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Source: Journal of Herpetology, 51(3) : 316-329

Published By: Society for the Study of Amphibians and Reptiles

URL: https://doi.org/10.1670/16-152

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Journal of Herpetology, Vol. 51, No. 3, 316–329, 2017
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Patterns of Variation in the Cranial Osteology of Three Species of Endemic Australian Lizards (*Ctenophorus*: Squamata: Agamidae): Implications for the Fossil Record and Morphological Analyses made with Limited Sample Sizes

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ABSTRACT.—**Australian Agamidae often are recovered from Australian Cenozoic fossil deposits but remain largely unidentified and unpublished. Accurate fossil identification could expand our understanding of the origin, distribution, evolution, and extinction of Australian agamid species over geologic time. We began to address this issue by critically examining skeletal morphologic features that were previously proposed for Australian Agamidae. We compared 60 morphological features (44 from the literature and 16 new features) for three taxa of the most speciose of the Australian agamid genera, *Ctenophorus caudicinctus* ($n = 18$), *Ctenophorus isolepis* ($n = 20$), and *Ctenophorus reticulatus* ($n = 20$). Of the 180 morphological features (60 per species) that were expected to be invariant for all specimens within a species, only 39 did not vary. All taxa have at least one unique feature that did not vary with ontogeny (i.e., apomorphy). Invariant features also are shared between two species or all three. Seventeen morphological features were invariant for all three taxa. In addition to invariant features, one to three morphological features varied within each species with either ontogeny or sex. We also found that few morphological features could be identified from disarticulated material. Given that the current museum collections are wholly inadequate for addressing these issues, larger collections of extant agamid skeletal material are needed to understand skeletal morphological variation. A fossil record of Australian Agamidae already exists; we just need to develop the tools to interpret it accurately.**

There are 480 extant lizard species currently recognized in the squamate clade Agamidae (Uetz et al., 2016). This increased from 350 a little over a decade ago (Heying, 2003). Species of the clade are present on Africa, Europe, Asia, and Australia as well as across insular Southeast Asia from the Malay Archipelago to New Guinea (Witten, 1993). Agamidae show lability of form and function that often is dependent on environment (Stuart-Fox and Owens, 2003; Melville et al., 2006; Östman and Stuart-Fox, 2011; Smith et al., 2011). Sexual dimorphism, ontogenetic variation, and other sources of phenotypic plasticity in the skeletal system remain largely unexplored for the group. Currently, agamids remain one of the most-poorly known of the major clades of lizards in terms of skeletal morphology (Conrad, 2008). The most-detailed studies of the skeletal anatomy of the group as a whole remain the pioneering work by Siebenrock (1895) and Moody (1980; unpubl. diss.). The compilation of morphological characteristics of Agamidae by Siebenrock (1895) included a list of 50 skeletal characteristics, 33 of which were from the cranium. Siebenrock reviewed 32 species and focused on morphological features he considered to be diagnostic at both the genus and species levels (Siebenrock, 1895). Subsequent reviews and observations of osteological features of Agamidae were made periodically through the decades by various authors including works on the skull (e.g., Camp, 1923; El-Toubi, 1945; Jollie, 1960; Evans, 2008) as well as more-holistic views of the skeleton (Waite, 1929; Badham, 1976; Greer, 1989b; Smirina and Ananjeva, 2007); however, all of these works relied heavily on Siebenrock's study as a foundation. The last systematic analysis of skeletal morphology of Agamidae was completed by Moody (1980), who identified and evaluated 70 cranial features as phylogenetically informative characters, including many of Siebenrock's original features. Moody (1980) examined a total of 861 specimens representing 120 species for osteological data and a subset of 317 specimens representing 45 genera to frame a hypothesis of relationships among them. In both the general and specific study, this meant that an average of seven individuals was observed for each taxon. Individual variation was not recorded by Moody (1980), and his scores for taxa presumably reflect the character state that occurred most often among specimens in his sample. Because his analysis was polarized by a hypothetical outgroup ancestor instead of an actual outgroup species, his results were ambiguous.

Subsequent work on osteology of agamids was completed as part of broader systematic analyses of Squamata as a whole (Estes et al., 1988; Caldwell, 1999; Conrad, 2008; Smith, 2011; Gauthier et al., 2012) as well as the reexamination of specific species (Harris, 1963; Pethiyagoda and Manamendra-Arachchi, 1998; Smirina and Ananjeva, 2007; Banzato et al., 2012). For Australian taxa in particular there are relatively few studies comparing agamid osteological diversity (Greer, 1989a; Hocknull, 2000; Fathinia et al., 2011; Smith et al., 2015) or the osteology of particular taxa (e.g., Cooper and Poole, 1973; Moazen et al., 2008; Bell et al., 2009; Porro et al., 2014), but a general synthesis still is lacking. In part, the relative paucity of modern data probably is because the group received little attention from Estes et al. (1988) in a work that laid the foundation for most modern morphological studies of squamates. The scant coverage in that work was a reflection of the uncertain phylogenetic position of the group within Iguania, itself a reflection of a general lack of systematically informative anatomical data.

A close relationship of Agamidae, Chameleonidae, and Iguanidae was recognized by Camp (1923), who aggregated the families into the suprafamilial group Iguania. Iguanians with acrodont tooth implantation—agamids and chamaeleonids—were united in Acrodonta by Estes et al. (1988) and were reconstructed as the sister taxon to Iguanidae (sensu lato). Phylogenetic relationships and nomenclature of the group Acrodonta are still being explored, but mitochondrial (Honda

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DOI: 10.1670/16-152

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et al., 2000; Macey et al., 2000) and nuclear (Hugall and Lee, 2004; Townsend et al., 2004; Wiens et al., 2012; Pyron et al., 2013) studies over the last 15 yr helped both to clarify relationships within the group and to establish its monophyly within Iguania. Molecular phylogenies of Agamidae coarsely follow geographic distribution, with endemic continent-level radiations (Honda et al., 2000).

Australian Agamidae.—The last major review of the Australian Agamidae recognized 78 species distributed within 14 genera (Wilson and Swan, 2013). Traditional classifications recognized several monotypic genera (e.g., *Moloch*, *Chelosania*, and *Chlamydosaurus*) as well as several speciose groups (e.g., *Diporiphora*, *Ctenophorus*, and *Amphibolurus*). Recent molecular phylogenies (Hugall et al., 2008; Rabosky et al., 2011; Melville et al., 2014) challenged the monophyly of many traditionally recognized genera, which was based primarily on soft-tissue characters, and a number of taxonomic rearrangements were proposed in recent years (Smith et al., 2011; Chen et al., 2012; Doughty et al., 2014; Edwards et al., 2015).

The diversity and increasingly recognized cryptic species of endemic Australian agamids is hypothesized to be a result of a relatively recent radiation. Agamids are thought to have reached Australia around 30 Ma, probably from insular Southeast Asia (Molnar, 1991; Hugall et al., 2008). Divergences within Australian Agamidae may have occurred after colonization to Australia, although this remains under study (Schulte et al., 2003; Hugall and Lee, 2004; Hugall et al., 2008).

Australian agamids are characterized by the early divergence of a relatively small number of specialized taxa compared to the huge diversity of desert specialists. Early divergences include the terrestrial *Moloch horridus*, the semiarboreal *Chelosania brunnea*, and several aquatic taxa within the genus *Hypsilurus* as well as in *Physignathus leseureii*. Among the remaining Australian agamids, the *Ctenophorus* clade is thought to have diverged around 21 Ma (Hugall et al., 2008) and perhaps diversified between 19 Ma (Hugall and Lee, 2004; Byrne et al., 2008; Hugall et al., 2008) and 12–11 Ma (Melville et al., 2001). Phylogenies constructed from mitochondrial DNA (Schulte et al., 2003; Collar et al., 2010; Rabosky et al., 2011; Smith et al., 2011) reveal great lability of habitat-associated traits and a number of cryptic species complexes which were not obvious from the data derived from nuclear DNA (Melville et al., 2001; Hugall et al., 2008; Levy et al., 2012; McLean et al., 2013). This is consistent with the hypothesis that clades containing cryptic species, such as *Ctenophorus*, diversified fairly recently with only enough time for the faster-evolving mitochondrial DNA to differentiate in some species, and implying a high degree of phenotypic plasticity.

Ctenophorus, as currently recognized, is the most speciose group of Australian agamids (Greer, 1989a; Melville et al., 2001; Doughty et al., 2007) with 28 currently recognized species (Wilson and Swan, 2013). The species are spread throughout the arid regions of Australia with the highest density in Western Australia (Cogger, 2014; Uetz et al., 2016). Species of *Ctenophorus* are known for their bright coloration, active lifestyle, and sexual dimorphism (Greer, 1989a). Males display greater color variation between species than do females (Melville et al., 2001), although color often varies with age, season, and temperature of the lizard (Greer, 1989a; Wilson, 2012). Body shape covaries with choice of retreat (burrows, no burrows, and rocks) in *Ctenophorus*, with the notable exception of *Ctenophorus caudicinctus* which was categorized as a generalist by Thompson and Withers (2005).

The three species considered here are *Ctenophorus caudicinctus* (Günther, 1875), *Ctenophorus isolepis* (Fischer, 1881), and *Ctenophorus reticulatus* (Gray, 1845). All are ground-dwelling lizards that exhibit bipedal running behavior (Greer, 1989a; Clemente et al., 2008). These three species are closely related and have similar ecological tolerances, increasing the potential for covariation.

Ctenophorus caudicinctus ranges across the Pilbara and Kimberley region of Western Australia, across much of the Northern Territory and into western Queensland (Cogger, 2014). *Ctenophorus caudicinctus* is a diurnal, saxicolous lizard species found on rocky slopes (Cogger, 1992) or hard soil (Greer, 1989a). The species is insectivorous (Cogger, 1992). The tail is 170–204% snout–vent length (SVL; Witten, 1993).

Ctenophorus isolepis, the most-widely distributed of these three taxa, is found across most of eastern and northern Western Australia, through the central portion of the continent, and into southwestern Queensland (Cogger, 2014). *Ctenophorus isolepis* is a ground-dwelling lizard species closely associated with arid habitats, sand dunes, and grasses of the genus *Triodia* (Witten, 1993; Doughty et al., 2007). The tail is 200–250% SVL (Cogger, 1992). This taxon may be an annual species (Greer, 1989a).

Ctenophorus reticulatus is found from the northern Gascoyne Coast and the Pilbara region of Western Australia across the central part of that state into north-central South Australia (Cogger, 2014). This is a ground-dwelling, herbivorous lizard species that hides under logs and in stony soils (Greer, 1989a; Cogger, 2000). The tail is about 150% SVL (Cogger, 2000). *Ctenophorus reticulatus* was traditionally considered to be a subspecies of *Ctenophorus nuchalis* (Storr, 1966; Greer, 1989a; Witten, 1993), but genetic data support a sister relationship (Melville et al., 2001).

The fossil record of Australian Agamidae is sparse and mostly unpublished (Molnar, 1991). Moreover, little currently can be understood regarding the fossil record because the variation within and between extant Australian Agamidae also remains unexplored, giving researchers the unique opportunity to systematically and holistically collect data from both modern and fossil specimens. An overview of the osteology of the Australian agamids was first described by Siebenrock (1895) and later Moody (1980). The osteology of a few specific Australian species has been described in depth (Beddard, 1905; Greer, 1987; Bell et al., 2009; Banzato et al., 2012). The most-serious limitation to the development of a rigorous understanding of the skeletal morphology of the group is lack of osteological preparations in museum collections (Bell and Mead, 2014). The recent and ongoing development of a collection at the Western Australian Museum (WAM) provides an opportunity to begin exploration of patterns of variation.

As a first step, we set out to answer three questions, all centered on previously published morphological characters used to frame phylogenetic hypotheses for Agamidae. First, how many of the previously published morphological characters are invariant for each of the three species we studied? Second, which states exhibiting no variation are shared among species and which are unique to a given species? Third, when morphological characters vary within a species, do the character states change (i.e., correlate) with ontogeny or sex of the individuals? We limit ourselves to these categories as a first pass at exploring variation in the skeletal system. There certainly are other factors that influence morphological expression, such as diet or terrain, but those are not addressed here.

Novel morphological features were added as needed to clarify or split features that were previously published as characters that we had a difficult time scoring. Because the

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TABLE 1. Data available on the three species of *Ctenophorus* in this study. All specimens are housed in the Western Australian Museum recent collection (WAM R). SVL = Snout–vent length (in mm). TL = Total length (in mm). Mass is in grams. NA = information not available.

Institution number (WAM R)	Species	SVL	TL	Mass	Sex	Date collected
162820	*caudicinctus*	NA	NA	NA	NA	NA
162819	*caudicinctus*	NA	NA	NA	NA	NA
167625	*caudicinctus*	38	109	2.05	F	5 Jun 2005
167626	*caudicinctus*	35	NA	1.6	M	5 Jun 2005
167673	*caudicinctus*	36	115	1.8	F	9 Jun 2005
167679	*caudicinctus*	32	95	1.55	F	11 Jun 2005
162822	*caudicinctus*	NA	NA	NA	NA	29 May 2006
167676	*caudicinctus*	39	119	1.95	F	11 Jun 2005
111747	*caudicinctus*	NA	NA	NA	NA	2 Oct 2005
162887	*caudicinctus*	46	151	4.45	F	11 June 2006
167665	*caudicinctus*	62	148	8.6	NA	8 Jun 2005
167670	*caudicinctus*	62	191	9.5	F	9 Jun 2005
167667	*caudicinctus*	64	206	11	M	9 Jun 2005
167672	*caudicinctus*	67	222	11.25	M	9 Jun 2005
167632	*caudicinctus*	72	217	16	M	5 Jun 2005
165036	*caudicinctus*	NA	NA	NA	NA	3 May 2005
93130	*caudicinctus*	NA	NA	NA	NA	NA
167652	*caudicinctus*	79	235	19.5	M	8 Jun 2005
149693	*isolepis gularis*	43	81	2.7	F	27 Sep 2008
149279	*isolepis gularis*	43	93	2.7	F	29 Sep 2008
149444	*isolepis gularis*	46	99	3.3	M	24 Sep 2008
162896	*isolepis*	40	125	2.15g	NA	9 Jun 2006
149574	*isolepis gularis*	46	55 (tip missing)	3.5	M	27 Sep 2008
149689	*isolepis gularis*	48	102	3.55	F	29 Sep 2008
149710	*isolepis gularis*	46	96	3.3	F	27 Sep 2008
149094	*isolepis gularis*	50	102	4.3	M	27 Sep 2008
149943	*isolepis gularis*	48	101	3.6	M	29 Sep 2008
149179	*isolepis gularis*	51	115	5.2	M	29 Sep 2008
149677	*isolepis gularis*	50	111	4.15	M	29 Sep 2008
149917	*isolepis gularis*	49	99	3.9	F	27 Sep 2008
149161	*isolepis gularis*	52	122	6.3	M	27 Sep 2008
111894	*isolepis gularis*	NA	NA	NA	M	NA
111903	*isolepis isolepis*	NA	NA	NA	M	NA
156956	*isolepis isolepis*	NA	NA	NA	NA	11 Oct 2005
162898	*isolepis isolepis*	35	107	1.8	M	9 Jun 2006
162895	*isolepis*	46	150	3.2	M	9 Jun 2006
162894	*isolepis*	51	171	4.6	F	9 Jun 2006
111736	*isolepis*	NA	NA	NA	NA	1 Oct 2005
162795	*reticulatus*	NA	NA	NA	NA	NA
162744	*reticulatus*	NA	NA	NA	NA	NA
162759	*reticulatus*	NA	NA	NA	NA	22 May 2006
162779	*reticulatus*	NA	NA	NA	NA	NA
162856	*reticulatus*	NA	NA	NA	NA	NA
167575	*reticulatus*	72	163	13.5	NA	2 Jun 2005
167589	*reticulatus*	61	140	10	F	4 Jun 2005
167590	*reticulatus*	75	181	16.5	F	4 Jun 2005
167591	*reticulatus*	73	163	14	F	4 Jun 2005
156678	*reticulatus*	77	192	17.8	M	25 May 2005
167503	*reticulatus*	80	~186	20.5	F	25 May 2005
167551	*reticulatus*	80	201	21	M	29 May 2005
162855	*reticulatus*	NA	NA	NA	F	31 May 2006
167514	*reticulatus*	95	243	29	M	27 May 2005
167563	*reticulatus*	94	258	37	M	2 Jun 2005
167567	*reticulatus*	98	264	40	M	2 Jun 2005
162760	*reticulatus*	NA	NA	NA	NA	23 May 2006
162878	*reticulatus*	NA	NA	NA	NA	2 Jun 2006
162821	*reticulatus*	NA	NA	NA	NA	29 May 2006

original author(s) did not necessarily intend for the character to be used in that way, it was classified as a novel character.

MATERIALS AND METHODS

All specimens we examined were collected as part of an ongoing effort to build and develop a skeletal collection at WAM that comprises skeletal specimens with associated tissue samples that are available for subsequent or concurrent molecular analysis. *Ctenophorus caudicinctus* is represented by 18 individuals and both *C. reticulatus* and *C. isolepis* are represented by 20 individuals (Table 1). All individual specimens were collected in Western Australia (Fig. 1) between 2005 and 2008, and all are registered in the collection of the WAM.

For convenience, and to facilitate comparisons, morphological data are recorded in a matrix format. We recognize that in the context of vertebrate morphology, the term 'character' now has a strong cognitive association with morphological conditions explicitly deemed to be of utility for phylogenetic analysis. Our

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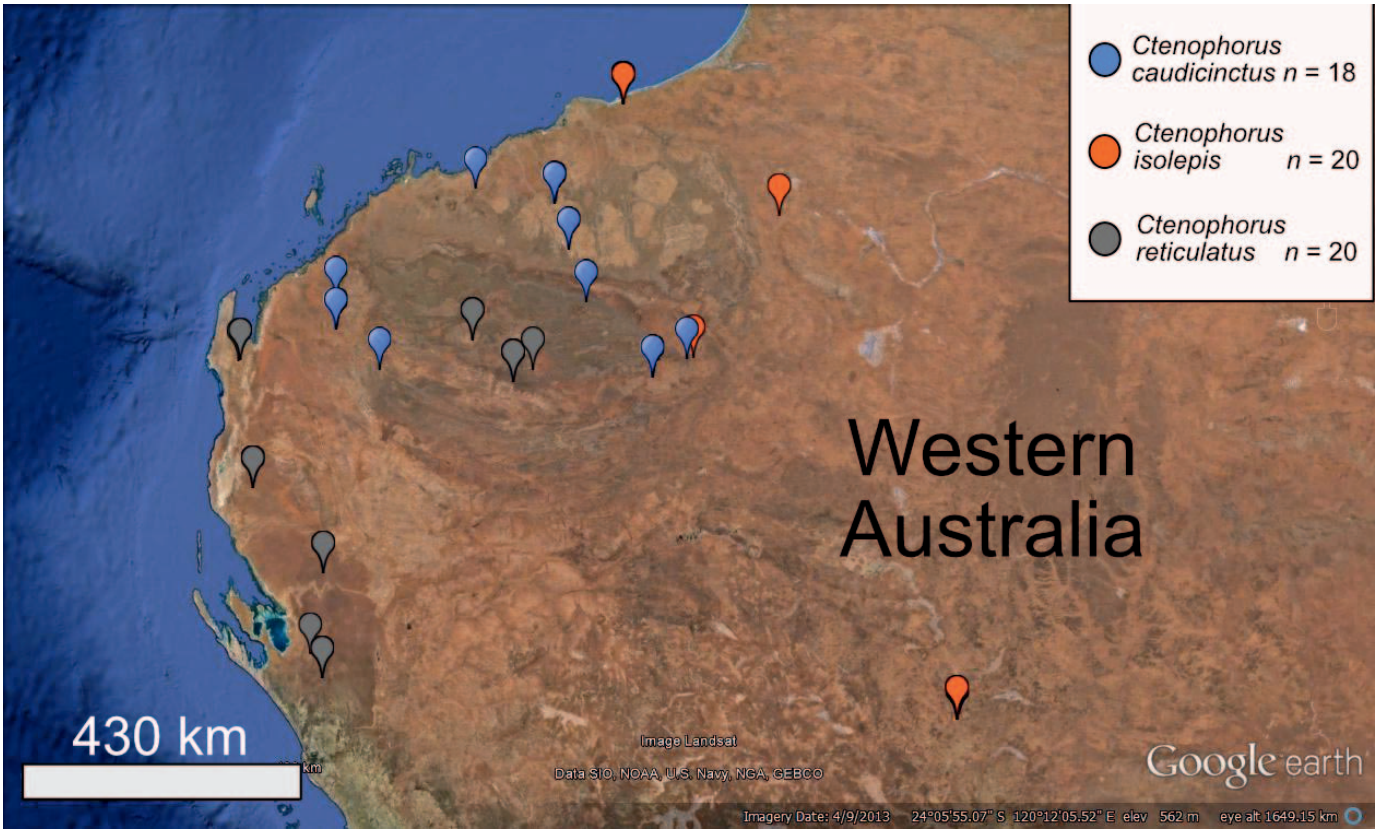


FIG. 1. Map of collected specimens in Western Australia. Latitude and longitude were collected concurrent with specimen capture. Indicators of collection location may overlap. The map was created using the DigitalGlobe feature of Google Maps (Data SIO, NOAA, U.S. Navy, NGA, GEBCO; Image Landsat; Imagery Date: 9 April 2013).

purpose was not to generate a phylogenetic hypothesis nor to summarize and evaluate data useful only for such a purpose. For the sake of clarity we adopted a terminological practice that makes this clear, and we refer to morphological 'features' to indicate our uncertainty about the propriety of including them in phylogenetic analysis. Although the potential phylogenetic utility of these features is discussed, a phylogenetic character analysis is beyond the scope of this study.

We selected morphological features from previously published studies that included Australian Agamidae and also the unpublished work by Moody (1980). We include his thesis because it is the primary source for the collected data and is referenced many times in the literature for phylogenetic analyses (e.g., Borsuk-Białynicka and Moody, 1984; Estes et al., 1988; Gauthier et al., 1988; Greer, 1989a) as well as comparative genetic studies (Melville et al., 2001; Lee, 2005; Smith et al., 2011; Gauthier et al., 2012), fossil analyses (Evans et al., 2002; Blain et al., 2014), morphologic studies (Hocknull, 2002; Stuart-Fox and Owens, 2003; Ord and Stuart-Fox, 2006; Ananjeva et al., 2007), species descriptions (Bell et al., 2009; Ananjeva et al., 2011), and phylogeographic analyses (Hugall and Lee, 2004; Hugall et al., 2008; Wagner et al., 2011). Features from different sources were combined if they described alternative states of the same anatomical system. A total of 51 morphological features initially were identified from the literature. We also added 16 novel features for an initial total of 67 morphological features. After we started scoring, seven morphological features were removed because the given feature on the observed skulls was not as easily categorized as originally anticipated (see Results). Anatomical terminology follows Evans (2008).

All morphological states were described a priori. All skulls were examined under a Zeiss microscope (Carl Zeiss International, Oberkochen, Germany). To ensure uniformity in scoring, each morphological feature was scored for each specimen of all three species before the next morphological feature was considered (figures depicting each morphological feature are provided in Supplementary File 1).

Two types of data were recorded for this study. Continuous data were collected from four measurements of the skull of each individual in dorsal view (Fig. 2), and categorical data were collected from the 60 morphological features. All measurements were recorded in Microsoft Excel 2017 (Microsoft Corporation,

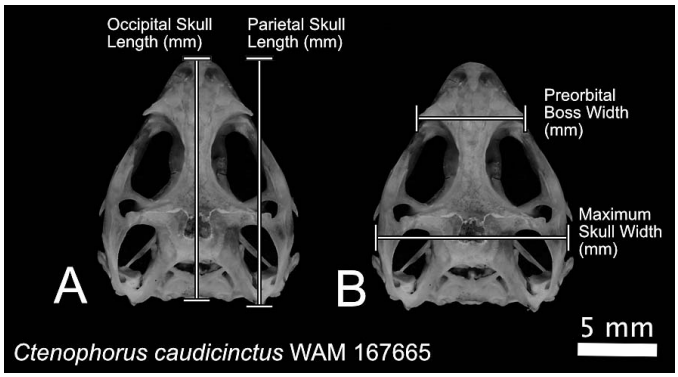


FIG. 2. Example of skull measurements used in this study (A and B). All measurements were taken in dorsal view using the program ImageJ 1.49 software (Schneider et al., 2012). Measurement labels correlate with Table 2.

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TABLE 2. Skull measurements (mm) for all specimens of the three species of *Ctenophorus* in this study. Specimens are housed in the Western Australian Museum recent collection (WAM R).

Institution number (WAM R)	Species	Occipital skull length	Parietal skull length	Maximum skull width	Preorbital boss width
162820	*caudicinctus*	9	9	8	3
162819	*caudicinctus*	10	9.5	8	4
167625	*caudicinctus*	10	10	8	5
167673	*caudicinctus*	10	10	8	5
167676	*caudicinctus*	10	10	9	5
167679	*caudicinctus*	10	10	8	4
167626	*caudicinctus*	10	10	8	5
162822	*caudicinctus*	10	10	9	5
162887	*caudicinctus*	13	13	10	5
167665	*caudicinctus*	15	16	12	7
167670	*caudicinctus*	15	16	12	7
167667	*caudicinctus*	16	16	13	7
167672	*caudicinctus*	17	18	12	8
167632	*caudicinctus*	18	19	14	8
111747	*caudicinctus*	18	19	6	8
165036	*caudicinctus*	19	20	16	8
93130	*caudicinctus*	19	20	16	8
167652	*caudicinctus*	20	21	17	9
162898	*isolepis*	10	9	8	4
149279	*isolepis*	11	10	9	5
162896	*isolepis*	11	11	9	4
149693	*isolepis*	11	11	8	5
149444	*isolepis*	11	11	9	5
149574	*isolepis*	12	11	9	4
149689	*isolepis*	12	12	9	5
149710	*isolepis*	12	12	9	4
149094	*isolepis*	12	12	10	5
149943	*isolepis*	12	12	10	5
162895	*isolepis*	12	12	9	5
149917	*isolepis*	13	12	10	5
149179	*isolepis*	13	12	10	5
162894	*isolepis*	13	13	10	5
149677	*isolepis*	13	13	10	5
149161	*isolepis*	15	14	11	6
111894	*isolepis*	15	15	12	6
111736	*isolepis*	15	15	12	6
111903	*isolepis*	16	16	12	?
156956	*isolepis*	16	17	12	6
162795	*reticulatus*	8	8	6	0.3 (broken?)
162821	*reticulatus*	9	0	8	4
162744	*reticulatus*	9	9	8	0.4 (broken?)
162759	*reticulatus*	10	10	9	5
162779	*reticulatus*	10	10	9	5
162856	*reticulatus*	12	12	11	5
162881	*reticulatus*	13	13	11	6
167589	*reticulatus*	15	15	13	8
167590	*reticulatus*	15	15	14	8
167575	*reticulatus*	15	15	13	8
167591	*reticulatus*	15	16	14	8
156678	*reticulatus*	16	16	15	9
167503	*reticulatus*	16	17	15	18
167551	*reticulatus*	17	18	16	9
162855	*reticulatus*	18	18	17	8
167514	*reticulatus*	18	20	17	9
167563	*reticulatus*	19	20	17	9
167567	*reticulatus*	20	22	19	10
162760	*reticulatus*	20	22	21	9
162878	*reticulatus*	21	22	22	0

Redmond, Washington). If the skull was not complete, measurements that could not be taken were scored as 'NA.' We photographed the skull of each individual with a Canon EOS 5D Mark 2 camera (Canon, Inc., Tokyo, Japan) and a Canon Macro Lens EF 100 mm 1:2.8 USM. Digital photos of each skull were taken in dorsal view; we photographed the mandible of each individual in labial and lingual view. All images were taken using the program Helicon Remote 2.4.4W (HeliconSoft, Ltd., Kharkiv, Ukraine) and stacked in Helicon Focus version 5.3 (HeliconSoft, Ltd.). Details of each skull were taken with the Zeiss microscope using the program Zen v8 (https://www.zeiss.com/microscopy/us/downloads/zen.html). All skull measurements (Table 2) were made from the dorsal view of each individual using the program ImageJ 1.49 (Schneider et al., 2012).

For our first question, 'invariant' is defined as 100% of the individuals of that species showing expression of only one morphologic state; not available (NA) scores were not included. Using discrete data, invariant morphologic states are easily identified within each species. This same method was used to identify invariant features between species.

Sex of the individual was coded as 1 for female and 2 for male. We used skull length as a proxy for ontogenetic age and evaluated it in two ways. The first (occipital skull length) was measured in dorsal view from the anteriormost tip of the skull to the posterior extent of the occipital condyles. We measured the second (parietal skull length) in dorsal view from the anteriormost tip of the skull to the posteriormost tip of the postparietal process of the parietal. For relatively smaller skulls the posteriormost portion of the skull often is the occipital condyle, but for relatively larger agamids the posteriormost portion of the skull is the postparietal process of the parietal. The means of those two sets of measurements were within one standard deviation (SD) of each other, so we arbitrarily chose parietal skull length for assessment of relative ontogenetic age.

To test if each morphological feature was independent of ontogeny or sexual dimorphism, we used Fisher's exact test (Zar, 2010) in RStudio (Racine, 2012) for all three species (R code in Supplementary File 2; data file for R code in Supplementary File 3). Skull length was binned into 0.5-mm intervals. The null hypothesis assumes independence of the two distributions and we rejected the null hypothesis if $P \leq 0.05$.

We attempted other statistical tests but ultimately found they yielded no additional meaningful information for the questions we wanted to answer (e.g., if skull length or the sex of the individual is influencing morphological variation). The common test of categorical variables is the chi-square Test (Zar, 2010), but that test fails if one or more character states have a frequency of zero (which often occurs in morphological character data); the test also requires an ideal distribution to compare against the collected data. Canonical correlation analysis cannot deal with missing values. The one-sided independent samples t-test also does not work because the data already are effectively binned, decreasing the degrees of freedom. Any sort of ranking test is not effective because of the way characters are scored. Sampling could have been increased by using a bootstrap method (Zar, 2010), but this would not have added any additional information pertaining to the questions addressed here (e.g., distribution of features and their variance within each species).

Abbreviations.—Institutional abbreviations include NT R, Museum and Art Gallery of the Northern Territory, Darwin, Northern Territory, Australia; WAM R, Western Australian Museum, Perth, Western Australia, Australia; VPL, Vertebrate Paleontology Lab, The University of Texas at Austin, Austin, Texas; JIM, James I. Mead Collection, East Tennessee State University, Tennessee.

Descriptions of Morphological Features.—The anatomical features are described in Appendix 1. Original data collection files, complete table of scores, statistical tests, and figures illustrating all states of the anatomical features are provided in Supplemen-

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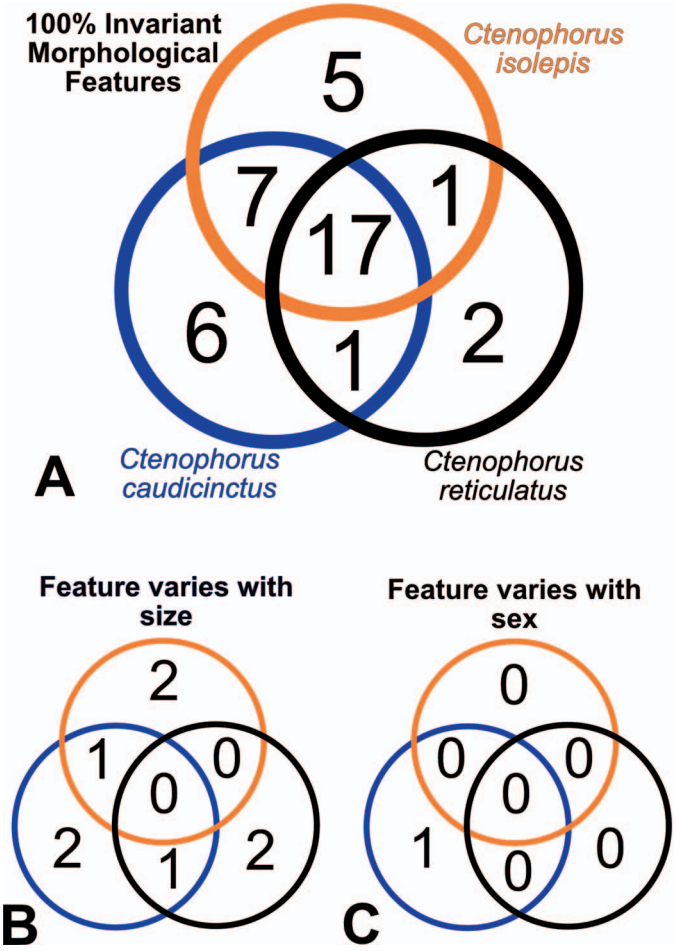


FIG. 3. Venn diagrams of shared and unique invariant morphological features (A; bolded) as well as significant morphological features using Fisher's exact test (Zar, 2010) for ontogenetic variation (B; highlighted) and sexual dimorphism (C; highlighted) per species. If a character was unscorable for an individual specimen, that datum did not count against correlation. Values were calculated in Microsoft Excel 2017 and using a script in RStudio (Racine, 2012).

tary Data File 1 and are archived online at Morphobank.org http://morphobank.org/permalink/?P1262 (O'Leary and Kaufman, 2012).

RESULTS

Sixty morphological features were retained for the analysis portion of this study and seven were not used. Features 63, 66, and 67 were discarded because the states we observed fell along subtle gradients that precluded meaningful classification as discrete states. Features 61, 62, 64, and 65 could not be reliably scored or interpreted in our specimens.

Each of the three species had at least one morphological state that was unique to that species (Fig. 3). Invariant morphological features are those that were always scored as the same state for all specimens of a given species, regardless of sex or ontogenetic age. Thirty-nine of the 60 morphological features are invariant for at least one of the three taxa (Table 3). Within this group of invariant features we recognize three categories. The first includes features with states that were unique to a single species. The second category includes features scored as the same state for two of the three species. The third category includes those features that were scored as the same state for all three species. Uniquely invariant features/states for *C. caudicinctus* are 5(1), 8(0), 28(1), 35(1), 51(0), and 59(1). Uniquely invariant features/states for *C. isolepis* are 10(2), 11(1), 17(0), 24(1), and 58(1). The uniquely invariant feature/state for *C. reticulatus* is 50(1). Among the second category of features, *C. caudicinctus* and *C. isolepis* were both invariant for features 13(0), 15(1), 19(1), 38(1), 47(0), 53(1), and 56(1). *Ctenophorus caudicinctus* and *C. reticulatus* were both invariant for feature 25(1). *Ctenophorus isolepis* and *C. reticulatus* were invariant for feature 2(0). Morphologically invariant features shared by all three taxa are 4(1), 9(0), 16(1), 21(0), 22(1), 23(1), 26(2), 27(1), 31(1), 37(1), 41(1), 42(0), 43(0), 48(1), 49(0), 54(1), and 57(1).

Morphological features that varied within taxa (hence excluding all invariant morphological features) may have varied with ontogeny (using skull length as a proxy) and sexual dimorphism. Nine of the 60 measured features varied with ontogeny for at least one taxon and one varied with sex for one taxon (Fig. 4). These measurements also can be divided into the three categories: those that are unique features for a single species; those that are the same for two species; and those shared by all three species. For only *C. caudicinctus*, features 7, 32, and 58 correlated with ontogeny and feature 17 correlated with sex. For only *C. isolepis*, features 44, 52, and 55 correlated with ontogeny and no features correlated with sex. For only *C. reticulatus*, features 39 and 40 varied with ontogeny and no features correlated with sex.

Features that varied with ontogeny or sexual dimorphism for groups of species also were evaluated. For *C. caudicinctus* and *C. isolepis* feature 55 varied with ontogeny. For *C. caudicinctus* and *C. reticulatus*, feature 17 varied with ontogeny. For *C. isolepis* and *C. reticulatus*, no features varied with ontogeny.

DISCUSSION

Morphological features examined here were not originally identified as being useful for distinguishing species of *Ctenophorus* or for distinguishing *Ctenophorus* from other endemic Australian agamids. They were, for the most part, proposed as morphological characteristics that varied in ways that were considered to be systematically informative for elucidating phylogenetic relationships among major clades within Agamidae. But they do afford an interesting opportunity to evaluate the degree to which such characteristics may be informative at other phylogenetic levels. Our initial expectation was that most of the morphological features would vary in comparable ways among the three species of *Ctenophorus* we assessed. Our major focus was to determine whether those features were subject to ontogenetic variation or to sexual dimorphism, neither of which has been seriously explored within the skeletal system of any of the Australian Agamidae.

We were, therefore, somewhat surprised to find the features we assessed show interesting patterns of variation among the three species of *Ctenophorus*. Each of the species has at least one uniquely invariant feature. Uniquely invariant morphological features may be important diagnostic characters for the identification of particular species and would be optimized as autapomorphies in a phylogenetic analysis of the group. If the feature and state can be assessed for isolated skeletal elements, those features would be particularly important for making reliable identifications of specimens preserved in the fossil record (Bell et al., 2010). The challenge, of course, is that such features must remain uniquely invariant as taxonomic sampling is increased.

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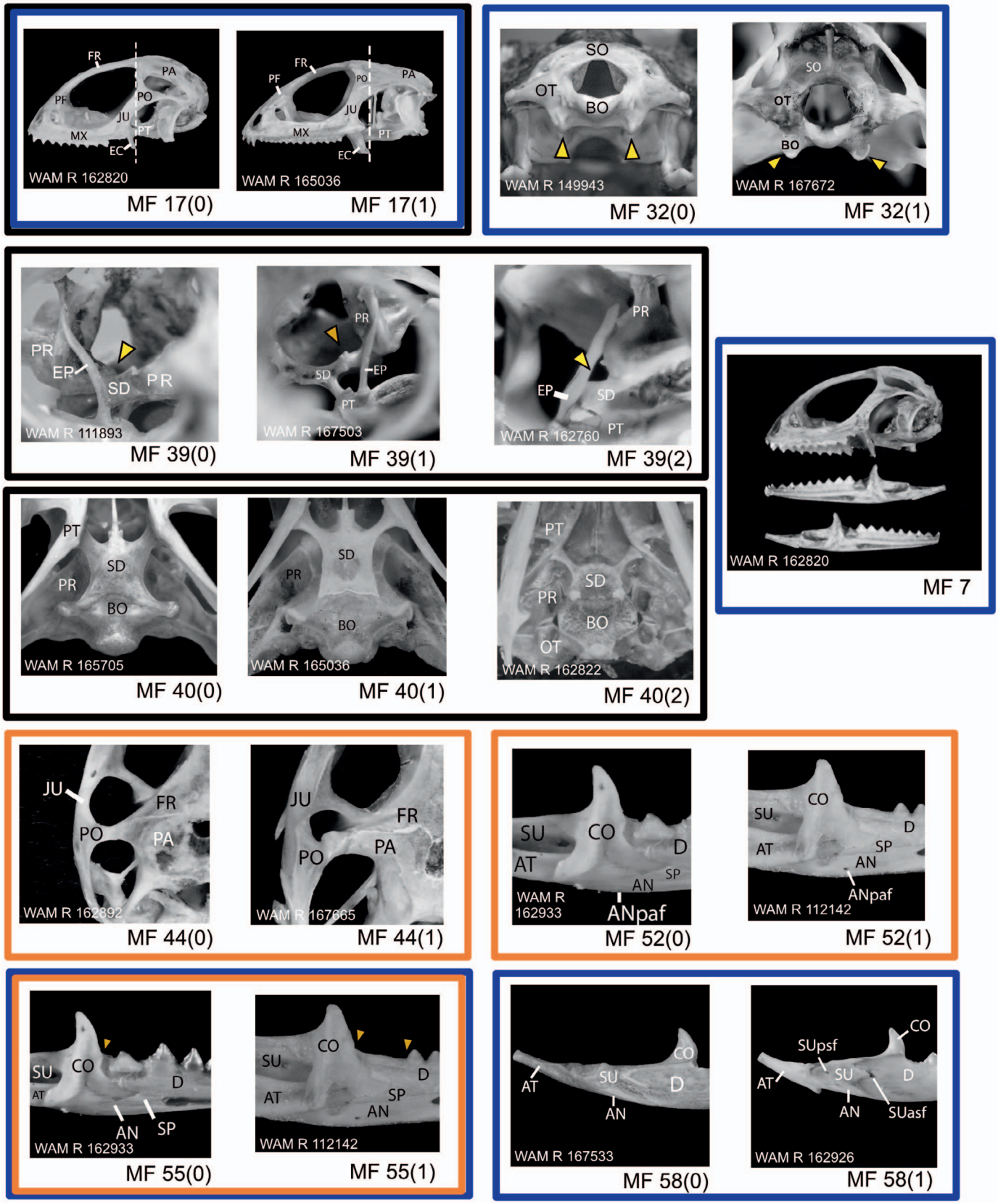


FIG. 4. Representative morphologic feature (MF) states for the nine characters that were found to be nonindependent of ontogeny (all features shown) and sex (feature 17). Colors correspond to species. Blue = *C. caudicinctus*; Orange = *C. isolepis*; Black = *C. caudicinctus*. Photos taken are representative examples and so may not be the same species as box color. MF 7: WAM R162820 *C. caudicinctus*, left view of skull, lingual view of right (upper) and left (lower) dentaries. MF 17(0): WAM R162820 *C. caudicinctus*, lateral view. 17(1): WAM R165036 *C. caudicinctus*, lateral view. MF 32(0): WAM R149943 *C. reticulatus*, posterior view. MF 32(1): WAM R167672 *C. caudicinctus*, posterior view. MF 39(0): WAM R111893 *C. nuchalis*, right anterolateral view. MF 39(1): WAM R167503 *C. reticulatus*, left anterolateral view. MF 39(2): WAM R162760 *C. reticulatus*, left lateral view. MF 40(0):

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Of the features unique to *C. caudicinctus*, 5(1) and 59(1) all could be readily identified in isolated skeletal elements and so could be useful for interpreting fossils. Features 8(0), 28(1), 35(1), and 51(0) are likely to be interpretable only from articulated or partially articulated skulls; their applicability to the interpretation of fossils would thus be dependent upon preservation and the degree to which disarticulation happened during fossilization. Of the features unique to *C. isolepis*, 24(1) and 58(1) could be readily identified on isolated skeletal elements while characters 10(2), 11(1), and 17(0) are likely to be interpretable only from articulated or partially articulated skulls. The feature unique to *C. reticulatus*, 50(1), is likely to be interpretable only from articulated or partially articulated dentaries.

The second category of features includes states that were invariant but shared by two of the three species. In a phylogenetic character analysis, those features are potential synapomorphies that might yield evidence of relationship. Determination of synapomorphic status would be dependent upon a phylogenetic analysis and the resolution of any character conflict that might be present within the data set. Again, the relative informative value of these features may change as taxon sampling is expanded.

The third category of features includes those that were invariant but were scored the same way in all three species. Clearly, those features are diagnostic at some deeper phylogenetic level (e.g., diagnostic of all *Ctenophorus*, or of larger species groups, or of the endemic Australian clade as a whole).

The sobering reality here is that our analysis included adequate sample sizes but only for three species of *Ctenophorus*. No fewer than 25 additional species of *Ctenophorus* must be evaluated and assessed before any reasonably confident statement can be made about the distribution of character states among species of the group.

Conclusion

The elucidation of patterns of morphological variation in the skeleton of Australian endemic agamids remains an important goal. A relatively rich but largely unstudied fossil record for the group is available. Efforts to interpret that fossil record reliably must be grounded in a solid understanding of the skeletal system of the group. That understanding can be developed only through the evaluation of relatively large sample sizes (certainly greater than only one or a few specimens) and with special attention paid to the intraspecific differences in skeletal morphology that result from differences in ontogenetic age and from sexual dimorphism (e.g., see Etheridge, 1962; Bell and Repenning, 1999). Such data are lacking for almost all clades of extant squamates, and existing holdings of skeletal specimens in museum collections are, for the most part, wholly inadequate for addressing this problem (Bell and Mead, 2014; Smith et al., 2015). A reliable interpretation of the fossil record must await a more refined understanding of the morphological patterns exhibited in the extant biota.

The importance of understanding interspecific and intraspecific patterns of skeletal variation is, therefore, acute. Agamids remain one of the most-poorly understood clades of squamates. No modern morphological database or matrix exists for the Australian endemics or for Agamidae as a whole. Efforts to gather, collate, and analyze such data sets must be initiated. The only attempts at summaries of the morphological patterns in the skull as a whole are those of Siebenrock (1895), Moody (1980), and Evans (2008). Detailed study of the maxilla and dentary of the Australian agamids was presented by Hocknull (2002) with the specific aim of building a framework from which fossils could be identified. Hocknull's data provide a crucial first step in shaping a list of morphological characters by which the Australian endemics may be evaluated and identified. Here we provide an addition to, not evaluation of, his seminal work. Our goal was to explore the patterns of variation of other previously published morphological features and to assess whether larger sample sizes were important for recording variant phenotypes. Some of those morphological features show some promise for taxon discrimination, even among closely related species within a speciose clade. Adequate sample sizes do not yet exist to test the broader utility of those morphological features for taxon discrimination; such sample sizes are desperately needed. Our preliminary efforts to develop an expanded data set centered on relatively small sample sizes of nine additional species of *Ctenophorus* (*adelaidensis*, *clayi*, *femoralis*, *maculatus*, *nuchalis*, *ornatus*, *parviceps*, *rubens*, and *scutulatus*). When we re-evaluated the features that in this study were unique to either *C. caudicinctus*, *C. reticulatus*, or *C. isolepis* in the context of the expanded data set, all were shared with at least one other species. This strengthens the argument that morphological data sets require rigorous evaluation, both within and between taxa, both to confirm and to more adequately understand morphological states before reliable phylogenetic analyses can be made. These data also are essential for reliable interpretations of the fossil record.

Alternative approaches also can and should be brought to bear on the problem. For example, morphometric analysis of skull shape certainly will yield interesting insights into ontogenetic transformations of the skull and might reveal subtle differences between the sexes that are not readily discernible from discrete character data alone. As evidenced by our data set, however, most morphological characters will not be invariantly scored for most taxa. Efforts to quantify and evaluate patterns of variation, and to explore differences in the tendency of particular lineages to express variation, will be important avenues of future work on the group. In all cases, more expansive collections will be required to gather the relevant data.

Our data confirm that published morphological characters of the skull in agamids do appear to vary in systematically informative ways, even when applied in contexts for which they were not originally conceptualized. But those data are simultaneously promising and sobering. They hold the promise that morphological characters of the skull may indeed permit species-level discrimination, even among speciose clades. But they also suggest that unambiguously diagnostic characters will likely remain elusive, and they emphasize the importance of relatively large sample sizes for documenting patterns of variation within agamids. The ability to resolve fine-scale

←
WAM R165705 *C. parviceps*, ventral view. MF 40(1): WAM R165036 *C. caudicinctus*, ventral view. MF 40(2): WAM R162822 *C. caudicinctus*, ventral view. MF 44(0): WAM R162892 *C. femoralis*, dorsal view. 44(1): WAM R167665 *C. caudicinctus*, dorsal view. MF 52(0): WAM R162933 *Lophognathus (Gowidon) longirostris*, left lingual view. MF 52(1): WAM R112142 *Pogona minor*, left lingual view. MF 55(0): WAM S162933 *Lophognathus (Gowidon) longirostris*, left lingual view. MF 55(1): WAM S112142 *Pogona minor*, left lingual view. MF 58(0): WAM R167533 *Ctenophorus scutulatus*, right labial view. MF 58(1): WAM R162926 *Lophognathus gilberti*, right labial view.

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TABLE 3. Invariant morphological features and Fisher's exact test (Zar, 2010) for all taxa. Invariant morphological features are those for which 100% of the individuals within a given species show expression of only one morphological state. Invariant features are recorded as 'INV (invariant state score).' The invariant state is indicated to allow comparison between taxa. We used parietal skull length (mm) for size and binned by 0.5 mm to satisfy the assumptions of the test. Both invariance and Fisher's exact test can be shown in one table because Fisher's exact test is nonapplicable when all the variables for one set of data are the same (that is, the character is invariant). *Values with an asterisk indicate a significant *P*-value of ≤ 0.05. MF = morphological feature.

Agamidae	*Ctenophorus caudicinctus*		*Ctenophorus isolepis*		*Ctenophorus reticulatus*	
MF	Size ($n = 18$)	Sex ($n = 11$)	Size ($n = 20$)	Sex ($n = 17$)	Size ($n = 20$)	Sex ($n = 10$)
1	0.882352941	1	0.383900929	0.514705882	0.797987616	1
2	0.5	0.454545455	INV (0)	INV (0)	INV (0)	INV (0)
3	0.671387436	1	0.474317165	0.949095023	0.375777396	1
4	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)
5	INV (1)	INV (1)	0.852631579	1	0.495665635	0.206349206
6	1	0.454545455	0.25	INV (0)	0.197239422	1
7	0.004180868*	0.74025974	0.986442876	0.707175178	0.115483574	1
8	INV (0)	INV (0)	0.130237358	1	0.738937842	1
9	INV (0)	INV (0)	INV (0)	INV (0)	INV (0)	INV (0)
10	0.277777778	INV (2)	INV (2)	INV (2)	0.11372549	INV (2)
11	0.352941176	0.545454545	INV (1)	INV (1)	0.47244582	1
12	0.949952009	0.350649351	0.510526316	1	0.296588899	1
13	INV (0)	INV (0)	INV (0)	INV (0)	0.55	1
14	0.757352941	1	0.913312693	0.161764706	0.510526316	INV (1)
15	INV (1)	INV (1)	INV (1)	INV (1)	0.068421053	INV (1)
16	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)
17	0.029411765*	0.015151515*	INV (0)	INV (0)	0.019473174*	0.523809524
18	0.6649429	1	0.790859296	0.619909502	0.805018511	0.523809524
19	INV (0)	INV (0)	INV (0)	INV (0)	0.526315789	1
20	0.932126697	1	0.761167625	1	0.62745098	1
21	INV (0)	INV (0)	INV (0)	INV (0)	INV (0)	INV (0)
22	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)
23	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)
24	0.277777778	0.454545455	INV (1)	INV (1)	0.881578947	0.444444444
25	INV (1)	INV (1)	1	1	INV (1)	INV (1)
26	INV (2)	INV (2)	INV (2)	INV (2)	INV (2)	INV (2)
27	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)
28	INV (1)	INV (1)	0.742105263	1	0.510526316	1
29	0.166666667	1	1	1	0.510526316	1
30	0.5	INV (0)	0.539473684	0.514705882	INV (0)	INV (0)
31	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)
32	0.030094905*	1	0.450980392	0.100899101	0.714285714	1
33	0.377777778	0.2	0.922997539	1	1	0.444444444
34	0.389495798	0.466666667	0.896155831	1	1	1
35	INV (1)	INV (1)	1	0.514705882	0.133436533	0.523809524
36	0.316176471	0.4	1	1	0.679050568	0.166666667
37	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)
38	INV (1)	INV (1)	INV (1)	INV (1)	0.456140351	INV (1)
39	0.084249084	0.428571429	0.125	1	0.015272309*	0.206349206
40	0.324095023	0.19047619	0.757720092	1	0.043702866*	1
41	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)
42	INV (0)	INV (0)	INV (0)	INV (0)	INV (0)	INV (0)
43	INV (0)	INV (0)	INV (0)	INV (0)	INV (0)	INV (0)
44	1	1	0.006227673*	1	0.065098833	1
45	0.485620915	0.454545455	0.294736842	1	0.566666667	1
46	0.606765783	1	0.440144479	1	0.057754681	1
47	INV (0)	INV (0)	INV (0)	INV (0)	1	INV (0)
48	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)
49	INV (0)	INV (0)	INV (0)	INV (0)	INV (0)	INV (0)
50	0.125619479	0.545454545	0.317698658	1	INV (1)	INV (1)
51	INV (0)	INV (0)	1	0.643665158	0.210526316	INV (0)
52	0.182435212	0.08008658	0.010415178*	1	0.094917441	1
53	INV (1)	INV (1)	INV (1)	INV (1)	1	INV (1)
54	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)
55	0.029411765*	0.08008658	0.001999484*	0.514705882	0.084325633	1
56	INV (0)	INV (0)	INV (0)	INV (0)	1	INV (0)
57	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)	INV (1)
58	0.010130719*	0.454545455	INV (1)	INV (1)	0.25	INV (1)
59	INV (1)	INV (1)	1	1	1	INV (0)
60	0.292251866	0.199134199	0.601511182	0.538461538	0.376572344	1

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taxonomic categories from isolated skeletal elements preserved in the fossil record may be limited in speciose clades. The occurrence of diagnostic characters in the several monotypic genera of Australian endemic agamids remains largely untested, but at least some diagnostic characters do occur in the iconic Thorny Devil, *Moloch horridus* (Bell et al., 2009).

Ultimately, the integration of detailed morphological data, from the fossil record and from the extant biota, with molecular data will provide a holistic perspective on the evolution of this interesting clade of lizards. The molecular data are increasingly more robust and are helping to shape new questions regarding biogeographic patterns (Melville et al., 2001, 2016; Byrne et al., 2008; Hugall et al., 2008) and the timing of divergence among the various lineages (Hugall and Lee, 2004; Doughty et al., 2014; Melville et al., 2014; Edwards et al., 2015). The fossil record can and will yield relevant data in both of those areas, but those data will be meaningful only if the fossil record is interpreted with care and in the context of a robust understanding of the skeletal morphology of the extant species.

Acknowledgments.—We thank C. Sagebiel (TMM), P. Doughty (WAM), and B. Maryan (WAM) for their assistance with specimen loans. A. Baynes, P. Doughty, W. Gelnaw, M. Hollenshead, B. Maryan, A. Power, and S. Swift assisted with field work and specimen collections associated with this project; without their efforts, the material component of this research would not exist. Technical assistance with, and helpful advice on, photographic techniques was received from A. Molineux and A. Thomson; we appreciate their efforts on our behalf. We benefited greatly from our discussions about agamid lizards with J. Clarke, P. Doughty, J. Gray, S. Hocknull, M. Hutchinson, M. Jones, T. LaDuc, J. Maisano, B. Maryan, J. Melville, R. Burroughs, and J. Müller. We also thank our reviewers, Reviewer 1 and M. Augé, as well as our editors J. Daza and T. Doan. Their contributions to our thoughts and education are gratefully acknowledged, but we attribute all errors of interpretation and fact to our own inadequacies.

Supplementary Data

Supplementary data associated with this article can be found online at http://dx.doi.org/10.1670/16-152

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Accepted: 22 May 2017.
Published online: 28 July 2017.

Appendix 1

Morphological feature descriptions used in the study. Citations are provided for features derived from the literature. Features from the literature were minimally modified. No attempt was made to correct for independence, but wording was changed where necessary for clarity. Novel features are marked with an asterisk.

1. Maxillary contact in palatal view; 0 = the maxillae do not contact each other posterior to the premaxilla and anterior to the vomers, see Supplementary Data Fig. S1; 1 = the maxillae contact, Fig. S2 (modified from Moody, 1980, character 40; Estes et al., 1988, Agamidae character 3).
2. *Contact of the internarial process of the premaxilla with the frontal; 0 = the internarial process of the premaxilla does not contact the frontal, Fig. S3; 1 = the internarial process of the premaxilla contacts the frontal, Fig. S4.
3. Number of pleurodont tooth positions on the premaxilla; Fig. S5 (Moody, 1980, character 69).
4. Contact of the facial process of the maxilla and the nasal; 0 = the facial process of the maxilla does not contact the nasal, Fig. S6; 1 = the facial process of the maxilla contacts the nasal, Fig. S7 (Moody, 1980, character 41).
5. Diastema between the lateralmost premaxillary tooth position and the premaxilla-maxilla suture; 0 = absent, Fig. S8; 1 = present, Fig. S9 (Hocknull, 2002).
6. *Distinct midline diastema between the premaxillary tooth positions; 0 = absent, Fig. S10; 1 = present, Fig. S11.
7. Total number of pleurodont tooth positions on the five tooth-bearing skeletal elements (azygous premaxilla, paired maxillae, and paired dentaries); Fig. S12 (Moody, 1980, character 67).
8. In palatal view, the labial margins of the premaxilla and maxilla; 0 = form a continuous arc, Fig. S13; 1 = the premaxilla is flat, Fig. S14; 2 = the premaxilla interrupts a continuous arc, Fig. S15 (modified from Moody, 1980, character 39).
9. Fenestra formed between the nasals and frontals; 0 = absent, Fig. S16; 1 = present, Fig. S17 (Siebenrock, 1895; El-Toubi, 1945, 1947).
10. *In dorsal view, the position of the pineal foramen relative to a straight line formed between the lateral margins of the frontoparietal suture; 0 = the pineal foramen is anterior, Fig. S18; 1 = the pineal foramen is in line, Fig. S19; 2 = the pineal foramen is posterior, Fig. S20.
11. In palatal view, contact of the vomer with the contralateral element; 0 = contact along less than half their length, Fig. S21; 1 = contact at least half, but less than the entire length, Fig. S22; 2 = contact along their entire length, Fig. S23 (modified from Siebenrock, 1895; Jollie, 1960).
12. *In palatal view, contact of the palatine with the contralateral element; 0 = no contact or contact along less than half the entire length, Fig. S24; 1 = contact along half or more than half the entire length, but less than the entire length, Fig. S25; 2 = contact along the entire length, Fig. S26.
13. In palatal view, anterior contact of the pterygoid with the contralateral element; 0 = do not contact each other anteriorly, Fig. S27; 1 = contact each other anteriorly, Fig. S28 (modified from Siebenrock, 1895, character 26).
14. Hooked ventral flange on the distal portion of the pterygoid anterior to the pterygoid-quadrate articulation; 0 = flange is absent, Fig. S29; 1 = flange is present, Fig. S30 (modified from Moody, 1980, character 47).
15. *Distal contact of the pterygoid with the quadrate; 0 = narrow, Fig. S31; 1 = broad, Fig. S32.
16. Size of the lacrimal duct relative to the infraorbital foramen; 0 = small, similar in size or not much larger than the infraorbital foramen, Fig. S33; 1 = large, significantly larger than the infraorbital foramen, Fig. S34 (Moody, 1980, character 35).
17. In lateral view of the skull, 0 = the distal tip of coronoid process of the ectopterygoid is anterior to or aligned with the posterior margin of the orbit, Fig. S35; 1 = the distal tip of coronoid process is posterior to the posterior margin of the orbit, Fig. S36 (Moody, 1980, character 48).
18. In anterior view of the skull, the contribution of the ectopterygoid to the pterygoid-ectopterygoid vertical flange; 0 = pterygoid distinctly forms the majority of the process, Fig. S37; 1 = pterygoid and ectopterygoid make approximately equal contribution, Fig. S38; 2 = ectopterygoid distinctly forms the majority of the process, Fig. S39 (modified from Moody, 1980, character 51).
19. In posterior view of the skull, the contribution of the ectopterygoid to the pterygoid-ectopterygoid vertical flange; 0 = pterygoid distinctly forms the majority of the process, Fig. S40; 1 = pterygoid and ectopterygoid make approximately equal contribution, Fig. S41; 2 = ectopterygoid distinctly forms the majority of the

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process, Fig. S42 (modified from Moody, 1980, character 51).

20. Dorsal process of the medial head of the ectopterygoid that overlaps the dorsolateral surface of the pterygoid; 0 = relatively short, Fig. S43; 1 = relatively long, completely overlaps the pterygoid surface to the midline, Fig. S44 (Moody, 1980, character 52).
21. *Base of the epipterygoid; 0 = articulates only with the pterygoid, Fig. S45; 1 = articulates with both the pterygoid and the basipterygoid process of the sphenoid, Fig. S46.
22. Dorsal epipterygoid contact; 0 = epipterygoid has a bony dorsal tip that closely approaches the ventral process of the parietal, Fig. S47; 1 = epipterygoid is short and does not closely approach the ventral process of the parietal, Fig. S48 (Moody, 1980, character 26).
23. Epipterygoid in lateral view; 0 = contacts the parietal or anterodorsal process of the prootic, Fig. S49; 1 = contacts the exterior of the anterior bulge of the anterior semicircular canal of the prootic or anteroventral surface of the prootic or does not contact the parietal or prootic, Fig. S50; (Moody, 1980, character 27).
24. Lateral cranial wall of parietal; 0 = possesses a sharply angled-downward process with which the epipterygoid has a ligamentous contact, Fig. S51; 1 = lateral wall is straight or with only a slightly rounded process, Fig. S52 (Moody, 1980, character 15).
25. In lateral view, the postparietal process of the parietal in the transverse plane; 0 = horizontal or with a slight curvature ventrally, Fig. S53; 1 = obvious ventral curvature, Fig. S54 (Moody, 1980, character 14).
26. In posterodorsal view of the skull, the posterior semicircular canals of the braincase; 0 = are not apparent, Fig. S55; 1 = are apparent only on the supraoccipital, Fig. S56; 2 = are apparent on both the supraoccipital and otooccipital, Fig. S57 (Moody, 1980, character 8).
27. Supratemporal; 0 = absent or extremely reduced, tiny element, Fig. S58; 1 = present, Fig. S59 (modified from Moody, 1980, character 17).
28. Squamosal contact with the jugal and postorbital; 0 = area of contact with the jugal and postorbital approximately equal, Fig. S60; 1 = the squamosal-jugal contact is larger than the postorbital, allowing only a small narrow process of the postorbital to contact the squamosal, Fig. S61; 2 = the squamosal contact with the jugal excludes any postorbital contact with the squamosal, Fig. S62 (Moody, 1980, character 28; Gauthier et al., 2012, character 154(2)).
29. Orbital portion of the jugal in lateral view; 0 = majority of the infraorbital margin formed by a broad jugal, Fig. S63; 1 = maxilla and jugal contribute approximately equally, Fig. S64 (Moody, 1980, character 29).
30. Jugal contribution to the infraorbital canal; 0 = absent, Fig. S65; 1 = present, Fig. S66 (Moody, 1980, character 30).
31. Quadrate notch that accommodates the squamosal articulation; 0 = absent, Fig. S67; 1 = present, Fig. S68 (Moody, 1980, character 23).
32. Transverse angle of the basal tubera of the basioccipital, one arm measured relative to the other from the midline of each tubera; 0 = approximately perpendicular, 90–110 degrees, Fig. S69; 1 = obtuse angle, 111–140 degrees, Fig. S70 (Moody, 1980, character 2).
33. In ventral view and perpendicular to the sagittal plane, the basal tubera of the basioccipital; 0 = project laterally, Fig. S71; 1 = project posteriorly, Fig. S72 (Moody, 1980, character 3).
34. In lateral view the fenestra ovalis, when compared to the lateral aperture of the recessus scalae tympani ('fenestra cochlea' of Moody, 1980, character 5); 0 = fenestra ovalis is obviously smaller than the lateral aperture of the recessus scalae tympani, Fig. S73; 1 = fenestra ovalis is approximately equal in size to the lateral aperture of the recessus scalae tympani, Fig. S74; 2 = fenestra ovalis is larger than the lateral aperture of the recessus scalae tympani, Fig. S75 (Moody, 1980, character 5).
35. The angle of the paroccipital (opisthotic) process of the otooccipital, when viewed in a lateral transverse plane; 0 = angled dorsolaterally, obviously above horizontal, Fig. S76; 1 = projects approximately horizontally, Fig. S77; 2 = angled ventrolaterally, obviously below horizontal, Fig. S78 (modified from Moody, 1980, character 4).
36. Size of the recess containing the fenestra ovalis and lateral aperture of the recessus scalae tympani (= the tympanic-occipital recess of Moody, 1980); 0 = recess large, including an excavation of the basioccipital, Fig. S79; 1 = recess large, but without excavation of the basioccipital, Fig. S80; 2 = absent, Fig. S81 (Moody, 1980, character 6).
37. Sphenoccipital foramen; 0 = absent, Fig. S82; 1 = present, Fig. S83 (Siebenrock, 1895; Moody, 1980, character 11; Borsuk-Białynicka and Moody, 1984, character 1; Gauthier et al., 2012, character 304(1)).
38. Anterodorsal (alar) process of the prootic; 0 = little or no prootic between the anterior semicircular canal bulge and the ventral process of the parietal with which it makes contact, Fig. S84; 1 = anterodorsal process of the prootic distinct between the anterior semicircular canal bulge and the ventral process of the parietal, Fig. S85 (Moody, 1980, character 9).
39. *Dorsal process formed by the anterior inferior process of the prootic and alar process of the sphenoid; 0 = absent, Fig. S86; 1 = distinctly small, Fig. S87; 2 = strongly projecting, Fig. S88.
40. Contribution of the parasphenoid portion of the sphenoid bone to the basal tubercle of the basioccipital; 0 = parasphenoid contributes to the process of the basal tubercle, Fig. S89; 1 = suture between the parasphenoid and basioccipital lies immediately anterior to the process, Fig. S90; 2 = suture far anterior to the processes, Fig. S91 (Moody, 1980, character 12).
41. Shape of the prefrontal margin of the orbit; 0 = round, follows the shape of the orbit, Fig. S92; 1 = knobbed or with a sharp process, Fig. S93 (modified from Moody, 1980, character 32).
42. Lacrimal; 0 = absent, Fig. S94; 1 = present, Fig. S95 (modified from Moody, 1980, character 33).
43. Postfrontal; 0 = absent, Fig. S96; 1 = present, Fig. S97 (Estes et al., 1988, character 1).
44. Anterodorsal process of the postorbital; 0 = lacking or only slightly rounded, Fig. S98; 1 = distinct knob or boss, Fig. S99 (modified from Moody, 1980, character 21).
45. Dorsal process of the squamosal extending along the medial wall of the upper temporal fenestra; 0 = absent, Fig. S100; 1 = present, Fig. S101 (Moody, 1980, character 22).

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46. Anterior margin conch of the quadrate; 0 = broadly arching lateral margin with a thickened edge, Fig. S102; 1 = broadly arching, but lateral margin without a thickened edge, Fig. S103; 2 = conch absent or rudimentary, lateral margin a sharp edge or absent, Fig. S104 (Moody, 1980, character 24).
47. Mandibular articulating head of the quadrate; 0 = medial condyle substantially larger than the lateral, Fig. S105; 1 = condyles approximately equal in size, Fig. S106 (Moody, 1980, character 25).
48. Meckelian groove; 0 = remains on medial surface of dentary at the symphysis, Fig. S107; 1 = rotates to the ventral edge, Fig. S108 (Moody, 1980, character 57).
49. Labial process on coronoid that overlaps the dentary; 0 = absent, Fig. S109; 1 = present, Fig. S110 (Moody, 1980, character 59; see also Estes et al., 1988, character 5; Gauthier et al., 1988, character 46).
50. Posterior medial process of the coronoid; 0 = short, not reaching the ventral edge of the mandible, Fig. S111; 1 = long, completely overlapping the prearticular and reaching the ventral edge of the mandible, Fig. S112; 2 = absent, Fig. S113 (modified from Moody, 1980, character 61).
51. Prearticular; 0 = absent, Fig. S114; 1 = present, Fig. S115 (modified from Gauthier et al., 2012, character 401).
52. Angular foramen (posterior mylohyoid foramen) location; 0 = on the ventral edge of the angular, Fig. S116; 1 = on the medial surface of the angular, Fig. S117 (Moody, 1980, character 65).
53. Splenial; 0 = absent, Fig. S118; 1 = present, Fig. S119 (Moody, 1980, character 66; Estes et al., 1988, character 2).
54. *Glenoid fossa; 0 = absent, Fig. S120; 1 = present, Fig. S121.
55. *Diastema present between last posterior acrodont tooth position and coronoid process. Diastema must not be the result of a tooth still forming and must be greater than the anteroposterior width of the most posterior acrodont tooth; 0 = absent, Fig. S122; 1 = present, Fig. S123.
56. *Lingual portion of the surangular pierced by the foramen for the mandibular division of cranial nerve V (SUasf; = anterior mylohyoid foramen of Oelrich, 1956); 0 = absent, Fig. S124; 1 = present, Fig. S125.
57. *From a labial view of the mandible, anterior supra-angular foramen (Oelrich, 1956); 0 = not visible, Fig. S126, 1 = present, Fig. S127.
58. *From a labial view of the mandible, posterior supra-angular foramen (Oelrich, 1956); 0 = not visible, Fig. S128; 1 = present, Fig. S129.
59. *Chorda tympani foramen in the glenoid fossa; 0 = not visible, Fig. S130; 1 = present, Fig. S131.
60. *Number of mental foramina visible in lateral view on right dentary (continuous value); Fig. S132.

Morphological Features not Addressed.—

61. *Septomaxilla; 0 = absent, Fig. S133; 1 = present, Fig. S134.
62. *Number of lateral maxillary foramina (continuous value); Fig. S135.
63. In palatal view, maxilla-palatine suture, as measured by a straight line from the most anterior to the most posterior visible contact points; 0 = parallel to maxillary tooth row, Fig. S136; 1 = acutely angled anteromedially, Fig. S137 (Moody, 1980, character 42).
64. Scleral ossicle number; 0 = 12, Fig. S138; 1 = 11, not illustrated (Underwood, 1970; Moody, 1980, character 56; Estes et al., 1988, character 8).
65. Postorbital and postfrontal; 0 = both bones present, Fig. S139; 1 = fusion of postorbital and postfrontal or loss of one bone, Fig. S140 (modified from Estes et al., 1988, character 14).
66. Posterior medial process of the coronoid; 0 = strongly ridged, not illustrated; 1 = weakly ridged or flat, not illustrated (Moody, 1980, character 61).
67. Supratrigeminal process of the prootic; 0 = absent, Fig. S86; 1 = distinctly small, Fig. S87; 2 = strongly projecting, Not illustrated (Moody, 1980, character 10).

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