Zootaxa 4344 (2): 333–344
http://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4344.2.8
http://zoobank.org/urn:lsid:zoobank.org:pub:F1E32F95-A711-48B8-96E8-CDC933535490

Additions to the description of *Paroplocephalus atriceps* (Serpentes: Elapidae) with a discussion on pupil shape in it and other Australian snakes

BRIAN BUSH
Snakes Harmful & Harmless, 9 Birch Place Stoneville WA 6081 Australia. E-mail: bush@iinet.net.au

Abstract

Morphometric data on an additional twelve individuals of *Paroplocephalus atriceps* Storr are included enlarging Keogh *et al*.'s 2000 description of the genus and further verifying its affinities with *Hoplocephalus*. Included are comments on its venom and observations confirming arboreality and although primarily nocturnal, it includes some diurnal activity. Various authors have erroneously suggested it has vertically elliptic pupils but they are round. During an examination of snake's eyes, it was found that several additional species have pupils that require re-describing, especially *Suta fasciata* Rosen, *S. punctata* Boulenger and *Echiopsis curta* Schlegel, all of which include individuals with round pupils. A standardised description is suggested for each of the three common pupil shapes in snakes as narrow elliptic where dilation and constriction is lateral or vertical only, wide elliptic where dilation and constriction is both lateral and vertical, and round where any dilation and constriction is equidistant from the centre around the pupil's circumference.

Key words: ecology, snake, venom, vertically elliptic

Introduction

Paroplocephalus atriceps was first described in 1980 by G.M. Storr from two specimens collected near Lake Cronin, Western Australia (WA) in 32º 23'S, 119º 45'E. The holotype (R67330) was collected by P. Griffin and G. Barron on 6 October 1979, and the paratype (R29770), the first formally known specimen, was collected by A.E. Jones on 24 August 1967. Storr tentatively placed it in *Brachyaspis* and stated at the time that the Australian Elapidae required urgent revision. The lack of stability in the generic classification of this species illustrates Storr's point, as in the next 20 years *atriceps* was placed in *Denisonia* (Storr 1984, Ehmann 1993), *Echiopsis* (Cogger *et al.* 1983), *Suta* (Golay *et al.* 1993) and *Paroplocephalus* (Keogh *et al.* 2000) its current genus.

Keogh *et al.* (2000) examined genetic, molecular and morphological evidence, and showed that *atriceps* needed to be recognized as a monotypic genus to avoid polyphyly of the elapid genera *Echiopsis*, *Denisonia* and *Suta*, and so described *Paroplocephalus* for that purpose. This name also reflects the close association *atriceps* has with eastern Australian *Hoplocephalus*.

At the time of their study, *atriceps* was poorly represented in collections allowing Keogh *et al.* (2000) only five preserved specimens to work with, although today, 12 are preserved in the WA Museum and three males and two females are being maintained in captivity for study by the author.

Various authors have erroneously described *Paroplocephalus* as having vertically elliptic pupils when this is obviously not so, therefore this study has been expanded to look more closely at the problem of incorrect pupil descriptions in three of the four genera that *atriceps* is currently or has been previously assigned (*Echiopsis*, *Paroplocephalus* and *Suta*). A snake's pupil shape is an important physical character that can provide an indication of some aspects of its ecology. In particular, elliptical pupils infer a sit and wait ambush hunting strategy and predominately nocturnal activity, while round pupils suggest a mobile foraging hunter that seeks out its prey and may be both diurnal and nocturnal (Brischoux *et al*. 2010).

Accepted by T. Nguyen: 4 Oct. 2017; published: 7 Nov. 2017

Materials and methods

This study commenced in 2009 after sourcing the relevant athorisation (Licence SF006959) to take and maintain alive for study purposes a series of five *P. atriceps*. The WA Department of Conservation and Land Management was the authority at the time, but is now the Department of Biodiversity, Conservation and Attractions. It has taken nine years to collect the five snakes, with one found in each of the following years 2009, 2013, 2014 and two in 2016. To find the study snakes, both hand searching during the day and spotlighting on foot or from motor vehicle at night were employed, with all five captive snakes being found in December using the latter technique. The area where all these snakes were located is between 10 and 35 kilometres south of Lake Cronin, WA.

All live snakes were ventrally scanned using a standard colour photocopier to provide a record of individual scale abnormalities and to allow for easy ventral and subcaudal scale counting. In both this sample and the preserved museum specimens, the first ventral was determined to be the first broad (wider than long) scale following the most posterior gular and the last ventral was that immediately preceding the anal plate. The first subcaudal was the first complete scale posterior to the anal plate and last was that preceding the terminal scale. Dorsal scales were counted at neck, defined as at the level of the first ventral; midbody was halfway between head and vent; and pre-vent which was immediately anterior to the vent at the level of the last ventral. To determine the position of the first scale row reduction and number of reductions, random counts were taken between the midbody and pre-vent.

Additional material examined. The earlier study by Keogh *et al.* (2000) examined five specimens: R29770 (paratype), R67330 (holotype), R124882, R126978 and R132047. Twelve additional specimens have been examined during this study, bringing the total to seventeen (5 female and 12 male). Five of these (2 female and 3 male) are being maintained alive, while seven (2 female and 5 male) are lodged in the Western Australian Museum with the registration numbers R82986, R119225, R123534, R151242, R151290, R175315 and R175316.

The eyes were examined in live, dead and preserved snakes and a sample from all groups were photographed to allow for more detailed examination. In species with pale irides (*E. curta, P. atriceps, S. fasciata* and some *S. punctata*) that allowed the pupil to be easily seen, they were categorized as round if the height and width were of similar measurement when constricted or dilated in live snakes. To determine this, the pupils were examined in poor light and then, while being observed, exposed to a bright light using an LED torch to determine if pupil during dilation expanded an equidistant from its center. Otherwise, if there was only lateral constriction or dilation they were vertically elliptic. In those genera or species with extremely dark irides that obscured the pupil (*Parasuta,* some *S. punctata* and *Vermicella*), overexposed photographs of the eye in live snakes would sometimes allow pupil to be discerned, although it was not so obvious nor easy to examine in freshly dead or preserved individuals as the cornea quickly becomes opaque concealing the pupil beneath.

Paroplocephalus description updated with additional data

Additions to the description of *Paroplocephalus* are required here to clarify pupil shape and to enlarge on the morphometrics contributed to by the additional 12 specimens available for examination during this study. The following diagnosis is reproduced (with permission) from Keogh *et al.* (2000) with amendments and additions from this study inserted.

Diagnosis. A monotypic genus containing *P. atriceps*, a terrestrial hydrophiine elapid snake with anal and all subcaudals undivided; dorsal scales smooth but not highly glossed; head moderately broad and distinct from neck; eye large, pupil round; 3 noncanaliculate maxillary teeth behind diastema; temporal scales 2 + 2 + 3 (N 7), 2 + 2 + 4 (N 8), 2 + 3 + 4 (N 1) and 2 + 3 + 5 (N 1) (formula follows definition in Scanlon, 2000); preocular without canthus rostralis, contacts undivided nasal and 2nd supralabial; 6 supralabials (41%), or 7 (59%) when temporolabial (lower anterior temporal) reaches lip between 5th and last; parietal separated from lower postocular; 7 infralabials. '*Oxyuranu*s type' of venom-gland musculature (*sensu* McDowell, 1967; main dorsal portion of *m. adductor externus medialis* reaching transverse crest of supraoccipital and overlapping anterior part of *m. depressor mandibulae*, but not attaching to quadrate). Neck and posterior trunk slender, and body somewhat laterally compressed; ventral scales extend to lower lateral surface of body, and their posterior edges arcuate (lateral parts concave; see Ehmann, 1993). Scale rows 21–23 at first ventral, sometimes reducing to 17 on neck, 17 (N 2) or 19 (N 15) at midbody; two or three reductions, (17–15–13) or (19–17–15–13) respectively posterior to midbody, sometimes increasing again to 15 rows at or just before last ventral. Ventrals 171–190 (N 17, mean 180), males 171–183 (N 12, mean 178.1), females 180–190 (N 5, mean 184.8). Subcaudals 41–52 (N 17, mean 47), males 44–52 (N 12, mean 48.1), females 40–48 (N 5, mean 42.8). Upper iris pale, reducing to a narrow pale band bordering remainder of pupil (golden orange in life: Storr, [1980] – see Figure 1B this study); body reddish brown, olive green (in eastern part of range), or blackish brown; head dull black or dark grey with pale spots on upper and lower labials, and denser black collar on neck, pale-edged posteriorly; dorsal bands or blotches absent (Figure 7); oral lining pale, tongue dark. Largest live specimen is a female (currently kept at Snakes Harmful & Harmless) with snout-vent length (SVL) 730 mm, undamaged tail length 90 mm (12.3% SVL vs. 16.1% in WAM R132047, a female examined by Keogh *et al.* 2000); the largest male (WAM R151290) has SVL 530 mm, tail 99 mm (18.7%). Presumed to be viviparous, but reproduction and natural diet unknown apart from a single prey record of an agamid lizard.

Most like *Hoplocephalus* spp. in body form and scalation (also cranial morphology, Keogh *et al.* 2000); distinguished by lower number of ventrals (171–190 vs. 190–250) and usually of subcaudals (41–52 vs 40–70), lower number of midbody scale rows (17–19 vs 19–21), only weakly angled and scalloped ventral scales (vs usually distinctly keeled and notched as an adaptation for climbing). Distribution restricted to arid eucalypt woodlands of Western Australia (Figure 2) v east coast, hinterland and arid eucalypt woodlands of New South Wales and Queensland.

Comments on *Paroplocephalus atriceps*

Morphologically, *Paroplocephalus atriceps* is most like *Hoplocephalus bitorquatus* Jan in sharing a low number of midbody scale rows, low number of ventrals, monotonal body colour and head of different colour to body. Ecologically, they both occur in dry eucalypt forests, with *P. atriceps* being solely found in this habitat, while *H. bitorquatus* also occurs in wet sclerophyll forests. The other two *Hoplocephalus* (*bungaroide*s Schlegel and *stephensii* Krefft) are generally only found in wet sclerophyll forests. Although all three *Hoplocephalus* spp. are arboreal, *H. bitorquatus* is most so compared to the other two.

Paroplocephalus atriceps represents a primitive, arid-adapted western *Hoplocephalus*-like species that, although displaying some similar ecological attributes to its eastern relatives, has not developed to the same degree the specialized climbing adaptation (distinctly keeled and notched ventrals) seen in *Hoplocephalus* spp.

Although *P. atriceps* lacks the distinctly keeled and notched ventrals in *Hoplocephalus*, recent observations of captive specimens suggest they are adept climbers, moving up and perching on vertically arranged bark and retaining purchase with variously spaced longitudinal lateral folds of skin along lower flanks where dorsal scales meet ventral scales (Figure 3). In addition, in December 2014, J. Vos and S. Patrick observed an adult male five metres above the ground active on the trunk of a smooth-barked eucalypt tree. In December 2016, D. Bromley, R. McGibbon and S. Tuckey saw a stationary individual elevated on the swollen base of a large eucalypt trunk in what they describe as an ambush position. Both these observations were near Cosmic Boy Mine, Forrestania in 32º 35' S, 119º 44' E.

Ehmann (1993) was the first to suggest *P. atriceps* was arboreal after finding a piece of sloughed skin on tree trunk 1.5 m above ground. After comparing a sloughed skin from a captive individual with the field-collected piece, he detected a weak notch at the outer surface of the shed skin.

This snake's distribution is centred on the Greater Western Woodlands and it occurs only 350 km from Perth, but we currently know little of its geographical range and ecology. Its abundance is difficult to assess on the numbers known and the time taken during this study to collect the study animals. Nearly all the individuals found to date were primarily discovered opportunistically at night on the ground, so the difficulty in finding it could be more a result of its arboreality—it may only infrequently foray on the ground moving between trees in the undisturbed densely vegetated woodlands it occupies.

Of those found on the ground during the day, two were discovered beneath rocks. The third, an adult snake was observed by R. Browne-Cooper (pers. comm.) basking on a cool winter's day at an air temperature of 20º Centigrade, at 13.55 hrs on 13 June 2017 about 5 km northwest of Lake Cronin Nature Reserve in 32º 23'S, 119º 45' E. It was observed in the sunshine within a north facing horizontal crevice between two large boulders approximately one metre above ground. When Browne-Cooper attempted to get closer, the snake quickly retreated out of sight.

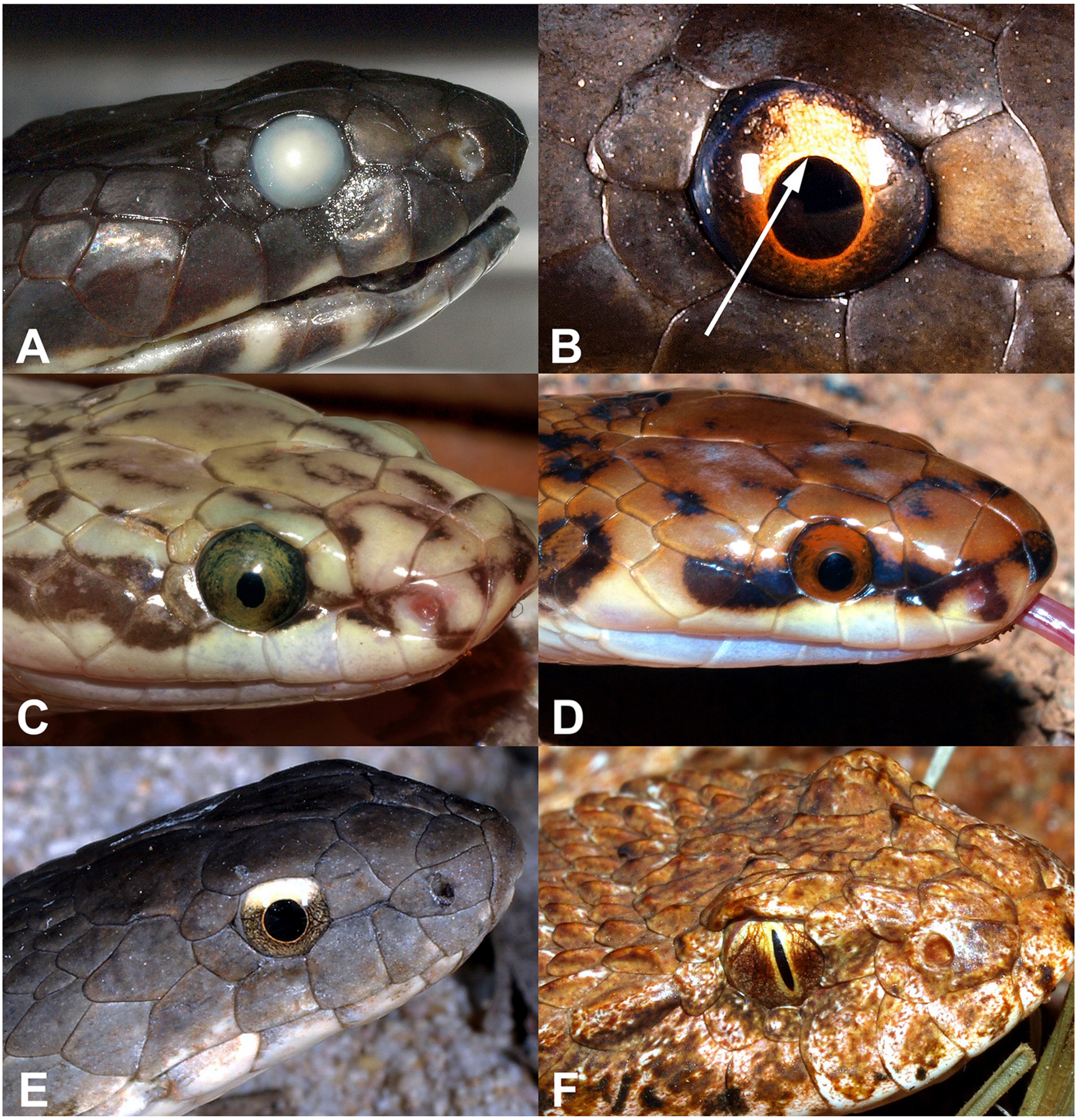

FIGURE 1. A, eye of preserved *Paroplocephalus atriceps* (R151290) showing the effect of ethanol on iris and pupil colour. In life, the iris has a large upper flare of golden-yellow that has gone altogether and the pupil has been changed from black to white. In some preserved individuals, the pupil is indiscernible from the iris altogether. B, eye of *Paroplocephalus atriceps* showing round pupil with slight apical bulge. During dilation and constriction pupil expands or reduces equidistantly from its centre maintaining a round shape. C, eye of *Suta fasciata* showing a rough-edged round pupil, while the individual in D has a smooth-edged round pupil although in some literature it is described as vertically elliptic. During dilation and constriction pupil expands or reduces equidistantly from its centre maintaining a round shape and any blemishes around its circumference. E, eye of *Echiopsis curta* showing round pupil, although in some literature it is described as vertically elliptic. During dilation and constriction pupil expands or reduces equidistantly from its centre maintaining a round shape. (Photo by B. Maryan). F, eye of *Acanthophis pyrrhus* showing narrow vertically elliptic pupil. During dilation and constriction pupil expands or narrows laterally.

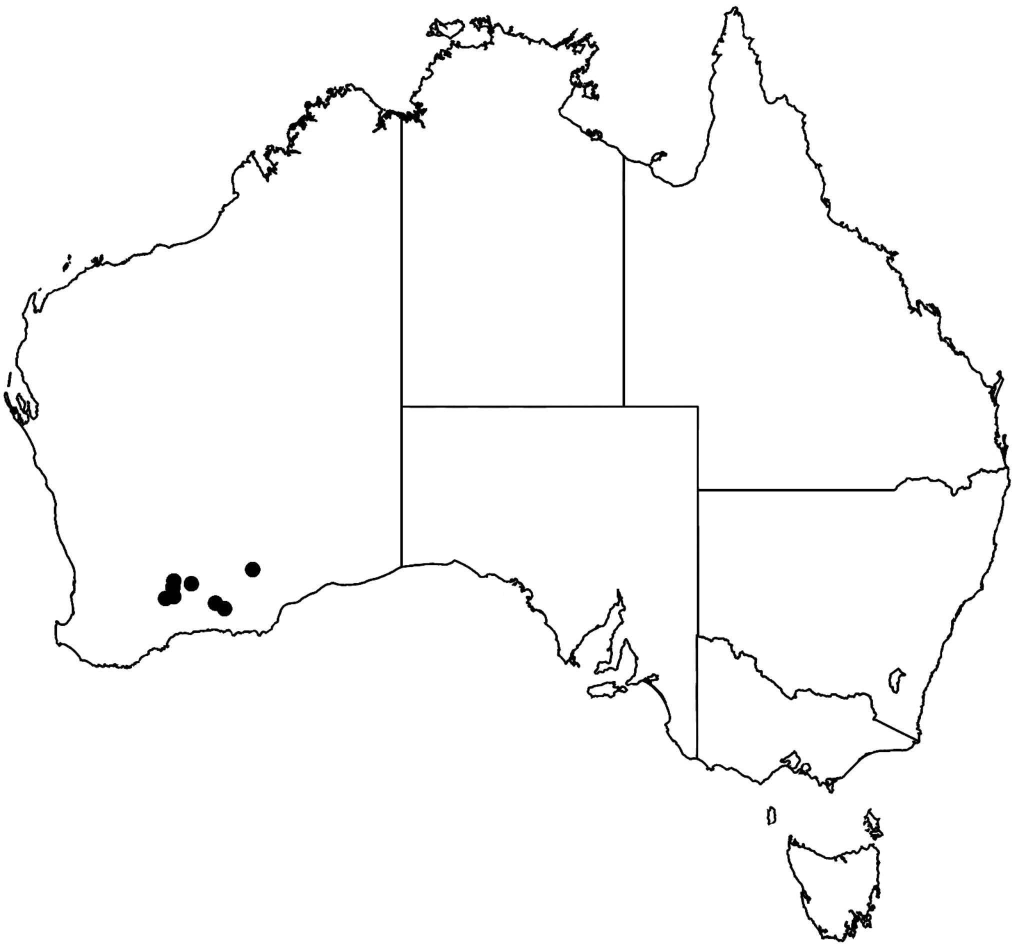

FIGURE 2. Map of Australia showing the known distribution of *Paroplocephalus atriceps* in Western Australia. The easterly dot represents the Fraser Range records.

While preparing this paper, two individuals were found by mine site staff in the Fraser Range 120 km east of all previous records in 31° 50'S, 123° 12'E. This distribution extension supports the current WA wildlife authority's conservation listing. It is a Priority 3 species (2015 a & b), a category for "*Poorly-known species (some on conservation lands) that are known from several locations and the species does not appear to be under imminent threat, or from few but widespread locations with either large population size or significant remaining areas of apparently suitable habitat, much of it not under imminent threat. Species may be included if they are comparatively well known from several locations but do not meet adequacy of survey requirements and known threatening processes exist that could affect them. Such species are in need of further survey.*" With this in mind, the current work is a prelude to an ongoing comprehensive ecological study of *P. atriceps.*

Storr's holotype and paratype are both adult males, with this collecting bias towards adult males continuing in the additional 15 individuals examined during this study (adult male 10, adult female 2 and subadult female 3). This bias may be due to sexually mature, reproductively ready males being far more active (on the ground) and easier to sample than conspecific females. In a study of southwestern Australian *Pseudonaja a. affinis* Maryan and Bush (1986) found a similar skewed sex ratio towards males (22 v 13), however in the similar-sized, although terrestrial *E. curta* Shine (1982) found the reverse was the case (38 v 60). However, with just 14 adult *P. atriceps* available for sexing to date, this discussion will be revisited when sample size is larger.

Venom—A preliminary investigation of *P. atriceps* venom was carried out in early 2016. It is broadly similar to *Hoplocephalus* in the molecular weight of its components, which suggested it to be a member of the Tiger Snake group of venoms (T. Jackson pers. comm.). This was confirmed in a recent study by Lister *et al*. (2017). As such, it is a medically significant species with one case history of an envenomation in an adult male reported by Allen *et al.* (2013). The victim experienced venom-induced consumption coagulopathy similar to the clinical features of *Hoplocephalus* envenoming. CSL polyvalent snake antivenom was administered and he made a full recovery.

Diet—There are no identifiable stomach contents in the twelve preserved specimens held at the WA Museum. The only confirmed natural prey recorded during this study is a large female *Ctenophorus cristatus* Gray regurgitated shortly after capture by a 614 mm male *P. atriceps* in December 2016. This dragon lizard is usually diurnally active and terrestrial, inferring the snake either actively hunted it during the day, or located it when it was at rest in its burrow or under cover and eaten it on the ground, rather than in a tree. Many types of diurnal and nocturnal lizard suitable as prey for this snake occur in the same area of the Greater Western Woodlands, including arboreal geckos.

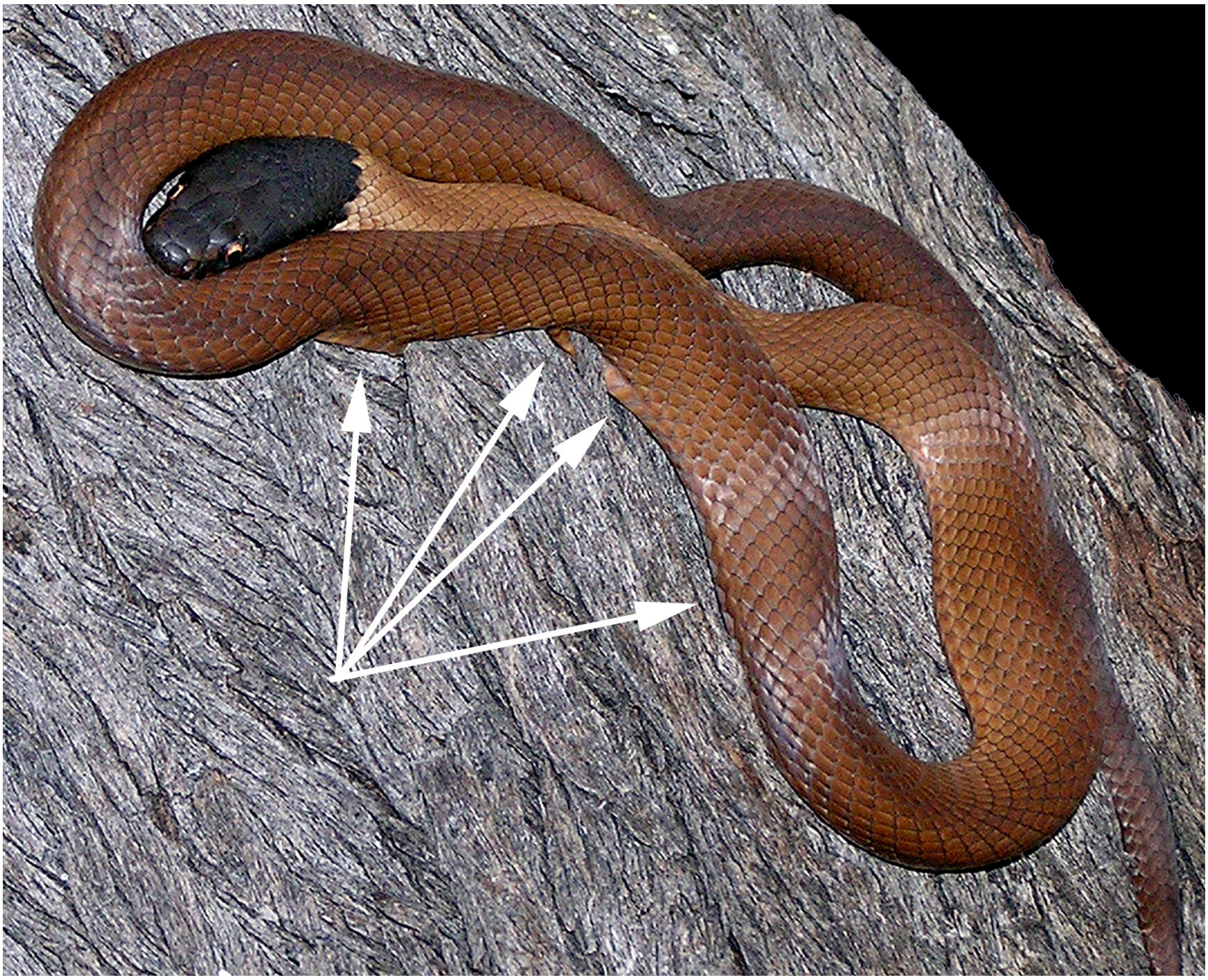

FIGURE 3. Observations of captive *Paroplocephalus atriceps* confirm its predilection for both climbing and perching on vertically positioned bark. Note the longitudinal lateral folds of skin (white arrowed) assisting the snake's grip on the rough bark.

General discussion on pupil shape in snakes

In his diagnosis of *atriceps*, Storr (1980: 397) limits his description of the eyes to, "large, somewhat obtrusive" and "iris entirely golden orange (rather than uppermost sector only)". This description must have been based on an examination of the holotype in life, or at least a photograph of it, as no golden colour is discernible in preserved specimens (Figure 1A). In addition, his description is not entirely accurate as only the upper part of the iris and a narrow margin around the pupil are golden in life (photograph of holotype in Storr 1980 and Figure 1B current study). There is no mention of pupil shape in this original description, however, in his 1984 (p. 250) revision of *Denisonia suta* Peters, of which he considered *atriceps* a congener, along with *devisi* Waite and Longman, *fasciata*, *maculata* Steindachner, *ordensis* Storr, *pallidiceps* Günther and *suta*, he describes member species as having "pale iris and vertically elliptic pupil" and this description has persisted in the literature since for all those species considered congeners by Storr at the time (e.g., Ehmann 1992; Scanlon *et al*. 2004; Wilson and Knowles 1988; Wilson and Swan 2013). Greer (1997: 193) in his data matrix correctly scored its pupil as round, but also incorrectly scored the pupil of *Echiopsis* and *Hoplocephalus* as vertically elliptic.

FIGURE 4. Left, pupil dilation in *Suta fasciata* from top: round, wide elliptic and round again when dilated; and right, *Acanthophis wellsi* from top showing lateral dilation only in narrow elliptic pupil.

Storr *et al.* (1986: 72) gave a more conservative description of the eye for *Denisonia*, "iris normally pale and pupil tending to be higher than wide", but the drawings they provided for all the four Western Australian species they included in this genus at the time (*atriceps*, *fasciata*, *ordensis* and *suta*) depict a pronounced vertically elliptic pupil. The same description for each species is given by Storr *et al.* (2002), however it is not the case for all of them in life. In *Paroplocephalus* (Figure 1B), the pupil is clearly round with at most a distortion in some individuals caused by a small apical bulge corresponding with the upper flare of golden-yellow iris colour. This slight distortion may have created the illusion of a somewhat compressed elliptical shape. When the eye is photographed in life to provide an accurately measurable image, the pupil's diameter is the same when recorded at any point around its circumference, except in height when the measurement includes the small apical bulge. The pupil's diameter increases and decreases minimally as it constricts and dilates but its lateral and horizontal measurement at any point in time remain the same showing no lateral narrowing as one would expect to see in a vertically elliptic pupil.

The eye in *Echiopsis curta* is similar to *atriceps* in sharing the pupil condition of the apical bulge and its iris in life also has the upper flare of golden colour, however Storr *et al*. (2002: 179), illustrate the pupil as round in this species, while Bush *et al.* (2010), Ehmann (1992), Wilson and Knowles (1988) and Wilson and Swan (2013) all describe it as vertically elliptic. Included here (Figure 1E) is a photograph of the eye with round pupil in *E. curta* showing its similarities to *P. atriceps*.

Suta fasciata (Figure 1C and 1D) has a very distinctive round pupil in a large bulbous eye, although the pupil can be rough-edged in some individuals when constricted in bright light. Three stages of progressive dilation of its pupil are shown in Figure 4 (left) with the upper two photos showing the rough edge of pupil often seen in this snake and the middle photo showing it as it changes to wide elliptic before returning to round again in the bottom photo.

FIGURE 5. *Suta fasciata* ingesting *Ctenophorus c. caudicinctus* found asleep on warm bitumen round at night.

Figure 1F depicts an eye with a typical vertically elliptic pupil in the elapid snake *Acanthophis pyrrhus* Boulenger photographed in daylight. During dilation and constriction in all *Acanthophis*, the pupil only expands or narrows laterally with little change in its height (Figure 4: right), whereas in a round pupil it expands or reduces equidistantly from its centre while maintaining its circular shape along with any bulges or blemishes around its circumference. Unless the pupil constricts laterally to an obvious narrow vertical bar (narrow elliptic), or constricts equally in on itself, retaining an oval shape (wide elliptic) then I believe it be best described as 'round'.

Some distortion of the eye and pupil occurs in preserved snakes. In some cases, even in specimens of the same species, it is impossible to distinguish the cornea from pupil with just a visual examination. Further, those species that, in life, have a dark iris with an upper flare of bright golden-yellow and a narrow halo surrounding the pupil lose this colour altogether in ethanol. In addition, the cornea and spectacle become opaque further concealing the iris and pupil (Figure 1A). This highlights the importance of observing live individuals when available, as well as examining photographs taken during the day of the relevant species in life, rather than relying solely on preserved museum specimens for descriptions.

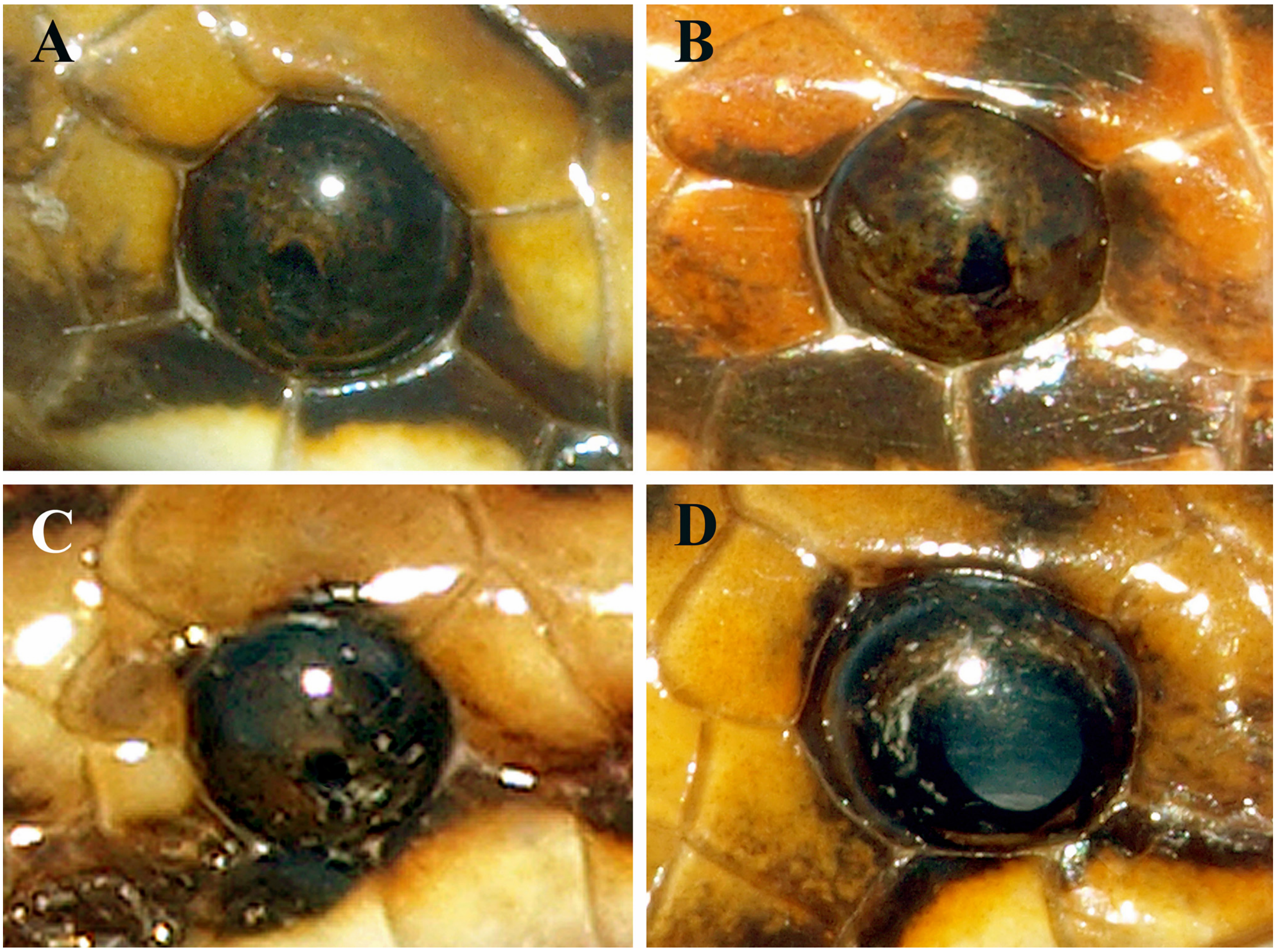

FIGURE 6. Eye in *Suta punctata* showing intraspecific variation in pupil shape. A and B wide elliptic. C round and D opaque cornea in recently deceased individual.

Field and captive observations of *P. atriceps* confirm it to be predominately nocturnal with some active diurnal hunting and opportunistic basking. An association between pupil shape and preferred activity time in Australian elapid snakes has been observed in several species. The nocturnal *Acanthophis*, *Cacophis* and *Denisonia* show little evidence of diurnal activity (Bush & Maryan 2011, Ehmann 1992, Wilson and Knowles 1988) and all have narrow vertically elliptic pupils. Shine (1983) found *D. devisi* and *D. maculata* were ambush hunters of nocturnal prey and more recent work by Brischoux *et al*. (2010) confirmed the connection between vertically elliptic pupils and this type of hunting strategy. *E. curta* has round pupils and is opportunistically active day or night dependant on temperature (Bush 1981, Bush *et al.* 2007, Wilson and Swan 2013). This opportunism rarely occurs in elapid snakes with vertically elliptic pupils. Both *Simoselaps bertholdi* Jan and *S. littoralis* Storr have been observed active during the day (Bush 1981, Browne-Cooper & Maryan 1988, Wilson and Knowles 1988) and are often described as having vertically elliptic pupils, but during present study it was found not to be consistent. Many individuals within the same population and under the same lighting conditions have round pupils, while others are wide elliptic. Polyphasic activity appears far more common in elapid snakes with round pupils, eg, the primarily diurnal *Drysdalia mastersii* Krefft (Bush 1981, Ehmann 1992), *D. coronoides* Günther (Ehmann 1992), *Elapognathus coronatus* Schlegel (Bush 1981, Bush *et al.* 2000, Ehmann 1992), *Pseudonaja* spp. (Bush *et al.* 2007, 2010) and *Demansia psammophis* Schlegel (Bush *et al.* 2010) have all been reported active at night during high temperatures. The exceptions are *S. fasciata* and *punctata* with their unique bulging eyes that contain small round to wide elliptic pupils in extremely large irides. I have never observed these snakes diurnally active, nor have I been able to find any published references to them being so. However, this does not detract from the pupil shape-activity link presented here as their eyes are unlike most other Australian elapids. Shine (1983) found *S. fasciata* to have a very specialized diet of agamids, which are found when asleep on warm substrates at night (Figure 5).

The uniqueness of *fasciata* and *punctata* eyes was further highlighted during this study when an intraspecific difference in pupil shape from round to wide vertically elliptic was recorded. In both species, this was generally found to be a result of the pupil shape changing during its transition from constricted, where it might be round, then as it enlarges it may become wide elliptic, before returning to round when nearly fully dilated (Figures 4: left and 6). This was observed in many adult individuals of both species randomly throughout their respective geographical distributions (*fasciata* 10 of 37–27%, and *punctata* 6 of 16–37.5%).

FIGURE 7. *Paroplocephalus atriceps* showing dominant brown dorsal colour in western population and green in eastern population. Bottom photo by S Thompson.

Conclusion on pupil shape

When describing the pupil shape in snakes, I suggest three standardised descriptions are used. These need to be specifically ascertained when constricted pupil can be examined in daylight conditions, as follows:

(1) **narrow elliptic** where constriction and dilation is vertical (some overseas genera, eg *Ahuetulla*) or lateral only (eg *Acanthophis* and *Denisonia*);
(2) **wide elliptic** where constriction and dilation includes both vertical and lateral enlargement with the height usually remaining greater than the width (eg *Cacophis,* some *Simoselaps bertholdi* and *S. littoralis* and some individuals of *Suta fasciata* and *S. punctata*); and
(3) **round** where during constriction and dilation, which is minimal in this group, the lateral and vertical measurement decreases or increases but both always remain the same (eg *Austrelaps, Demansia, Drysdalia, Echiopsis*, *Elapognathus*, *Hemiaspis, Hoplocephalus, Notechis*, *Oxyuranus, Paroplocephalus, Pseudechis*, *Pseudonaja*, some individuals of *Simoselaps bertholdi*, *S. littoralis*, *Suta fasciata* and *S. punctata*, and *Tropidechis*).

In many species, the pupil is indiscernible within a black iris, so accurately documenting the shape is problematic. Genera with such hidden pupils are *Antairoserpens, Brachyurophis, Cryptophis*, *Furina*, *Neelaps*, *Parasuta, Rhinoplocephalus, Simoselaps* (part) and *Vermicella*.

Before my involvement in this study, I wandered how pupil descriptions in both the popular books and scientific literature for Australian snakes could be so inconsistent. Now I have a completely new perspective on the problem and understand why this has occurred.

Acknowledgements

I thank Scott Keogh for comments and suggestions on the original draft and providing permission to reproduce the 2000 *Paroplocephalus* diagnosis here. Bruce Budrey, Brad Maryan and Robert Browne-Cooper for their encouragement, while Jackson Bishop and Josh Maher provided me with a greater insight to *Hoplocephalus* species. Matt Clancy, Loki Fenner, Lockie Gilding, Mark Neath, Steven Patrick, Trent Snow, Gary Stephenson and Jordan Vos allowed me to examine some of their great photos of *Echiopsis curta, Denisonia* and *Suta* species in life. For sharing their observations of *atriceps* in the wild, I thank Daniel Bromley, Ross McGibbon, Steven Patrick, Steve Tuckey and Jordan Vos. Timothy Jackson examined the *atriceps* venom I provided and Harald Ehmann examined a sloughed skin of one of my study snakes for comparison with the piece of skin that was the basis for his 1993 paper. Scott Thompson provided the photograph and information on the Fraser Range records of *P. atriceps*. Paul Doughty allowed me access to the collection to examine the additional *P. atriceps* lodged there since 2000 and along with Graham Thompson provided invaluable comments on an earlier draft of this paper. I thank Glenn Shea for his amazingly thorough attention to detail during his review of the final draft. On several field trips to the Forrestania area, Brad Maryan, Jy and Nathan Garbin provided company. The WA Department of Biodiversity, Conservation and Attractions provided the required athorisation (#SF008976) to allow the taking of the five live snakes held for observation.

References

Allen, G.E., Wilson, S.K. & Isbister, G.K. (2013) *Paroplocephalus* envenoming: a previously unrecognised highly venomous snake in Australia. *Medical Journal of Australia*, 199 (11), 792–793.
https://doi.org/10.5694/mja13.10985

Brischoux, L., Pizzatto, L. & Shine, R (2010) Insights into the adaptive significance of vertical pupil shape in snakes. *Journal of Evolutionary Biology*, 23, 1878–85.
https://doi.org/10.1111/j.1420-9101.2010.02046.x

Browne-Cooper, R. & Maryan, B. (1988) Record of diurnal feeding in *Vermicella bertholdi (*Jan, 1859) (Serpentes: Elapidae). *Herpetofauna*, 18 (2), 25.

Bush, B. (1981) *Reptiles of the Kalgoorlie-Esperance Region*. Bush, Esperance, WA, 46 pp.

Bush, B., Maryan, B., Browne-Cooper, R. & Robinson, D. (2007) *Reptiles and Frogs in the Bush: Southwestern Australia.* UWA Press, Nedlands, WA, 302 pp.

Bush, B., Maryan, B., Browne-Cooper, R. & Robinson, D. (2010) *Field Guide to Reptiles & Frogs of the Perth Region.* WA Museum, Welshpool, WA, 185 pp.

Bush, B. & Maryan, B. (2011) *Field Guide to Snakes of the Pilbara.* WA Museum, Welshpool, WA, 112 pp.

Bush, B. (2013) Perseverance Prevails: Captive Reproduction in the Spotted Mulga Snake. *Scales and Tails*, 29, 29-32.

Cogger, H.G., Cameron, E.E. & Cogger, H.M. (1983) *Zoological Catalogue of Australia. Vol. 1. Amphibia and Reptilia*. Australian Government Publishing Service, Camberra, 313 pp.

Ehmann, H. (1992) *Encyclopedia of Australian: Reptiles.* Collins Angus & Robertson, Sydney, 495 pp.

Ehmann, H. (1993) A field observation on the Lake Cronin Snake (*Denisonia atriceps*) and mineral exploration within its range. *In*: Lunney, D. & Ayres, D. (Ed.), *Herpetology in Australia – A Diverse Discipline*. Transactions of the Royal Zoological Society, NSW, pp. 346-348.

Golay, P., Smith, H.M., Broadley, D.G., Dixon, J.R., McCarthy, C., Rage, J.C., Schätti, B. & Toriba, M. (1993) *Endoglyphs and other major venomous snakes of the world. A Checklist.* Azemiops, SA, Geneva, 497 pp.

Greer, A. (1997) *The Biology and Evolution of Australian Snakes.* Surrey Beatty & Sons Pty Ltd, Chipping Norton, 358 pp.

Keogh, S.J., Scott, I.A.W. & Scanlon, J.D. (2000) Molecular phylogeny of viviparous Australian elapid snakes: affinities of *Echiopsis atriceps* (Storr, 1980) and *Drysdalia coronata* (Schlegel, 1837), with a description of a new genus. *Journal of Zoology London*, 252, 317–326.
https://doi.org/10.1111/j.1469-7998.2000.tb00626.x

Lister, C., Arbuckle, K., Jackson, T.N.W., Debono, J., Zdenek, C.N., Dashevsky, D., Dunstan, N., Allen, L., Hay, C., Bush, B. & Gillett, A. (2017) Catch a tiger snake by the tail: Differential toxicity, co-factor dependence and antivenom efficacy in a procoagulant clade of Australian venomous snakes. *Comparative Biochemistry and Physiology*, Part C, 202, 39–54.
https://doi.org/10.1016/j.cbpc.2017.07.005

Maryan, B. & Bush, B. (1996) The Dugite or Spotted Brown Snake *Pseudonaja affinis*. *Herpetofauna*, 26 (2), 22-34.

Scanlon, J.D. (2003) The Australian elapid genus *Cacophis*: Morphology and phylogeny of rainforest crowned snakes. *Herpetological Journal*, 13, 1-20.

Scanlon, J.D. & Lee, M.S.Y. (2004) Phylogeny of Australasian venomous snakes (Colubroidea, Elapidae, Hydrophiinae) based on phenotypic and molecular evidence. *Zoologica Scripta*, 33 (4), 335–366.
https://doi.org/10.1111/j.0300-3256.2004.00151.x

Shine, R. (1982) Ecology of the Australian elapid snake *Echiopsis curta*. *Journal of Herpetology*, 16 (4), 388–193.
https://doi.org/10.2307/1563569

Shine, R. (1983) Food habits and reproductive biology of Australian elapid snakes of the genus *Denisonia*. *Journal of Herpetology*, 17 (2), 171-175.
https://doi.org/10.2307/1563458

Storr, G.M. (1980) A new *Brachyaspis* (Serpentes: Elapidae) from Western Australia. *Records of the Western Australian Museum*, 8 (3), 397-399.

Storr, G.M. (1984) Revision of *Denisonia suta* (Serpentes: Elapidae) and a description of a new species closely related to it. *Records of the Western Australian Mus*eum, 11 (3), 249-257.

Storr, G.M., Smith, L.A. & Johnstone, R.E. (1986) *Snakes of Western Australia.* Western Australian Museum, Perth, WA, 187 pp.

Storr, G.M., Smith, L.A. & Johnstone, R.E. (2002) *Snakes of Western Australia. 2nd Edition*. Western Australian Museum, Perth, WA, 309 pp.

Western Australian Department of Parks and Wildlife (2015a) Critically endangered fauna (Schedule 1 of the Wildlife Conservation (Specially Protected Fauna) *WA Department of Parks and Wildlife Notice 2015*, 1–23.

Western Australian Department of Parks and Wildlife (2015b) Wildlife Conservation (Specially Protected Fauna) Notice 2015. *WA Government Gazette*, 2015, 4532-4543.

Wilson, S.K. & Knowles, D.G. (1998) *Australia's Reptiles: A Photographic Reference to the Terrestrial Reptiles of Australia.* Collins Publishers, Sydney, NSW, 447 pp.

Wilson, S. & Swan, G. (2013) *A Complete Guide to Reptiles of Australia. 4th Edition*. New Holland, Chatswood, NSW, 592 pp.