetation. The salt lake environment is particularly harsh with high temperatures, high reflectance off the white bed of the lake, a lack of water, and exceptionally saline conditions. Despite these conditions, two species of *Ctenophorus* are known to occur on and around these lakes. One highly

divergent species, *C. maculosus*, occupies Lake Eyre and other largely featureless salt lakes in the arid interior of South Australia (Mitchell, 1973). This unusual dragon has a number of behavioral and morphological traits that allow it to occupy the lake surface, and excavates burrows below the salt crust. The only other species currently known to be strongly associated with salt lakes is *C. salinarum*. Originally described as a subspecies of *C. pictus*, *C. salinarum* is associated with the halophytic vegetation on or around the margins of salt lakes as its specific name indicates (Storr, 1966; Wilson and Knowles, 1988; B. Maryan, personal observation). However, *C. pictus* and *C. reticulatus*, which also have been observed on claypans and salt lakes, do not show the extreme association with salt lakes as in *C. maculosus* and *C. salinarum*.

Here we describe a new species of agamid from a remote salt lake in central Western Australia. In 1996, a single specimen was collected when biologists stopped for vehicle repairs near Lake Disappointment on the Canning Stock Route. A recent collecting expedition was made in September 2004 where 11 further specimens were collected and new observations were made to provide sufficient material for our description. We also discuss the ecological, morphological and

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TABLE 1.—Primers used in amplification and sequencing of mitochondrial DNA. R = G or A; H and L = primers whose extensions produce heavy and light strands, respectively.

Human position	Gene	Sequence (5'→3')	Reference
L3914	ND1	5'-GCCCATTTGACCTCACAGAAGG-3'	Macey et al., 1998 <sup>1</sup>
H4980	ND2	5'-ATTTTCGTAGTTGGGTTTGRIT-3'	Macey et al., 1997a
H4419	tRNA MET	5'-AAGCAGTTGGCCCATRCC-3'	Macey et al., 2000
H5934a	CO1	5'-AGRGTCCAATGTCTTTGTGRIT-3'	Macey et al., 1997a

<sup>1</sup> L3914 was incorrectly referred to as L3878 in Macey et al., (1998), as noted by Melville et al., (2001).

physiological features associated with salt lake specialization in the genus *Ctenophorus*.

## MATERIALS AND METHODS

### *Morphometrics*

This study is based on the examination of material held in the Western Australian Museum (hereafter, WAM; Appendix 1; the R prefixes are excluded below). The terminology for most morphometric measurements and meristic counts follows (Johnston, 1992). A total of 17 linear measurements and 10 meristic counts were made on the 12 available specimens of the new taxon along with a selection of *C. salinarum* ( $n = 41$ ) and *C. pictus* ( $n = 34$ ) for comparison. We chose these species for comparison based on previous accounts of species groups within *Ctenophorus* and on preliminary genetic results.

The following linear measurements were taken with digital vernier calipers to the nearest 0.1 mm: snout-vent length (SVL), tail length (TL), head length from tip of snout to posterior margin of tympanum (HL), head width at tympanum (HW), head depth immediately behind eye (HD), snout length from tip of snout to anterior margin of eye (SL), snout width at nostrils (SW), eye length (EyeL), axilla-groin length (AG), forelimb length (FLL), hand length (from wrist to tip of 4<sup>th</sup> finger, excluding claw and sheath; HL), 4<sup>th</sup> finger length (4FL), claw length of 4<sup>th</sup> finger (CLF), hindlimb length (HLL), foot length (from base of foot to tip of 4<sup>th</sup> toe, excluding claw and sheath; FL), 4<sup>th</sup> toe length (4TL), and claw length of 4<sup>th</sup> toe (CLT).

The following meristic counts were made: number of scales between rostral and nasal (prenasal), subnasal scale rows between nasal and supralabials, number of internasal scales across top of snout between nostrils, number

of supralabial and infralabial scales, number of subdigital lamellae on 4<sup>th</sup> finger (SL4<sup>th</sup>F) and 4<sup>th</sup> toe (SL4<sup>th</sup>T) from point of divergence of the digit up to (but not including) the claw-sheath, number of femoral and preanal pores, number of midbody scale rows (MBS) counted midway between axilla and groin and number of paravertebral (PV) scales counted from immediately behind head to a point opposite the vent.

### *Molecular Systematics*

*Specimen information.*—Museum numbers and localities of voucher specimens from which morphological measurements were taken and DNA was extracted are provided in Appendix 2.

*Laboratory protocols and alignment of DNA sequences.*—Genomic DNA was extracted from liver, or muscle using Qiagen QIAamp tissue kits. Different primer combinations were used to amplify from genomic DNA (Table 1). Amplification of genomic DNA was performed by an initial denaturing and enzyme activation step at 95 C for 15 min followed by 40 cycles of denaturing at 95 C for 20 s, annealing at 50 C (or 55 C) for 20 s, and extension at 72 C for 60 s. All successful amplifications were sequenced by a commercial company (Macrogen, Korea) using the same forward and reverse primers used in the PCR reactions (Table 1). Sequence chromatograms were edited and a single contiguous sequence for each specimen produced using Sequencher (Gene Codes Corporation, USA). DNA sequences were aligned using tRNA secondary structure models (Macey et al., 1997b) and amino acid translations (for protein coding regions).

*Phylogenetic analyses.*—Phylogenetic trees were estimated using PAUP\* beta version 4.0b410a (Swofford, 2002). Maximum likeli-

TABLE 2.—Morphological characteristics and sexual dimorphism in *Ctenophorus nguyarna* sp. nov., *C. salinarum*, and *C. pictus*. The first line presents the mean ( $\pm$ SD), with ranges on the second line.

Character:	<i>C. nguyarna</i> sp. nov.		<i>C. salinarum</i>		<i>C. pictus</i>	
	Males (N = 8)	Females (4)	Males (23)	Females (18)	Males (20)	Females (14)
Snout-vent length (mm)	73.4 $\pm$ 3.4 (68.4–78.4)	56.3 $\pm$ 3.9 (52.1–60.8)	65.9 $\pm$ 6.2 (54.5–77.9)	61.7 $\pm$ 3.7 (55.2–71.0)	59.7 $\pm$ 6.0 (51.5–74.9)	60.3 $\pm$ 5.8 (48.7–70.8)
Tail length (mm)	127.2 $\pm$ 6.6 (119.9–140)	94.3 $\pm$ 9.1 (86–104)	106.2 $\pm$ 9.9 (91–128)	82.6 $\pm$ 8.4 (64.5–97.0)	111.2 $\pm$ 14.0 (90–144)	104.7 $\pm$ 9 (89–127)
Head length (mm)	19.7 $\pm$ 1.4 (18.4–22.5)	14.8 $\pm$ 1.2 (13.5–16.0)	18.8 $\pm$ 1.7 (15.5–22.5)	16.1 $\pm$ 1.4 (14.5–19.4)	17.2 $\pm$ 1.6 (14.7–20.6)	15.9 $\pm$ 1.1 (14.5–18.1)
Head width (mm)	14.5 $\pm$ 1.3 (12.8–16.8)	10.5 $\pm$ 1.2 (9.3–12.2)	14.0 $\pm$ 1.3 (11.5–16.5)	12.2 $\pm$ 0.9 (11.0–14.1)	12.5 $\pm$ 0.9 (11.3–14.0)	11.6 $\pm$ 0.8 (10.1–13.3)
Axilla-groin (mm)	32.5 $\pm$ 2.3 (29.0–35.3)	26.3 $\pm$ 2.7 (22.8–29.2)	27.5 $\pm$ 4.0 (20.5–36.7)	28.6 $\pm$ 3.1 (24.4–34.9)	25.9 $\pm$ 3.1 (21.5–33.2)	27.4 $\pm$ 3.4 (21.9–34.9)
Supralabial scales	15.9 $\pm$ 0.6 (15–17)	15.6 $\pm$ 1.2 (14–17)	16.9 $\pm$ 1.3 (15–19)	16.5 $\pm$ 1.1 (14–18)	15.1 $\pm$ 1.0 (14–17)	15.5 $\pm$ 0.9 (14–17)
Subdigital lamellae:						
4 <sup>th</sup> finger	16.9 $\pm$ 1.8 (13–19)	16.8 $\pm$ 1.3 (15–18)	13.6 $\pm$ 1.3 (12–16)	13.1 $\pm$ 1.2 (12–16)	14.5 $\pm$ 2.0 (12–19)	14.1 $\pm$ 1.4 (12–16)
4 <sup>th</sup> toe	26.3 $\pm$ 0.9 (25–28)	23.8 $\pm$ 0.5 (23–24)	23.6 $\pm$ 1.5 (20–28)	22.9 $\pm$ 1.9 (20–26)	25.6 $\pm$ 2.1 (22–28)	26.4 $\pm$ 1.7 (24–28)
Femoral pores	17 $\pm$ 1 (16–18)	—	17 $\pm$ 2 (13–21)	16 (N = 1)	15 $\pm$ 1 (13–19)	14 $\pm$ 2 (N = 5) (12–16)
Preanal pores	10.5 $\pm$ 1.3 (9–12)	—	9.3 $\pm$ 2.2 (4–14)	—	8.9 $\pm$ 2.0 (4–14)	7 $\pm$ 1.2 (N = 4) (12–17)
Midbody scale rows	116.1 $\pm$ 8.5 (105–133)	103.5 $\pm$ 8.5 (98–116)	125.3 $\pm$ 6.1 (116–140)	122 $\pm$ 8.1 (110–143)	107.6 $\pm$ 6.6 (93–118)	105.9 $\pm$ 7.5 (95–122)
Paravertebral scales	64.0 $\pm$ 5.2 (56–70)	60.8 $\pm$ 4.2 (55–64)	67.9 $\pm$ 6.1 (60–84)	69.3 $\pm$ 5.7 (57–80)	57.6 $\pm$ 4.0 (52–64)	59 $\pm$ 4.3 (52–66)

hood was used to estimate a phylogenetic tree that maximized the probability of the observed data. ModelTest version 3.06 (Posada and Crandall, 1998) was used to compare goodness-of-fit of different models of sequence evolution to the data, and to generate optimal likelihood settings. The best-fitting model parameters were fixed and the overall most parsimonious tree(s) were used as starting trees for branch swapping in 25 heuristic searches with random addition of taxa to find the overall best likelihood topology. Bootstrap resampling was applied to assess support for individual nodes using 500 bootstrap replicates with 10 heuristic searches featuring random addition of sequences.

The SH test (Shimodaira and Hasegawa, 1999), a likelihood-based test of topologies, was used to evaluate the statistical significance of the favored tree relative to alternative hypotheses. Phylogenetic topologies were constructed in MacClade (Maddison and Maddison, 1992) and used as constraints in PAUP\*. A search, using the maximum-likelihood settings deter-

mined previously in ModelTest and starting from a neighbor-joining tree, was used to estimate a phylogenetic tree that maximized the probability based on the alternative hypothesis. An SH test, using 10,000 replications, was then run to determine whether the favored likelihood tree is significantly better than an alternative or whether their differences are attributed to chance alone.

## RESULTS

### *Morphometrics*

Table 2 summarizes the characters that varied most strongly among *Ctenophorus* sp. nov., *C. salinarum*, and *C. pictus*. *Ctenophorus* sp. nov. reaches the largest maximum size of the three, has a longer tail, and more subdigital lamellae under the 4<sup>th</sup> finger. *Ctenophorus pictus* has a much narrower head than the other two species. Midbody scale rows and paravertebral scales decreased in the order: *C. salinarum*, *Ctenophorus* sp. nov., and *C. pictus*. Further elaboration of morphological traits is described below.

*Molecular systematics*

Five sequences of *Ctenophorus* sp. nov., two new sequences of *C. salinarum* and 11 previously published sequences of *Ctenophorus* species, representing ~1573 bases of the mitochondrial genome, were analysed. Two further Amphibolurinae taxa were included as outgroups: *Pogona vitticeps* and *Diporiphora bilineata*. Of the 1573 unambiguous sites in 20 aligned sequences, 724 were variable and 528 were parsimony informative.

Among 56 likelihood models TVM + G had the highest likelihood and was significantly favored over alternatives by hierarchical likelihood-ratio tests. Model parameters were: alpha = 0.3679; substitution rates AC = 1.6745, AG = 9.0517, AT = 1.127, CG = 0.001 and CT = 10.3918; and empirical base frequencies A = 0.3679, C = 0.3079, G = 0.1136, and T = 0.2106. Twenty-five random-addition heuristic searches using a neighbor-joining tree as the starting topology yielded a single optimal tree with a log-likelihood score of -9987.68 (Fig. 1).

Maximum-likelihood bootstrap resampling using 500 bootstrap replicates (Fig. 1) supports monophyly of *Ctenophorus* sp. nov. (bootstrap 100%). The monophyly of *Ctenophorus* sp. nov. is supported by an SH test (difference in  $-\ln L$ : 85.72;  $P < 0.001$ ). Within *Ctenophorus* sp. nov. there was virtually no genetic divergence, with four of the lizards having identical mtDNA sequence and one (157970) being  $\approx 0.03\%$  divergent from other individuals. *Ctenophorus salinarum* is strongly supported as the sister taxa of *Ctenophorus* sp. nov. (bootstrap 100%). The phylogenetic separation of these two taxa is also strongly supported, with the three individuals of *C. salinarum* sampled forming a monophyletic group (bootstrap 100%).

## SPECIES ACCOUNT

*Ctenophorus nguyarna* sp. nov.  
(Lake Disappointment Dragon)

*Holotype*.—157979 in the Western Australian Museum, an adult male collected on 14 September 2004 by B. Maryan and B. Budrey at the Savory Creek Mouth, Lake Disappointment Western Australia (23° 21' 08" S; 122° 40' 03" E). Liver stored at -75 C.

*Paratypes*.—All collected at Lake Disappointment: 126970 (male), near Onegunyah Rockhole (23° 38' 37" S, 122° 44' 33" E) in May 1996; 157970 (male), Lake Views near Savory Creek Mouth (23° 22' 17" S, 122° 40' 29" E) on 15 September 2004; 157971 and 157972 (males), Lake Views (23° 17' 54" S, 122° 42' 06" E) on 17 September 2004; 157973 and 157974 (females), northwestern tip (23° 14' 02" S, 122° 42' 12" E) on 14 September 2004; 157975 (female) and 157976 (male), northwestern tip (23° 14' 02" S, 122° 42' 12" E) on 19 September 2004; 157977 and 157978 (males), northwestern tip (23° 14' 02" S, 122° 42' 12" E) on 14 September 2004; and 157980 (female), Savory Creek Mouth (23° 21' 08" S, 122° 40' 03" E) on 14 September 2004.

*Diagnosis*.—A member of the Australian genus *Ctenophorus* (Fitzinger 1838), characterized by a row of tectiform scales that starts from the nostril, extends back below eye, and ends above the tympanum. *Ctenophorus nguyarna* is a medium-sized robust burrowing dragon with a blunt head and moderately built short limbs. Within *Ctenophorus*, possession of heterogeneous dorsal scales distinguishes *C. nguyarna* from *C. caudicinctus*, *C. femoralis*, *C. fordi*, *C. isolepis*, *C. maculatus*, *C. mckenziei*, *C. ornatus*, *C. rubens*, *C. scutulatus*, and *C. yinnietharra*. Possession of a stout (non-depressed) head distinguishes *C. nguyarna* from the rock-dwelling species *C. decresii*, *C. fionni*, *C. rufescens*, *C. tjantjalka*, and *C. vadnappa*. Within *Ctenophorus*, only *C. cristatus* possesses a strong vertical nuchal crest and dorsolateral fold with spines. A lack of a row of spines on the basal portion of the tail distinguishes *C. nguyarna* from *C.* (= *Rankinia* [Wells and Wellington, 1985] or *Tympanocryptis* [Peters, 1864]) *adelaidensis* and *C. parviceps*.

The remaining species of *Ctenophorus* have been placed in to a *C. reticulatus* group or the more exclusive *C. pictus* group consisting of just *C. pictus* and *C. salinarum*. In *C. nuchalis* and *C. reticulatus* the nostril is on a rounded canthus rostralis (versus below a sharp canthus rostralis in *C. nguyarna*). The more obscure less colorful pattern and smaller ear of *C. gibba* distinguishes it from *C. nguyarna*. The nostrils of *C. clayi* are elongate (versus

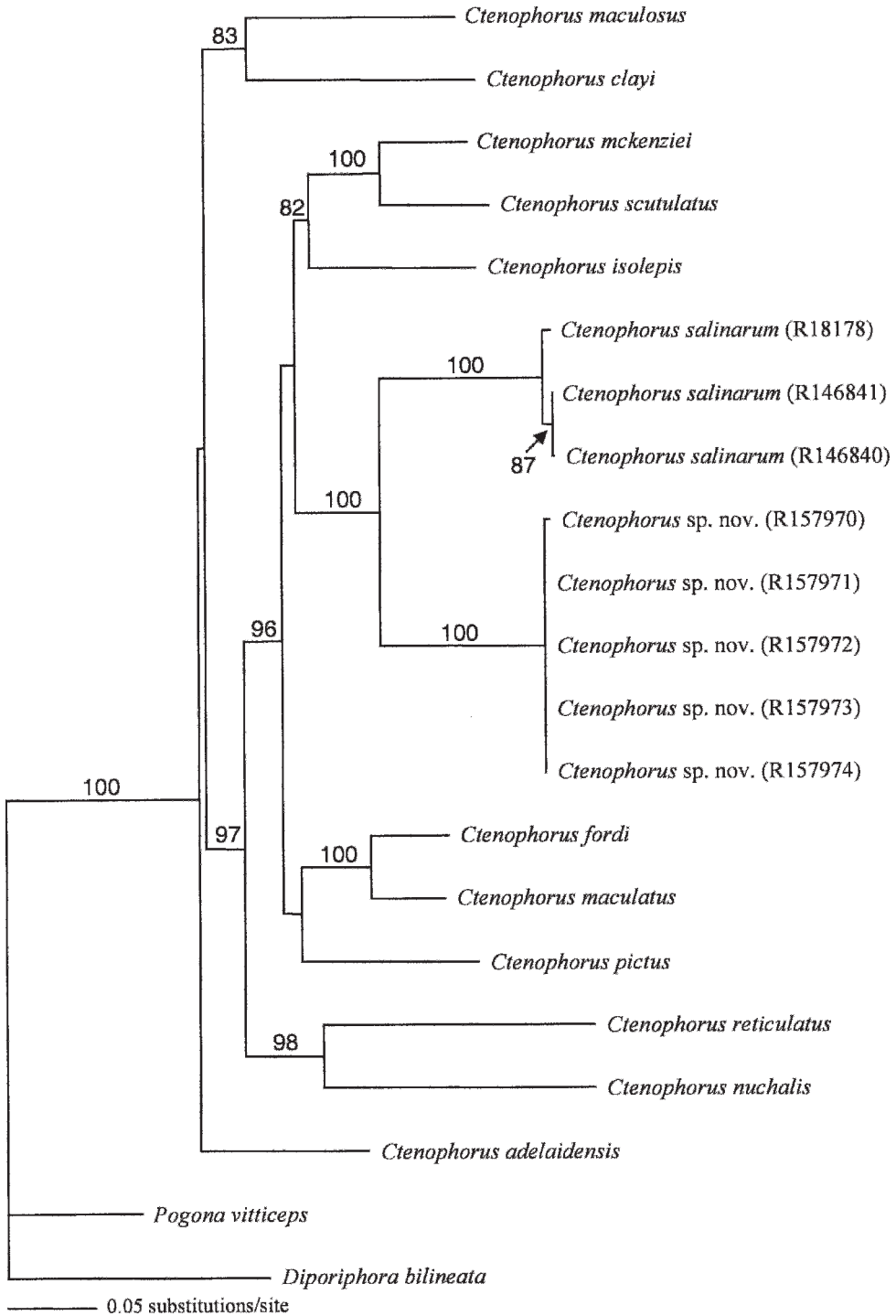


FIG. 1.—Phylogram of the maximum-likelihood tree under the TVM + G model, which indicates phylogenetic relationships between *Ctenophorus nguyarna* sp. nov. and other *Ctenophorus* species. Bootstrap values are presented above branches.

round in *C. nguyarna*), and *C. maculosus* has a covered tympanum (versus exposed).

*Ctenophorus nguyarna* is distinguished from both *C. salinarum* and *C. pictus* by larger body size, less prominent ridge of tectiform scales below eyes, longer eyelids (especially lower), and a different color pattern including thin white vertical bars on the sides and strong vertical bars on the tail. It is further distinguished from *C. salinarum* by having a narrower head with weakly keeled scales (versus smooth head scales), more numerous scattered enlarged dorsal scales tending to form transverse bars on sides (versus fewer enlarged scales tending to form transverse bars on dorsum near midline), vertebral scales along midline weakly keeled (versus smooth), and sexual dimorphism in color pattern (versus monomorphic). It is further distinguished from *C. pictus* by having a wider head, scattered enlarged dorsal scales (versus homogeneous scales) and pale short narrow claws (versus long thick claws with dark culmen on upper surface).

*Description of holotype.*—Male; SVL = 76.8 mm; TL = 131 mm; HL = 20.81 mm; HW = 15.5 mm; HD = 12.7 mm; SL = 8.7 mm; SW = 7.2 mm; EyeL = 4.8 mm; AG = 31.8 mm; FLL = 32.2 mm; HL = 11.1 mm; 4FL = 7.0 mm; CLF = 1.5 mm; HLL = 50.5 mm; FL = 24.7 mm; 4TL = 12.6 mm; CLT = 1.6 mm; SL<sup>4th</sup>F = 17; SL<sup>4th</sup>T = 25; prenasal = 5L/5R; subnasal = 4L/4R; internasals = 12; supralabials = 15; infralabials = 16; femoral pores = 16L/16R; preanal pores = 10; MBS = 116; PV = 60. Figure 2A shows the holotype in life.

A robust, medium-sized dragon lizard. Head relatively short, wide and deep, slightly rounded profile of snout; nostril located below acute canthus rostralis (Fig. 3). Body and basal half of tail moderately dorsoventrally depressed; adpressed hindlimb reaches tympanum; toes compressed laterally, their outer edge denticulate. Scales on top of head and snout low in lateral profile (not protruding), smoothest and largest along midline and smaller above orbit. Occipital scales and those on nape much smaller and subconical than head scales. Series of enlarged tectiform scales extends back from nostril, continues below eye, then rising and terminates above

tympanum; scales are flat and smooth near nostril, become more shelf-like beneath orbit, and increase in size as they curve up towards top of tympanum. Outer margins of eyelids fringed with row of acute scales with a reduction in length in the center of the upper eye lid and projecting scales on the lower eyelid. On the sides of the head there are loose folds of skin with small conical scales and occasionally larger scales; these folds extend obliquely up from above and behind tympanum, joining on the middle of neck with the dorsolateral fold. A strong gular fold curves back to above shoulder. Vertebral row of scales possess weak keels. Scales on flanks are small and subconical, mixed with pale smooth scales 2–3 times larger that are scattered towards midline and tending to be arranged transversely towards the ventral surface. Dorsal scales increase in size towards midline and are larger, flatter and more imbricate than nuchals with some scales being feebly keeled. Scales within the darker colored vertebral zone are homogeneous (unlike condition of lateral scales). Ventral scales smooth, imbricate and much larger than gulars and lateral scales (except the large white scales on back and sides). Scales on tail and dorsal surfaces of limbs are imbricate, moderately keeled and much larger than dorsal scales. Femoral and preanal pores are evenly spaced and slightly raised when gorged; each is located in a posterior notch on edge of scale and separated by much narrower scales. Pores arranged along full length of thigh in a more or less straight line and interrupted medially above vent. Subdigital lamellae bicarinate. Palmar and plantar scales very small and spinose. Claws relatively short and pale. Testes turgid with convolutions clearly visible (size of left testis: 5.3 × 3.6 mm; right: 4.9 × 3.6 mm). Vas deferens convoluted and thickened. The specimen has a longitudinal incision on the ventral surface, with perpendicular incisions on either end to create flaps for removing the liver and checking the condition of the testes. Both hemipenes everted but flaccid.

*Pattern in life.*—Ground color orange suffused with black, extending to basal portion of tail and fading on lower flanks. Unbroken broad silvery grey vertebral stripe extends



FIG. 2.—(A) holotype (157979) of *Ctenophorus nguyarna* sp. nov. from Lake Disappointment, Western Australia; (B) female *Ctenophorus nguyarna* sp. nov. (157980); (C) ventral view of male (157971); (D) male *Ctenophorus nguyarna* sp. nov. perched in samphire bush (*Halosarcia h. halocnemoides*); (E) typical habitat where the type series was collected on the edge of Lake Disappointment, Western Australia.

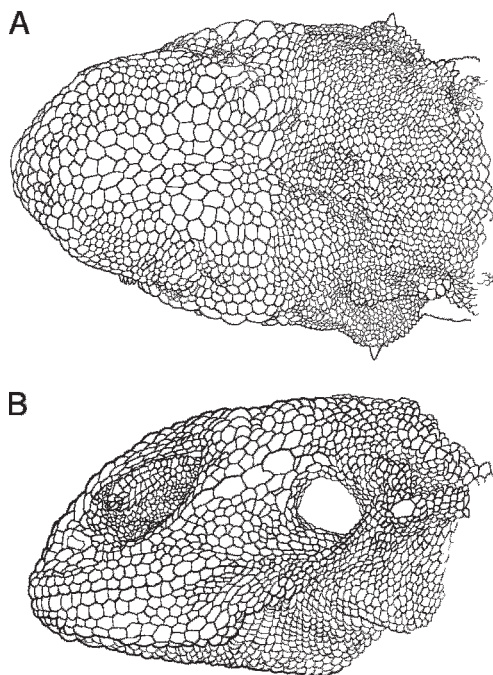


FIG. 3.—Dorsal (a) and lateral (b) views of the head scalation of the *Ctenophorus nguyarna* sp. nov. holotype (157979).

from nape and terminates diffusely on basal portion of tail. Vertebral stripe encloses series of eight large black straight to slightly angled bars. Remainder of body bears irregular small brown-edged yellow spots alternating with dark brown to black variegations. Towards the ventral surface, spots coalesce toward the ventral surface to form vertical bars along ventrolateral surface. On the sides of the tail, evenly spaced dark brown to black lateral bars (that fade distally) contrast sharply with white to silver gray interspaces. Similar to tail, the limbs are paler than rest of body with indications of dark variegations on forelimbs and bars on hindlimbs. The upper surfaces of the hands and feet are much paler than the rest of the limbs. Ventral surfaces are white, bearing black triangle on throat (diffuse and spotted), and broad kite-shaped patch on chest descending narrowly and broadening again before termination above groin.

*Pattern in spirit.*—The pattern remains strong after two years, but the vertebral stripe has turned a bluish gray and ground color is

darker than at capture. There is only a hint of yellow pigment around the spots and the orange is duller with considerable fading.

*Variation.*—Table 2 summarizes the morphological differences between male and female *C. nguyarna*. Ground color of non-holotype males is less vivid with duller orange hues, tending towards a salmon pink. One specimen has an orange flush only near hindlimbs that fades towards the middle of the back. Vertebral stripe or band relatively consistent among specimens in width and darkness; it extends to tail where it fades out basally or continues to nearly half the length of the tail. The number of large dark spots along midline range from 7 to 11. These spots are either paired across midline, are slightly offset, or staggered from each other across midline; some specimens show a combination of these arrangements. Transition from upper dorsal to lateral zone varies from very diffuse reticulations to a coarser, speckled pattern of orange, black and white. On the sides, the large white scales form weak to strong vertical bars, but some barring evident in all specimens. Ground color of tail ranges from mostly pale to grey proximally tending to orange distally. Vertical black bars on tail contrast strongly with ground color but gradually fade from the middle of the tail to nearly the tip. Width of the bars relative to interspaces near the proximal portion of the tail ranges from almost equal to 2–3 times narrower. Bars extend to near midline of tail (almost touching) to being widely separated medially. Forelimbs range from fairly light (similar to vertebral area) to light with contrasting dark black barring. Similarly, the rear limbs can have diffuse variegations from up to 9 transverse black bars on each leg with a hint of barring on the foot and toes. Non-holotype males possess a more extensive triangular black patch on the chin, roughly mirroring shape of jaw and asymmetric in two individuals (157970, 157976). Black patch on underside of body begins broadly at shoulders, constricting 1/4 to 1/3 along chest towards groin, then widening again before terminating 1/2 way to nearly all the way to groin. Posterior end of patch either tapers sharply or fades broadly. Basking males develop varying levels of a yellow flush on shoulders, anterior chest, forelimbs, and lower flanks.



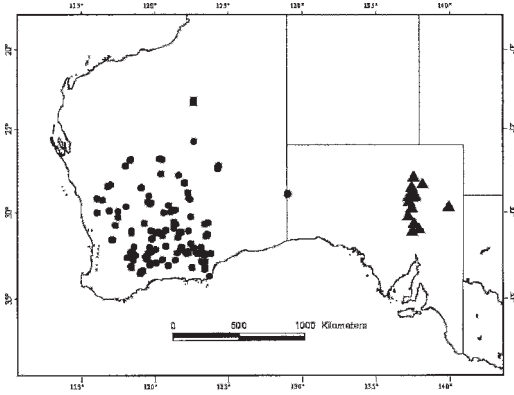


FIG. 4.—Map of Australia showing the distribution of *Ctenophorus salinarum* from south Western Australia (●), *C. maculosus* from Lake Eyre, South Australia (▲), and *C. nguyarna* sp. nov. from Lake Disappointment (■).

Adult females (Fig. 2B) are less strongly patterned than breeding males. Ground color is grayish orange extending along tail and fading on lower flanks. Vertebral gray band is less dark (sometimes suffused with white) and narrower than in males. Series of up to eight staggered black spots occur from nape to basal portion of tail, the spots often extending outside the vertebral gray band. Dark vertebral spots and bars on tail slightly margined with orange (not seen in any of the males). A series of up to seven dorsolateral brown spots between axilla and groin (only a hint apparent in males). Sides bear scattered enlarged cream-colored scales alternating with dark brown variegations; spots coalesce to form weak bars on one specimen (157980). Limbs and lateral sides of tail bear evenly spaced dark brown bars. Ventral surfaces are white (no black patches as in males).

Owing to lack of material, it is unknown whether juveniles are similar to females in aspects of morphology and coloration as for other *Ctenophorus* (Storr et al., 1983).

*Coloration in spirit.*—The adult male (126970) that has been in preservative for 9 yr has faded considerably so that the ground color is pale gray and the spots on dorsum and bars on tail are barely visible. The only remaining pattern is four black bars on vertebral region, with only traces of other bars. In recently preserved (<2 y) specimens the vertebral stripe becomes a bluish gray and

ground color appears darker. There is no yellow pigment around the spots and the orange has almost entirely faded (the holotype retains more orange coloration).

*Distribution and ecology.*—*Ctenophorus nguyarna* sp. nov. is known only from Lake Disappointment, a large salt lake basin located in the Little Sandy Desert in Western Australia (Fig. 4). The lake is accessible from the Canning Stock Route which runs along the western edge of the lake between Wells 18–20. Museum collections of agamids in the regions around the lake do not contain specimens of *C. nguyarna*. Searches of the areas immediately adjacent to the lake during the collecting trip in September 2004 failed to produce any *C. nguyarna*. Lizards collected by hand during the collecting trip inhabited samphire vegetation (*Halosarcia h. halocnemoides*) on the lake shoreline (there was no water in the lake at this time). Males were usually observed perched on the crowns of clumps, while females were active on the ground and were usually observed running from clump to clump on the bare salt-crust. *Ctenophorus nguyarna* was observed in areas supporting both sparse and moderately dense clumping *Halosarcia* (Figs. 2D,E). These observations suggest that *C. nguyarna* is closely tied to the habitat fringing the lake itself.

The first specimen (126970) was opportunistically collected during a ‘vehicle bog’ approximately 20 m from the edge of the lake in *Triodia* sandplain (M. Craig, personal communication). This suggests that *C. nguyarna* forages away from the lake shoreline in the marginal vegetated zone. *Ctenophorus maculosus* from Lake Eyre moves in this vegetated zone when seasonal flooding occurs (Houston, 1978), and *C. nguyarna* may also do this.

Similar to *C. pictus*, *C. salinarum* and *C. maculosus*, the new species also excavates a shallow burrow with an oblique entrance with an adjacent escape exit that terminates just below the surface (Ehmann, 1992; Greer, 1989; Mitchell, 1973). All burrow entrances were at the base of low vegetation within or near the edge of the *Halosarcia* clump. The timing of capture of most specimens of this species in September 2004 suggests that most activity occurs during mid-morning and late

afternoon. Males were easily observed basking in elevated positions (>1 m) perched on top of *Halosarcia* clumps, with some individuals allowing a close enough approach for in-situ photography (Fig. 2D). Characteristic head-bobbing behavior of males was combined with vigorous back-arching and tail-waving.

The holotype male raised his nuchal and dorsal crests once, and was photographed (Fig. 2A). The positioning of the black blotches along the midline creates a strongly contrasting pattern when the dorsal crest is raised. However, further observations are necessary to better determine the frequency and social contexts of the various display components. In areas where *Halosarcia* clumps were dense, males were regularly spaced (~20 m apart) suggesting the existence of exclusive territories.

When moving between clumps, some males would resume the elevated position momentarily and then return to the original clump when first seen. By contrast, females were rarely seen, were never observed perched in clumps and were seen only on the open ground between clumps close to a burrow entrance that they retreated in to when approached too closely. Several dragons were observed feeding on black harvester ants on the surface of the salt crust.

**Reproduction.**—All the males collected in spring in September 2004 had large testes (width: 2.8–3.7 mm; length: 5.2–5.8 mm) with convoluted surfaces (tubules clearly visible) and convoluted, thickened vas deferens. The male collected in autumn in May 1996 had small smooth testes (2.8–3.1 × 4.3–4.6) with convoluted but thin vas deferens indicating this individual was not reproductively active at this time.

All four paratype females collected in September 2004 were clearly reproductively active with varying stages of egg development. Female 157980 (60.4 mm SVL) contained four eggs measuring 12.7 × 6.1 mm, 12.1 × 7.4 mm, 11.2 × 5.4 mm and 10.9 × 5.9 mm, female 157975 (51.7 mm snout–vent length) contained two eggs measuring 14.1 × 6.5 mm and 15.4 × 5.7 mm, female 157973 (57.3 mm SVL) contained a single undeveloped egg measuring 7.0 × 6.4 mm, and female 157974 (54.0 mm SVL) possessed four small non-

yielding follicles. These observations suggest that females have full-term eggs during spring with a clutch size of 1–4. In 2004 two major cyclones passed through this region and may have led to a favorable year for reproduction.

**Comparison with other species.**—*Ctenophorus nguyarna* is a medium-sized robust burrowing dragon with a blunt head and moderately built short limbs. The diagnosis reviews how *C. nguyarna* differs from the other 24 currently recognized species of *Ctenophorus*. Rock-dwelling *Ctenophorus* (the *C. caudicinctus*, *C. decresii*, and *C. ornatus* groups; Wilson and Knowles, 1988; see also Ehmann, 1992; Houston, 1978; Houston and Hutchinson, 1998; Storr et al., 1983 and in “Taxonomic issues in *Ctenophorus*” below) possess a dorsoventrally flattened head, presumably to penetrate crevices when retreating. In contrast, the head of *C. nguyarna* is robust with no indication of flattening. The “military dragons” (*C. maculatus* and *C. scutulatus* groups) are swift dragons with long limbs and tails that possess homogeneous dorsal scales, whereas *C. nguyarna* has shorter limbs and tail and has heterogeneous scales. The large-bodied *C. cristatus* possess a prominent spinose nuchal crest and dorso-lateral folds, absent in *C. nguyarna*. The allopatric *C. gibba* has a much less colorful and distinctive dorsal pattern, has a much blunter snout, and a small tympanum.

Our morphological and molecular results suggest *C. nguyarna* is closely related to *C. salinarum* and *C. pictus*, and we focus on these two species below. *Ctenophorus nguyarna* shares similar body proportions and meristic characters with *C. pictus* and *C. salinarum*, with extensive overlap (Table 2). It is readily separated from these other species of *Ctenophorus* by the combination of characters given in the diagnosis. *Ctenophorus nguyarna* differs in having much shorter and paler claws lacking a dark upper culmen or pale brown appearance. In *C. nguyarna* the enlarged tectiform scales curving up from below eye to above ear are weakly keeled and appear smaller and flatter below eye.

The presence of heterogeneous dorsal scales distinguishes *C. nguyarna* and *C. salinarum* from *C. pictus*. In *C. nguyarna* there are large scales scattered across the

dorsum that tend to form transverse bars on the sides, especially towards ventral surface. Most of these larger scales are coincident with pale spots that do not encroach upon midline of dorsum. In *C. salinarum*, the larger scales tend to be arranged in transverse rows especially towards midline, and are also usually coincident with pale bars or spots.

Some aspects of color pattern are similar in all three species. However, the pale pigment of *C. nguyarna* is more irregular, consisting of finer randomly scattered spots (particularly in males), compared to the regular transverse bars or rows of pale spots in *C. pictus* and *C. salinarum* that alternate with a series of dark spots on the dorsum. *Ctenophorus nguyarna* has a combination of dark bars or spots (when bars are broken along midline) on dorsum and distinct lateral bars on tail. Both *C. pictus* and *C. salinarum* have less prominent dark spots on dorsum and mostly pale rings encircling tail. In addition to these morphological differences, *Ctenophorus nguyarna* appears to be entirely allopatric to both *C. pictus* and *C. salinarum* (Fig. 4).

In September 2004, no other *Ctenophorus* species were observed in direct syntopy with *C. nguyarna*. However, *C. i. isolepis* and *C. nuchalis* occupy the adjacent *Triodia* sandplain habitat. Female *C. i. isolepis* are similar to female *C. nguyarna* but differ in having much longer tails and a color pattern that includes a clear dorsolateral stripe. *Ctenophorus nuchalis* has a similar build but possess a reticulate color pattern and widely spaced femoral pores that curve upwards on thigh. *Ctenophorus reticulatus* is geographically distant to *C. nguyarna*, but is superficially similar in aspects of color pattern and scalation; it can be distinguished from *C. nguyarna* by larger size, dark claws and position of nostril on (rather than below) canthus rostralis.

The Lake Eyre Dragon, *C. maculosus*, occurs in similar habitat to *C. nguyarna*, but is only distantly related (Melville et al., 2001; Fig. 1). *Ctenophorus maculosus* also has black blotches on the back, but they are more widely separated than in *C. nguyarna*. The tympanum is covered in *C. maculosus*, whereas it is clearly visible in *C. nguyarna*. Both species share a relatively long lower eyelid for *Ctenophorus*.

*Etymology*.—The specific epithet *nguyarna* is a name used by the Kartujarra people to refer to Lake Disappointment. Pronunciation—the first “n” is silent.

#### DISCUSSION

The *Ctenophorus* dragon lizards of Australia are a fascinating example of a continent-wide adaptive radiation (Melville et al., 2006). The description of *C. nguyarna* sp. nov. from the remote Lake Disappointment in Western Australia brings the number of species within the genus *Ctenophorus* to 25 (Melville et al., 2001; Wilson and Swan, 2003). Morphological and molecular evidence indicates *C. nguyarna*'s sister taxon is *C. salinarum*, a member of the *C. reticulatus* species group, or the more exclusive *C. pictus* group. Our molecular phylogeny also provided evidence for two independent origins of associations with salt lakes in the arid zone. Below we review current conceptions of species groups within *Ctenophorus* in light of our results, then discuss the origins of salt lake specialization within this genus.

#### *Taxonomic Issues in Ctenophorus*

Our morphological and molecular work supports *C. nguyarna* as a distinct species. *Ctenophorus nguyarna* is currently only known from Lake Disappointment but exploration of other remote salt lakes such as Lake McKay in northern Western Australia may increase its range. The sister species is *C. salinarum*, with a 12.5% sequence divergence between them. Previously, several authors have proposed various species groups within *Ctenophorus* on morphological and behavioral grounds. For example, previous treatments have suggested that *C. salinarum* is a member of a group of burrowing species, known as the “*reticulatus*-group” (Ehmann, 1992; Greer, 1989; see also Wilson and Knowles, 1988) which consists of seven species: *C. pictus*, *C. salinarum*, *C. clayi*, *C. gibba*, *C. nuchalis*, *C. maculosus*, and *C. reticulatus*. All have short limbs and tails, stocky bodies and inhabit burrows. In addition, there is a tendency in this proposed group for species to have small or covered eardrums (Greer, 1989). Our molecular work suggests that *C. nguyarna* is a member of this putative species group, as it

is the sister species of *C. salinarum*. However, previous molecular work, using the same segment of mtDNA as our study rejects the phylogenetic affinities between the species of the “*reticulatus* group” (Melville et al., 2001). This previous report showed that *C. clayi* and *C. maculosus* are basal species within *Ctenophorus* and found little molecular evidence for any of the previously defined species groups, including the *C. decresii*, *C. maculatus*, *C. reticulatus* and *C. scutulatus* groups. Our study supports this molecular work, providing no further evidence for the phylogenetic validity of these species groups.

Another traditional taxonomic grouping, known as the “*pictus* group”, includes *C. pictus* and *C. salinarum*. Our study, along with previous molecular work (Melville et al., 2001) does not support this phylogenetic relationship. This result is somewhat surprising, as *C. salinarum* was originally described as a subspecies of *C. pictus* based on morphological and behavioural traits (Storr, 1966). These species, including *C. nguyarna*, are ground-dwelling and are associated with low, sparse shrubs and dig short burrows for shelter (Greer, 1989). However, the molecular phylogenies place these burrowing species in clades with fleet, non-burrowing taxa such as *C. isolepis* and *C. fordi*. Overall, molecular studies have not strongly supported long-standing *Ctenophorus* species group concepts based on morphology. Further molecular work on agamid dragons is necessary to better resolve relationships within this genus.

#### *Evolution of Salt Lake Association in Ctenophorus*

Our phylogenetic analyses and statistical hypothesis testing has shown that salt lake associations have evolved independently on at least two occasions in *Ctenophorus* (*C. maculosus* and *C. salinarum* + *C. nguyarna*). These lineages separated early in the radiation of *Ctenophorus*, with molecular divergences between these species greater than 17%. Using a molecular clock estimate of 1.3% divergence between lineages per million years (Macey et al., 1998; Weisrock et al., 2001) or a more conservative estimate of 2% per million years (Brown et al., 1979; Wilson et al., 1985), these two populations diverged

between 8.5 to 13 mya. This period corresponds to a burst of speciation in *Ctenophorus* that was probably associated with the late Miocene, a time of climatic and vegetational changes (Melville et al., 2001). This was a period of global drying and cooling, as ice rapidly accumulated at the poles, sea levels fell, rainfall decreased and forests retreated (White, 1994). Prior to these climate changes, the central Australian vegetation consisted of rainforests and coniferous forests. When the Miocene climate began to cool, the vegetation changed dramatically. Evidence for these changes comes from records of grass pollen in northwestern Australia indicating an open savannah by the mid Miocene (Kershaw et al., 1994). Plants now associated with salt lakes, such as the Australian endemic Salicornioideae (halophytic plant species), are believed to have diversified during the late Miocene to Pliocene. Increasing aridity caused the formation of extensive salt lakes within the last 1 my along endorheic paleodrainage channels (White, 1994; Shepherd et al., 2004).

The Lake Eyre Dragon, *C. maculosus*, is extremely specialized for life on salt lakes and has no close relatives (Fig. 1). It diverged from its closest extant relative, *C. clayi*, during the mid-late Miocene. There are many characteristics that align *C. maculosus* and *C. clayi*—both species have small stocky bodies, short blunt heads, and have very long comb-like scales on the lower eyelid. It was the subject of a detailed study by Mitchell (1973) and as a result is one of the more well-known agamids. Behaviorally, *C. maculosus* digs short burrows like *C. clayi*, except these burrows are under the crust of salt lakes in areas where the cracking crust is very dry and with a damp sandy substrate below (Mitchell, 1973). *Ctenophorus maculosus* has a number of unique characters within *Ctenophorus*: a covered tympanum and an extremely pale dorsal patterning that provides camouflage on the salt lake surface. In addition, *C. maculosus* is the only Australian dragon to have a submissive behavioral display that involves flipping on to the dorsal surface when a dominant conspecific approaches (Mitchell, 1973).

In the west, *C. salinarum* and *C. nguyarna* seem to have diverged in the late Miocene,

which coincides with the stabilization of drainage patterns (Bunting et al., 1973). There was 12.3–12.7% sequence divergence between these species. Using the rates of sequence divergence as above, this translates to divergences from 6–10 mya, much earlier than when salt lakes are believed to have formed (ca. 1 mya). This points to three separate origins of salt lake dwelling, with two sister species adapting to salt lakes independently in the western lineage. Further speculation of such biogeographic hypotheses should be tested by sequencing different genes that evolve at different rates, using multiple fossil calibration points, and better understanding of the physiogeographic evolution of the arid zone.

An interesting difference between these two salt lake dwellers from western Australia is the degree of sexual dimorphism. *Ctenophorus nguyarna* displays dimorphism in size, coloration and behaviour similar to most other congeners (Greer, 1989). In contrast, male and female *C. salinarum* are similar in appearance and males are less conspicuous than other *Ctenophorus* species. The causes and consequences of the lack of sexual dimorphism in *C. salinarum* are unknown.

Association with salt lakes may have evolved through a progression, with dragons moving into open areas and inhabiting peripheral salt lake habitat. For example, *C. salinarum* is common in salt lakes and clay pans in Western Australia, but they also occur in other habitat types (Wilson and Knowles, 1988; B. Maryan, personal observation). However, *C. nguyarna* appears to be more closely associated with salt lakes as it has been observed only on the fringes of Lake Disappointment. Finally, *C. maculosus* is the most specialized of the salt lake species, occurring both on the edges and on and below the salt crust of the lakes. These scenarios are speculative as salt lake associations have evolved only a few times within agamid lizards. The discovery of *C. nguyarna* at the isolated Lake Disappointment highlights the need for further exploration of other salt lakes in Australia's arid interior.

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## APPENDIX I

## Comparative Material Examined for Morphology

*Ctenophorus salinarum* (Storr, 1966)

Sex indicated in brackets.

- 59760 (M) 50 km E Clear Streak Well (32° 26' 00" S 122° 55' 00" E); 59864 (M) Boingaring Rocks (32° 28' 00" S 123° 11' 00" E); 62336 (M) 21 km E Jindabinbin Rockhole (32° 25' 00" S 122° 19' 00" E); 65205 (F) 2 km N Lake Cronin (32° 21' 30" S 119° 45' 30" E); 65212 (M) 3 km N Lake Cronin (32° 21' 00" S 119° 45' 00" E); 65279 (F) 30 km E Forrestania (32° 14' 00" S 120° 05' 00" E); 65324 (F), 65325 (M), 65335 (M) 3 km E McDermid Rock (32° 00' 45" S 120° 45' 50" E); 65503 (F), 65518 (M), 65554 (F) 9 km NNE Buningtonia Spring (31° 21' 20" S 123° 36' 10" E); 67518 (F) Bending Nature Reserve (32° 21' 00" S 118° 27' 00" E); 68270 (M) 19 km S Queen Victoria Rocks (30° 38' 00" S 123° 41' 00" E); 72297 (M) Boorabbin (31° 12' 00" S 120° 18' 00" E); 72325 (M) 23 km NE Heartbreak Ridge (31° 53' 00" S 122° 28' 00" E); 72519 (F), 72521 (M), 72523 (F) 11.5 km ENE Buningtonia Spring (31° 19' 30" S 123° 36' 30" E); 72684 (M) 13.7 km ENE Comet Vale (29° 54' 00" S 121° 15' 05" E); 72822 (M), 72870 (F) 6.7 km NNW Mount Linden (29° 15' 55" S 122° 24' 00" E); 72871 (M) 6.2 km NNW Mount Linden (29° 16' 15" S 122° 24' 00" E); 78580 (M) 13 km NW Eristoun Homestead (28° 16' 00" S 122° 03' 00" E); 78743 (F) 14 km S Woolgangie (31° 17' 00" S 120° 33' 00" E); 87438 (M) Lake Barlee (29° 04' 00" S 119° 36' 00" E); 89979–980 (M's) Lake Magenta (33° 27' 00" S 119° 11' 00" E); 93272 (M) 11 km NE Mount Heywood (33° 16' 00" S 122° 35' 00" E); 93393 (M), 93394–396 (F's), 93397 (M), 93398 (F) Boingaring Rocks (32° 28' 00" S 123° 11' 00" E); 93412 (F) 22 km S Mount Malcolm (32° 22' 00" S 122° 51' 00" E); 93847 (F) Juranda Rockhole (33° 13' 00" S 123° 27' 00" E); 94296 (F) 1 km W Mordetta (32° 51' 00" S 118° 33' 00" E); 96608 (M) 27 km SSW Mouroubra Homestead (29° 59' 00" S 117° 31' 00" E); 119587 (F) 5 km E Norseman (32° 12' 00" S 121° 46' 00" E).

*Ctenophorus pictus* (Peters 1866)

Sex indicated in brackets.

- 19033 (M) Iltoon near Lake Ell (29° 14' 00" S 127° 43' 00" E); 24055 (M) Pidinga, South Australia (30° 52' 00" S 132° 06' 00" E); 31878 (F) Eucla (31° 43' 00" S 128° 54' 00" E); 34520 (M) Serpentine Lakes (28° 30' 00" S 129° 01' 00" E); 37684 (F), 37685 (M) Coopers Creek, South Australia (28° 00' 00" S 139° 00' 00" E); 44932 (F) Etadunna Station, South Australia (28° 43' 00" S 138° 38' 00" E); 44945 (F), 44946 (M) Near Etadunna Homestead, South Australia (28° 36' 00" S 138° 31' 00" E); 45359 (M) Lake Gidgi (29° 03' 00" S 126° 01' 00" E); 55813 (F) 34 km NE Etadunna Homestead, South Australia (28° 29' 00" S 138° 42' 00" E); 66450 (M) 40 km SW Eucla (31° 47' 00" S 128° 29' 00" E); 66906 (F) 4 km S Eucla (31° 43' 00" S 128° 54' 00" E); 80992 (F) 10 km SSE Cocklebidy (32° 12' 00" S 126° 12' 00" E); 91759 (M), 91763 (F), 91847 (F) 7 km ESE Kildwerinia Granite Rock (32° 04' 25" S 123° 59' 38" E); 91843 (M) 13 km E Kildwerinia Granite Rock (32° 04' 05" S 124° 04' 25" E); 91848 (M) 15 km E Kildwerinia Granite Rock (32° 03' 41" S 124° 05' 49" E); 101439 (M) Lake Ilma (29° 15' 00" S 127° 43' 00" E); 137663 (M) Eucla Telegraph Station (31° 42' 00" S 128° 53' 00" E).

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## APPENDIX 2

*Specimen Information for Genotyped Individuals*

Museum numbers, localities and GenBank accession numbers of voucher specimens from which DNA was extracted are provided below.

*Ctenophorus salinarum*: 146841, Goongarrie Station, Western Australia, GenBank# DQ683730; *C. salinarum*: 146840, Menzies to Sandstone Rd, Western Australia, GenBank# DQ683731; *C. nguyarna* sp. nov.: 157970–974, Lake Disappointment, Western Australia, GenBank#s DQ683732–6 (in that order).

Mitochondrial sequences of 10 previously published *Ctenophorus* species were used to determine the phylogenetic position of *C. nguyarna* sp. nov. within the genus (Melville et al., 2001). (SAMA = South Australian Museum, Adelaide.) *Ctenophorus clayi*: SAMA48593,

GenBank# AF375620, 12.2 km northwest of Mt. Cheesman, South Australia; *C. fordi*: SAMA31886, GenBank# AF375626, Mt. Finke, South Australia; *C. gibba*: SAMA45990, GenBank# AF375625, William Creek Rd., 20 km east of Coober Pedy, South Australia; *C. isolepis*: SAMA26194, GenBank# AF375629, 25 km southwest of Mabel Creek homestead, South Australia; *C. maculatus*: SAMA29397, GenBank# AF375628, 34 km south of Denham, Western Australia; *C. maculosus*: SAMA25909, GenBank# AF375621, Lake Eyre, South Australia; *C. mckenziei*: SAMA32266, GenBank# AF375631, Mitcherie Rockhole, South Australia; *C. pictus*: SAMA28208, GenBank# AF375635, 73 km north of Oodnadatta, South Australia; *C. salinarum*: SAMA18178, GenBank# AF375640, north of Serpentine Lakes, South Australia; *C. scutulatus*: SAMA29402, GenBank# AF375632, 1 km south of Wannoo, Western Australia.