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# A new genus for four myobatrachid frogs from the South Western Australian Ecoregion

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## Abstract

The southern Australian endemic genus *Geocrinia* Blake 1973 (Anura: Myobatrachidae) currently contains seven species, with five restricted to Western Australia and two in the south-eastern states covering parts of New South Wales, Victoria, Tasmania and South Australia. All species have a modified life history with at least some or all of the larval stage being completed terrestrially. Four of the Western Australian species have terrestrial, non-feeding tadpoles nourished by yolk until metamorphosis. The remaining species have a biphasic development with embryos developing on land followed by an aquatic tadpole stage. The presence of species groups within the *Geocrinia* has been recognised since the 1970s, with all relevant subsequent studies supporting a model of two groups within the genus, recovered as reciprocally monophyletic in phylogenetic analyses. We examined character traits of the seven recognised *Geocrinia* species, concluding that distinction of the two monophyletic groups is supported by differences in life history strategy, larval morphology, adult morphology, call structure, breeding season and geographic distribution. The differences between the two groups correspond to phylogenetic structuring for all traits except distribution. Given reciprocal monophyly, and greater variation in traits than present within other myobatrachid genera, we conclude that the two groups should be given generic distinction. We therefore describe a new genus, *Anstisia* **gen. nov.**, for four Western Australian *Geocrinia* species, retaining three species in *Geocrinia*. This increases the number of recognised myobatrachid genera to 14: five are endemic to south-western Australia.

**Key words:** generic concept, global biodiversity hotspot, Amphibia, Myobatrachinae

## Introduction

The classification of species into genera can be a problematic aspect of taxonomy. Unlike species classification, where appropriate taxonomic decisions are guided by well refined and widely supported "species concepts", notwithstanding some inherent applicational imprecision, there is no singular uniformly applied "genus concept" (Dobzhansky 1935, Mayr 1942, Cain 1956, Dubois 1988, Wilkins 2002). Rather, individual taxonomists often assign species into genera based on their interpretation of the significance of morphological, ecological and behaviour traits, with the only strict requirement for a genus being genetic monophyly (Hennig 1950, Cain 1956, Inger 1958, Mayr 1981, Dubois 1988). In recognition of the lack of clarity to genus definition, Dubois (1988) presented a synthesis of genus concepts in zoology and suggested criteria for genera recognition. He proposed a generic concept constrained by hybridisation, where species able to produce viable hybrids should be placed into the same genus, while suggesting that genera should be defined as phenotypic, cladistic and ecological units that represent real, rather than interpreted, patterns in nature.

While phenotypic and cladistics approaches to genera are broadly applied, the importance of ecological traits, which correspond to environmental niches, has been particularly highlighted in anuran taxonomy. The "adaptive approach" to genus recognition proposed by Inger (1958) uses life history strategy, indicated by reproductive behaviour

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and larval development, as a defining character for genera, where species within a genus feature a uniform strategy. Under this model monophyletic species groups with distinctly different life histories or ecological niches can/should be placed in separate genera. Globally, species within anuran genera largely have uniform life history strategies, referred to broadly as "developmental guilds", and exceptions to this are rare (Thibaudeau & Altig 1999). Congruent with Dubois' hybridisation model, species featuring differing life history strategies are unlikely to hybridise, given different requirements for reproduction or development. A notable exception to these ecological approaches is the Australo-papuan anuran family Myobatrachidae Schlegel 1850, where some genera lack uniformity in life history strategy, suggesting the possibility for recognition of further genera if supported by genetic monophyly.

The family Myobatrachidae currently contains 91 described species (Frost 2021) of primarily small, and fossorial or terrestrial frogs (Anstis 2017, Sanders 2021), across 13 genera (Frost 2021). Recognition of Myobatrachidae as a family distinct from Limnodynastidae Lynch 1969 is also disputed, with some authors considering the limnodynastids as a myobatrachid subfamily (Vidal-García *et al*. 2014, Vidal-García & Keogh 2017, Dubois *et al*. 2021, Gould *et al.* 2022), although considerable ecological and morphological differences exist between the two groups (Frost *et al*. 2006, Anstis 2017). The family Myobatrachidae sensu stricto inhabits temperate and tropical ecosystems, including deserts, forests, montane areas and rainforests, being widely distributed in Australia (Anstis 2017, Sanders 2021) with some species also occurring in New Guinea (Menzies 2006).

Myobatrachids have both conventional, and very atypical, anuran life histories, varying primarily between genera (Anstis 2017). Compared to the other widely distributed Australian frog families, Pelodryadidae Günther 1858 and Limnodynastidae, which show little variation in life history between genera and species (Anstis 2017), the life history strategies of Myobatrachidae tend to differ between, and in some cases, within genera. Among the 13 currently recognised myobatrachid genera there are seven documented life history (reproductive cycle) strategies (summarised in Anstis 2013) (Table 1). Within genera, the life history strategy is uniform, with the exception of *Geocrinia* and *Crinia* (Anstis 2017, Sanders 2021). Within *Crinia,* a single species, *C. nimba* Rounsevell, Ziegeler, Brown, Davies & Littlejohn, features a nidicolous life history, while the remainder are aquatic (Anstis 2017). The former placement of *C. nimba* in *Bryobatrachus* renders *Crinia* paraphyletic (Read *et al*. 2001); consequently further taxonomic resolution of this clade may be appropriate following the genus concepts of Inger (1958) and Dubois (1988). To a much lesser extent, the life history strategies of *Pseudophryne* and *Mixophyes* may also be considered non-uniform (Main 1965, Thumm 2004, Anstis 2013), however differences between species within these genera are confined to egg deposition sites and not embryonic or larval development (M. Anstis, pers. comm.).

**TABLE 1.** The known life history strategies of Australian myobatrachids classified following Anstis (2013). Some *Mixophyes* species are better classed as "aquatic (terrestrial oviposition)" as eggs are often deposited onto terrestrial stream banks, however hatching occurs during embryo stages like other "aquatic" developing species, rather than during larval stages as occurs in "terrestrial/aquatic" species. Two species of *Pseudophryne* can also lay eggs in water during drier conditions (Main 1965, Thumm 2004, J. Walsh, pers. comm.), but in both species hatching begins from larval stages and feature embryological development which is consistent for this genus. *Indicates genera where life history strategy has not been documented for all species.

| Life history strategy | Genera | Species |
|---|---|---|
| Aquatic | *Crinia, Mixophyes, Paracrinia, Spicospina, Taudactylus*, Uperoleia*, Pseudophryne** | *M. balbus*, *M. fleayi*, *P. australis*, *P. douglasi*. All documented *Crinia* (other than *C. nimba*), *Paracrinia*, *Spicospina*, *Taudactylus* and *Uperoleia* species. |
| Aquatic (terrestrial oviposition) | *Mixophyes* | *M. carbinensis, M. coggeri, M. fasciolatus, M. iteratus, M. schevilli.* |
| Terrestrial/aquatic | *Geocrinia, Pseudophryne** | *G. laevis, G. leai, G. victoriana*. All documented *Pseudophryne* species. |
| Nidicolous | *Crinia, Geocrinia* | *C. nimba, G. alba, G. lutea, G. rosea, G. vitellina.* |
| Paraviviparous | *Rheobatrachus* | All species. |
| Exoviviparous | *Assa* | All species. |
| Direct development | *Arenophryne, Metacrinia, Myobatrachus* | All species. |

The myobatrachid genus *Geocrinia* forms an obvious exception to this pattern, where two clades, commonly referred to as "species groups", with different life history strategies and morphology have been identified in the literature (Blake 1973, Roberts & Maxson 1985, Read *et al*. 2001, Driscoll & Roberts 2007, Anstis 2010). The genus currently comprises of seven species restricted to southern Australia and features life histories that are apparently adapted to temporary inundations or remnant moisture resulting from predictable autumn and winter rains. Species in the *Geocrinia laevis* group (*G. laevis* Günther 1864, *G. leai* Fletcher 1898 and *G. victoriana* Boulenger 1888), utilise a terrestrial/aquatic life history, while the four species in the *G. rosea* group (*G. alba* Wardell-Johnson and Roberts 1989, *G. lutea* Main 1963, *G. rosea* Harrison 1927 and *G. vitellina* Wardell-Johnson and Roberts 1989), utilise a nidicolous life history (Anstis 2010); an anuran developmental guild where free-living and non-feeding larvae do not interact with the parents, and remain within the nest site until metamorphosis (Altig & Johnston 1989). These two groups are reciprocally monophyletic (Read *et al.* 2001, Driscoll & Roberts 2007) and there are a number of other differences between them, including larval morphology, adult morphology, mating system, call structure and breeding season (Anstis 2013, Clulow & Swan 2018, Sanders 2021).

The earliest molecular investigation into phylogenetic relationships within *Geocrinia* was Roberts & Maxson (1985), who found deep immunological distinction between the one eastern Australian species they sampled (*G. victoriana*) and all four Western Australian (WA) species sampled (*G. leai*, *G. rosea*, *G. lutea* and one of either *G. vitellina* or *G. alba*, both undescribed at the time). With only one-way comparisons, they were unable to assess the relationships of the WA species to each other. Subsequently Read *et al*. (2001) presented a molecular study of relationships among the Myobatrachidae. Their work, which included all *Geocrinia* species other than *G. lutea*, but had only single specimen representation of species other than *G. leai*, and used two mitochondrial genes, recovered monophyly of *Geocrinia* and within it, the *G. laevis* group inclusive of *G. leai*, and sampled members of the *G. rosea* group. Driscoll & Roberts (2007) investigated molecular systematics of the *G. rosea* group in more detail, confirming the reciprocal monophyly of the *G. rosea* and *G. laevis* groups. All three studies found support for the concept of 'groups' within *Geocrinia*, which was first inferred on morphological grounds by Blake (1973), although Blake suggested a third group, containing only *G. leai,* may be justified. Read *et al*. (2001) found support for Blake's model, recovering *G. leai* as the most basal member of the *G. laevis* group, but concluded that only two supported lineages, corresponding to the two species groups, were present.

Within the Myobatrachidae, Read *et al*. (2001) identified the exoviviparous *Assa* as the sister to *Geocrinia* with strong support. Dubois *et al*. (2021) provided another phylogenetic analysis of Myobatrachidae, which recovered *Assa* and *Geocrinia* as sister taxa in a broader radiation that also included *Crinia* and *Paracrinia,* with *Paracrinia* as the sister taxon to *Assa* and *Geocrinia*, and *Crinia* as the basal member of the clade. The inclusion of *Paracrinia* and *Crinia* within the same radiation as *Assa* and *Geocrinia* is very strongly supported (Dubois *et al*. 2021). Expectedly, the close relationship between *Paracrinia*, *Geocrinia* and *Assa* is also recovered by Frost *et al*. (2006), Pyron & Wiens (2011) and Vidal-García & Keogh (2017) given these analyses were conducted using similar datasets to Dubois *et al*. (2021).

Historically, there have also been a number of taxonomic changes to *Geocrinia* species, with the first described *Geocrinia, G. laevis,* originally placed in the genus *Pterophrynus* by Günther (1864). Keferstein (1868) synonymized *Pterophrynus* with *Crinia*, in recognition of similarities with *Crinia georgiana* Tschudi, and the next four species to be described, *G. victoriana*, *G. leai*, *G. rosea* and *G. lutea*, were also placed in *Crinia.* Blake (1973) moved this distinct group of five species with terrestrial egg deposition into a new genus, *Geocrinia*, to which the remaining two species, *G. alba* and *G. vitellina* were assigned when described. A summary of the taxonomic history of all *Geocrinia* species is presented in the Supplementary Material (Table S1).

The significance of life history and ecological factors in genus recognition, as per the concepts of Cain (1956), Inger (1958) and Dubois (1988), is particularly validated as a case study in the taxonomic and nomenclatural history of Myobatrachidae. This variation in life history between myobatrachid genera also corresponds to objective natural structuring, i.e. real genetic, rather than inferred, differences (Read *et al.* 2001, Frost *et al.* 2006, Vidal-García & Keogh 2017, Dubois *et al*. 2021). Species contained in *Assa* and *Geocrinia* were originally included in *Crinia*, until recognition of the unique life histories and morphology, demonstrated as distinct from all other *Crinia* species, prompted the creation of the new genera by Tyler (1972) and Blake (1973). The placement of *Metacrinia nichollsi* Harrison into a monotypic genus by Parker (1940), when it had been previously included in the morphologically similar *Pseudophryne,* is supported by the difference in life history strategy between the two genera (Anstis 2008, 2013). Further, *Metacrinia* is more closely related to *Arenophryne* and *Myobatrachus* with the three genera forming

a distinct Western Australian myobatrachid lineage that share life history strategies (Read *et al.* 2001, Anstis *et al*. 2007, Anstis 2008, 2013, Vidal-García & Keogh 2017, Dubois *et al*. 2021).

Herein we review *Geocrinia*, investigating whether phenotypic and ecological traits correspond with phylogenetics, and find support for recognition of separate genera for the two groups.

## Materials and methods

We examined all relevant literature on *Geocrinia* to investigate phylogenetic structuring in the genus. We used the analysis of relationships, including branch lengths and confidence values, provided by Read *et al*. (2001), with the position of *G. lutea* inferred following the analysis by Driscoll & Roberts (2007). We then compared character systems covering behavioural and ecological traits of the species, sourced from the literature and our own observations. These traits and reference sources are presented in Table 2.

**TABLE 2.** Description of traits examined for *Geocrinia* species and relevant references.

| Trait | Description | Sources |
|---|---|---|
| Genetic grouping (mitochondrial ND2/12S; 17 allozyme loci) | Placement in the *G. laevis* or *G. rosea* group, and broader relationships according to genetic data. | Roberts & Maxson 1985, Driscoll 1998b, Read *et al*. 2001, Driscoll & Roberts 2007, Pyron & Wiens 2011, Vidal-García & Keogh 2017, Dubois *et al*. 2021 |
| Life history | Reproductive cycle/life history strategy as classified by Anstis (2013). | Main 1957, 1963, 1965, Littlejohn & Martin 1964, Roberts *et al*. 1990, Gollmann & Gollmann 1991, Anstis 2010, 2013, Gould *et al*. 2022 |
| Larval morphology | Morphology of the larvae including mouthparts and body shape/size, as classified by Anstis (2013). | Anstis 2010, 2013 |
| Frog morphology and mating system | Absolute testes mass, morphometrics and evidence of polyandry. | Wardell-Johnson & Roberts 1996, Byrne *et al*. 2002, Roberts & Byrne 2011, Vidal-García *et al*. 2014, Vidal-García & Keogh 2015, Roberts 2020 |
| Call type | Call structure—either monophasic (single repeated note) or biphasic (two note types—introductory and secondary, repeated in call sequence). | Littlejohn & Martin 1964, Littlejohn *et al*. 1971, Littlejohn & Harrison 1985, Harrison & Littlejohn 1985, Littlejohn & Watson 1985, Roberts *et al*. 1990, Roberts & Wardell-Johnson 1995, Scroggie & Littlejohn 2005, Clulow & Swan 2018, Webster & Bool (this study), Roberts 2020, Sanders 2021 |
| Breeding season | Time of year when calling and reproduction are known to occur. | Main 1957, 1963, 1965, Littlejohn & Martin 1964, Roberts *et al*. 1990, Driscoll 1998a, Conroy 2001, Anstis 2010, 2013, Rowley & Callaghan 2020, I. Bool, pers. obs., G. Webster, pers. obs. |
| Distribution | Geographic range of the species. | Roberts *et al*. 1990, Wardell-Johnson & Roberts 1993, Roberts & Wardell-Johnson 1995, Atlas of Living Australia 2020a–g |

In addition to existing literature, calls recorded by G. Webster of *G. alba* (n=3), *G. vitellina* (n=3), *G. lutea* (n=2) and *G. rosea* (n=1) were examined in Raven Pro 1.5. Additional call recordings of *G. leai* (n=4) and *G. laevis* (n=2) provided by M. Anstis, and *G. victoriana* (n=2) provided by M. Clancy, were also examined. Corresponding values for frog snout-vent length and temperature were not available and consequently analysis incorporating covariates was not possible. Calls were recorded and processed in WAV format (44.1 kHz with 16 bits per sample) with audiospectrograms calculated using a fast-Fourier transformation (FFT) of 512 points, 50% overlap and 86.1 Hz grid spacing, and Hanning windows. Using these recordings, waveforms of advertisement calls for each species were produced. Advertisement calls were identified as a grouped sequence of notes together forming a single cohesive vocalisation repeated at regular intervals and emitted in the context of mating, consistent with Köhler *et al*. (2017). Locality data for these recordings are presented in Table 3.

**TABLE 3.** Locality data for recordings of *Geocrinia* used to quantify and describe call properties and to produce waveforms presented in Figure 4.

| Species | Locality | Latitude | Longitude | Date |
|---|---|---|---|---|
| *G. laevis* | Garvoc, Vic. | -38.35 | 142.79 | 28/05/2008 |
| *G. leai* | Pemberton, Vic. | -34.42 | 116.03 | 28/03/2006 |
| *G. victoriana* | Panton Hill, Vic. | -37.64 | 145.24 | 04/2018 |
| *G. alba* | Davis Rd, Rosa Glen, WA | -34.04 | 115.14 | 17/10/2016 |
| *G. lutea* | Angove Rd, North Walpole, WA | -34.97 | 116.70 | 19/10/2016 |
| *G. rosea* | Maiden Bush Track, Yeagarup, WA | -34.51 | 115.95 | 18/10/2016 |
| *G. vitellina* | Denny Rd, Schroeder, WA | -34.07 | 115.31 | 17/10/2016 |

Morphometric data of preserved specimens from Vidal-García *et al*. (2014) was provided to us, including all *Geocrinia* species, and the close relative *Assa darlingtoni*, and analysed using generalised linear models with Tukey's pairwise comparisons between species, and a principal components analysis (PCA). Five individuals of each species were included in the PCA with the exception of *G. alba* (n=6) and *G. lutea* (n=4). Due to scarcity of material, measurements of female specimens were primarily used; however male specimens of the *G. rosea* group were also used as females were largely unavailable. Specimens of both sexes were used only for *G. rosea* (f=1, m=4). The use of both sexes in our analysis is justified as males and females of the *G. rosea* group species are morphologically similar (supporting statistical analysis is provided in Table 4) and sexual dimorphism, other than of ventral colouration in *G. lutea* and *G. rosea*, is not known in these species (Wardell-Johnson & Roberts 1996). There were 29 morphometric variables used in the PCA with some variables transformed for normality (refer to Table 5 for details on the variables and transformations used).

Additionally, geographic distribution maps for the *Geocrinia* species were compiled using records in the literature and from the Atlas of Living Australia (Atlas of Living Australia 2020a–g).

**TABLE 4.** Comparison of SVL measurements, with supporting statistics (generalised linear mixed model), between sexes for species in the *Geocrinia rosea* group.

| Variable | Male | Female | Model | SVL ~ Sex, Species |
|---|---|---|---|---|
| Mean SVL (mm) | 21.05 | 21.58 | Fixed Effects | SVL; Sex |
| SD | 1.9577 | 3.3206 | Random Effects | Species |
| SEm | 0.4491 | 1.3556 | t-value | 0.4833 |
| N | 19 | 6 | P-value | 0.6341 |
| Range (mm) | 17.74–24.27 | 17.00–25.00 | DF | 20 |

**TABLE 5.** Morphological variables and transformations used in the principal components analysis (PCA). All measurements are in millimetres (mm) unless otherwise stated. Variables and descriptions are adapted from Vidal-García *et al*. (2014). The transformations used were chosen as they were able to fit the data of each specific variable to a normal distribution.

| Variable | Description | Transf. |
|---|---|---|
| Body mass | Mass in grams (g). | 1/sqrt(x) |
| SVL | Tip of snout to posterior tip of urostyle. | 1/sqrt(x) |
| Head length | Tip of snout to angle of jaw. | - |
| Head width | Width of head immediately posterior to lateral canthus of eyes. | - |
| Eye-naris | Anterior corner of eye to posterior edge of naris. | Sqrt(x) |
| Naris-snout | Anterior edge of naris to tip of snout. | - |
| Eye length | Distance between medial and lateral canthus of eyelids. | - |
| Mouth width | Between corners of mouth. | - |
| Humerus length | Midpoint of pectoral girdle to elbow. | - |
| Forearm length | Between elbow and wrist. | - |
| Wrist width | At widest point. | - |
| Hand length | Between midpart of wrist and tip of third finger. | - |
| Thumb length | Thumb length from tip to base. | - |
| Finger 4 length | Fourth finger length from tip to base. | - |
| Thigh length | From midpart of urostyle to knee. | - |
| Thigh width | Maximum width of thigh. | - |
| Crus width | Maximum width of crus. | Log(x) |
| Foot length | Junction of the first toe and foot to tip of fourth toe. | 1/(x) |
| Toe 1 length | Junction between first and second toe to tip of first toe. | Sqrt(x) |
| Toe 5 length | Junction between fourth and fifth toe to tip of fifth toe. | Sqrt(x) |
| Finger 2 length | Second finger length from tip to base. | - |
| Toe 2 length | Junction between second and third toe to tip of second toe. | 1/sqrt(x) |
| Toe 3 length | Junction between third and fourth toe to tip of third toe. | Sqrt(x) |
| Toe 4 length | Junction between fourth and fifth toe to tip of fourth toe. | 1/sqrt(x) |
| Finger 3 length | Third finger length from tip to base. | - |
| Arm length/SVL | Arm (humerus+forearm+hand) length/SVL. | - |
| Leg length/ SVL | Leg (foot+tibia+femur) length/SVL. | 1/(x) |
| Relative limb length | Arm length/leg length. | - |
| Crus/thigh ratio | Crus length/thigh length. | - |

**Results**

The two reciprocally monophyletic groups within *Geocrinia* differed in all character systems examined. The results are summarised in Table 6 and discussed in detail below.

**TABLE 6.** Character systems of *Geocrinia* species examined. The column labeled "mouthparts" refers to the structure/function of the oral disc of the tadpoles (larval morphology) and the "testes" column refers to the relative mass of the testes of mature male frogs (frog morphology and mating system). Clades in the "genetics" column correspond to branch colouration in Figure 1.

| Species | Genetics | Life history | Mouthparts | Testes | Call type | Breeding | Range |
|---|---|---|---|---|---|---|---|
| *G. laevis* group | | | | | | | |
| *G. laevis* | Clade 1b | Terrestrial/ aquatic | Feeding | Moderate | Biphasic-B | Autumn | SE Aus |
| *G. leai* | Clade 1a | Terrestrial/ aquatic | Feeding | Large | Biphasic-A | Autumn | SW WA |
| *G. victoriana* | Clade 1b | Terrestrial/ aquatic | Feeding | Large | Biphasic-A | Autumn | SE Aus |
| *G. rosea* group | | | | | | | |
| *G. alba* | Clade 2b | Nidicolous | Vestigial | Small | Monophasic | Spring | SW WA |
| *G. lutea* | Clade 2a | Nidicolous | Vestigial | Small | Monophasic | Spring | SW WA |
| *G. rosea* | Clade 2a | Nidicolous | Vestigial | Small | Monophasic | Spring | SW WA |
| *G. vitellina* | Clade 2b | Nidicolous | Vestigial | Small | Monophasic | Spring | SW WA |

**Genetic groupings.** Based on the mitochondrial ND2 and 12S rRNA gene fragments, there are two strongly supported lineages forming clades within *Geocrinia* (Read *et al*. 2001), that correspond to the *G. laevis* group (Clade 1) and the *G. rosea* group (Clade 2) (Figure 1). Although their analysis did not include *G. lutea,* the monophyly of the *G. rosea* group was very strongly supported. Read *et al.* (2001) showed that *G. leai* forms the sister clade (Clade 1a) to *G. laevis* and *G. victoriana* which themselves are very strongly supported sister species (Clade 1b) (Figure 1). Although *Geocrinia* sensu lato was recovered as monophyletic, the support for this was less than for the two groups within *Geocrinia*. Analysis of 17 distinct allozyme loci isolated by Driscoll (1998b) demonstrated monophyly of all species within the *G. rosea* group (Driscoll & Roberts 2007). They identified *G. lutea* as the sister species to *G. rosea* (Clade 2a) and together these species form the sister clade to *G. alba* and *G. vitellina*, which are also sister species (Clade 2b) (Figure 1). Roberts & Maxson (1985) also found support for both groups, as well as Clade 1a and 1b, through immunological distance, showing *G. leai* as potentially distinct from other *G. laevis* group species and from the *G. rosea* group, with less divergence, albeit marginally, between *G. leai* and *G. victoriana* than between *G. victoriana* and *G. rosea* group species.

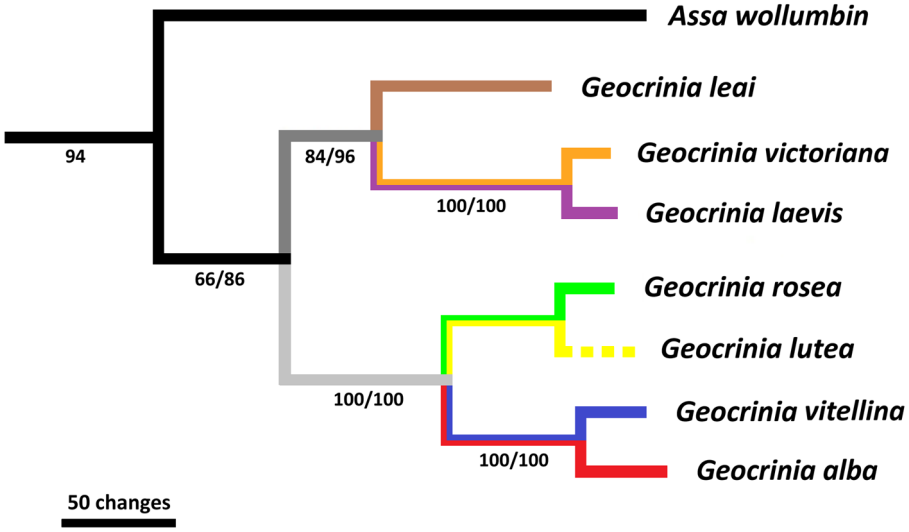


**FIGURE 1.** Phylogenetic relationships between members of the sister genera *Geocrinia* and *Assa*. Adapted from Molecular Phylogenetics and Evolution, 21, Read, K., Keogh, J.S., Scott, I.A.W, Roberts, J.D. & Doughty, P., Molecular phylogeny of the Australian frog genera *Crinia*, *Geocrinia*, and allied taxa (Anura: Myobatrachidae), 294–308, Copyright Elsevier (2001). The placement of *G. lutea* follows Driscoll & Roberts (2007). This tree shows the known phylogenetic relationships between all seven *Geocrinia* species and the allied taxon, *Assa wollumbin*. Clade 1 (the *G. laevis* group) is coloured dark grey, with Clade 1a (*G. leai*) in brown and Clade 1b (*G. victoriana* and *G. laevis*) in orange and purple. Clade 2 (the *G. rosea* group) is coloured light grey, with Clade 2a (*G. rosea* and *G. lutea*) in green and yellow and with Clade 2b (*G. vitelllina* and *G. alba*) in blue and red.

**Life history.** The life history of all three species in the *G. laevis* group is terrestrial/aquatic, while the life history of all four species in the *G. rosea* group is nidicolous (Anstis 2010, 2013). Data on life history and reproductive development are presented in Table 7.

**TABLE 7.** Comparative summary of larval development between *Geocrinia* species including: clutch size (average number of eggs with range in parentheses), hatching (days from egg deposition to when hatching occurs), hatching stage (development stage at which hatching occurs with approximate equivalent Gosner stages of limb development in parentheses for *G. rosea* group species), larval days (total number of days for completion of larval development) and metamorphosis (months when metamorphosis occurs). NA = value not available.

| Species | Clutch Size | Hatching | Hatching stage | Larval days | Metamorphosis |
|---|---|---|---|---|---|
| *G. laevis* group | | | | | |
| *G. laevis* | 145 (76–183) | 26–47 | 26–27 | 150–163 | Sep–Nov |
| *G. leai* | 68 (38–96) | 15–22 | 22–27 | 149–174 | Sep–Nov |
| *G. victoriana* | 121 (90–162) | 27–53 | 26–27 | 150–178 | Sep–Oct |
| *G. rosea* group | | | | | |
| *G. alba* | 11 (1–19) | NA | NA | 28–98 | Oct–Dec |
| *G. lutea* | 13 (11–17) | NA | NA | 35–~46 | Nov–Jan |
| *G. rosea* | 20 (11–32) | NA | 22–23 (28–29) | 42–~60 | Nov–Dec |
| *G. vitellina* | 11 (3–18) | 19–26 | 22–25 (28–31) | 86–87 | Oct–Nov |

Frogs in the *G. laevis* group deposit their pigmented eggs as a sticky coherent cluster or clump(s) in moist terrestrial environments, such as within damp leaf litter or mud, or attached within sedges, and the embryos begin development within the egg capsule, hatching as larvae following inundation of the nest site and complete their development as free-swimming and feeding (exotrophic) aquatic tadpoles (Littlejohn & Martin 1964, Main 1965, Anstis 2010, 2013). Hatching of tadpoles in the *G. laevis* group mostly occurs at early larval stages, usually stages 26–27 (*G. laevis* and *G. victoriana*) and stages 25–26 (*G. leai*) but may occur as early as stages 22–23 or as late as stage 27 in *G. leai* (Anstis 2013). Hatching usually occurs anywhere from two to six weeks after eggs are laid, depending on rainfall (Main 1957, Anstis 2010, 2013), but can be delayed as long as four months in both *G. laevis* and *G. victoriana* (Littlejohn & Martin 1964, Gollmann & Gollmann 1991). It is possible that hatching in *G. leai* can also be delayed if conditions are unfavourable, but this is presently unstudied. Hatching in *G. laevis* and *G. victoriana* also occurs in a staggered fashion. Tadpoles of *G. laevis* begin to emerge within 12 hours of nest inundation, and continue hatching over 24–47 days, while those of *G. victoriana* emerge over 1–27 days post immersion (Anstis 2010).

Frogs in the *G. rosea* group have nidicolous larvae, where large, unpigmented eggs are laid in moist terrestrial environments, usually in an excavated nest basin or burrow constructed by the male in mud (Main 1965, Roberts *et al*. 1990, Anstis 2010, 2013). The eggs are laid singularly in large jelly capsules then adhere, forming a single clutch in the nest (Anstis 2010, 2013). Tadpoles complete embryonic development entirely within the jelly capsule initially before hatching into the broken-down liquefied jelly, and while capable of free swimming within this jelly medium, they are not free feeding (endotrophic) and rely entirely on yolk reserves for nourishment (Anstis 2010, 2013). Hatching in *G. vitellina* is reported to occur 19–26 days after eggs are laid at a controlled temperature of 15°C (Mitchell 2001). Hatching occurs at Anstis stages 22–25 (roughly equivalent to Gosner stages 28–31 in hind limb development) although this has only been observed in *G. rosea* and *G. vitellina*, with the process likely to be similar in *G. alba* and *G. lutea* (Anstis 2013), given close similarities between the species. Unlike the *G. laevis* group, eggs of *G. rosea* group species do not require rainfall and nest inundation for hatching (Anstis 2010, 2013), potentially because the nest site is usually in an area where seepage occurs (M. Anstis, pers. comm.). It is not known whether hatching in the *G. rosea* group can be delayed in a similar manner to the *G. laevis* group; however as hatching is not dependent on subsequent rainfall for *G. rosea* group species, and as nest sites are in seepages, delayed hatching may not be required. Presently, the only species in the *G. rosea* group with available data on hatching time is *G. vitellina*, with no hatching delay observed for this species (Mitchell 2001).

Tadpole development also differs between the two groups, with the larger, aquatic *G. laevis* group tadpoles

developing predominately as per standard Gosner stages (Gosner 1960) while the diminutive, endotrophic tadpoles of the *G. rosea* group do not, so a specific staging system was developed for, and applied to this group, by Anstis (2010). The difficulty in applying Gosner stages to *G. rosea* group tadpoles was earlier noted by Mitchell (2001) who applied a modified version of the De Bavay (1993) staging system to *G. vitellina* larvae. The Anstis (2010) system was designed to further simplify the staging and to include reference to the equivalent and universally adopted hind limb developmental stages of Gosner as a comparative guide (Anstis 2010, 2013). Additionally, early in the larval development of all *G. laevis* group species Gosner stages cannot be applied due to lack of synchronicity with standard aquatic tadpole development, arising from slower mouthpart, gut and limb bud growth (Anstis 2010), and a staging system developed by Gollmann & Gollmann (1991) is used between Gosner stages 20–26. The duration of larval development is also considerably longer in the *G. laevis* group (149–178 days) compared to the *G. rosea* group (28–98 days) (Littlejohn & Martin 1964, Mitchell 2001, Anstis 2013). Tadpoles of the *G. laevis* group species metamorphose during spring approximately five to eight months from egg deposition, while metamorphosis for the *G. rosea* group species takes place from October to January around one to three months after eggs are deposited (Main 1965, Mitchell 2001, Anstis 2010, 2013).

Differences in relative reproductive investment are also evident between the groups, in terms of both size of clutches and embryos. Frogs in the *G. laevis* group feature larger clutches of over 100 eggs in *G. laevis* and *G. victoriana* and over 50 eggs in *G. leai* (Anstis 2010, 2013), while frogs in the *G. rosea* group have smaller clutches, usually containing less than 20 larger eggs, although clutches of up to 32 eggs have been observed in *G. rosea* (Main 1957, Anstis 2013). Pooled values of recorded ovum diameters for the *G. laevis* group species range from 1.5–3.1 mm (mean = 2.0 mm) while the *G. rosea* group species are larger, from 2.4–3.5 mm (mean = 2.9 mm) (Anstis 2010). Analysis of reproductive investment, inferred by clutch and embryo size, supports this distinction, with *G. rosea* group species having greater investment than the *G. laevis* group and aligning more closely to *Assa darlingtoni* (Gould *et al.* 2022).

**Larval morphology.** There are consistent differences in larval morphology between the groups, particularly evident in the structure of the oral disc, body form and maximum size, with larvae of *G. laevis* group species growing much larger than those of the *G. rosea* group. Data on larval morphology are presented in Table 8.

**TABLE 8.** Comparison of larval morphology between *Geocrinia* species including: labial tooth row formula (LTRF); oral disc type and body type according to Anstis (2013); and measurements (in mm) for average total length of hatchlings, maximum tadpole total length (body length in parentheses) and average size at metamorphosis (Anstis 2010, 2013). Ranges for hatchling and metamorph measures are contained in parentheses. Morphometric data for western (W) and southern (S) populations of *G. leai* are presented where available. NA = value not available.

| Species | LTRF | Oral Disc | Body | Hatchling | Tadpole | Metamorph |
|---|---|---|---|---|---|---|
| *G. laevis* group | | | | | | |
| *G. laevis* | 2(2)/3(±1) | Type 14 | Type 17 | 9.6 (8.5–11.4) | 30.3 (10.9) | 9.3 (8.4–10.1) |
| *G. leai* (W) | 2(2)/3[±1] | Type 15 | Type 17 | 8.6 (6.9–10.5) | NA | 7.9 (7.4–8.5) |
| *G. leai* (S) | | | | 9.2 (8.7–10.6) | 37 (11.5) | 11.0 (9.6–12.4) |
| *G. victoriana* | 2(2)/3(±1) | Type 14 | Type 17 | 11.7 (10.0–13.4) | 37.4 (12.4) | 10.2 (9.7–11.1) |
| *G. rosea* group | | | | | | |
| *G. alba* | 0/0 | Type 19 | Type 20 | NA | 16.3 (5.6) | 6.2 (5.9–6.4) |
| *G. lutea* | 0/0 | Type 19 | Type 20 | NA | 15.6 (5.0) | 5.6 (5.5–5.6) |
| *G. rosea* | 0/0 | Type 19 | Type 20 | 10.2 (9–11.6) | 15.6 (5.2) | 5.7 (5.6–6.2) |
| *G. vitellina* | 0/0 | Type 19 | Type 20 | 11.0 (9.5–13.0) | 18.2 (5.5) | 6.1 (6.0–6.3) |

Tadpoles of the *G. laevis* group have keratinised feeding mouthparts, clearly differing from tadpoles of all species in the *G. rosea* group which feature vestigial, non-feeding mouthparts that lack keratin (Figure 2). The *G. laevis* group species have two anterior and three posterior labial tooth rows and keratinised jaw sheaths, while those of the *G. rosea* group have a diminutive oral disc lacking both tooth rows and keratinised jaw sheaths (Anstis 2013). Within species there is little variation in oral disc structure, particularly in the *G. rosea* group. However, larvae of all *G. laevis* group species vary in the presence or absence of a gap in the first posterior tooth row.

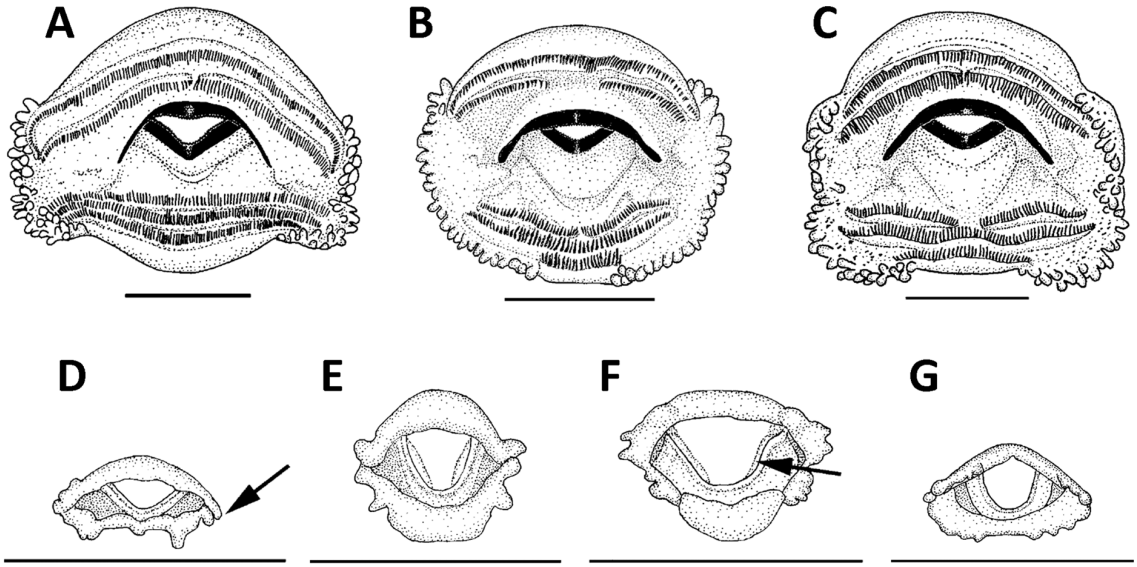


**FIGURE 2.** Oral disc illustrations of all *Geocrinia* species by M. Anstis, reproduced with permission from the author. The *G. laevis* group species are in the top row with the *G. rosea* group species in the bottom row: A) *G. leai*; B) *G. laevis*; C) *G. victoriana*; D) *G. alba*; E) *G. lutea*; F) *G. rosea*; and G) *G. vitellina*. The scale bar under each illustration represents 1 mm. The arrow in D) indicates papillae and the arrow in F) indicates the lower jaw.

According to Anstis (2013), larval body form, tadpole length and size at metamorphosis differ significantly between the groups, conversely, hatchling size is relatively similar among *Geocrinia*, perhaps slightly larger in the *G. rosea* group species, although data are unavailable for *G. alba* and *G. lutea*. Tadpoles of the *G. laevis* group species feature a small, aquatic body form while the *G. rosea* group species feature a very small, endotrophic body form. Tadpoles of the *G. rosea* group are markedly smaller in maximum size, being about half the length of the *G. laevis* group species. Maximum lengths of tadpoles of the *G. laevis* group species range between 30.3–37.4 mm (body length ranging from 10.9–12.4 mm) while maximum lengths of the *G. rosea* group species range between 15.6–18.2 mm (body length from 5.0–5.6 mm). This difference in larval size is also carried into metamorphosis, with metamorphs of the *G. laevis* group being consistently larger on average than those of the *G. rosea* group. Mean size at metamorphosis for the three *G. laevis* group species is 9.6 mm (with range of species/population means of 7.9–11.0 mm) while the mean for the four *G. rosea* group species is 5.9 mm (range of means 5.6–6.2 mm).

**Frog morphology and mating system.** Morphology of adult frogs varied between *Geocrinia* species, with species in the *G. laevis* group generally larger in overall body size than those in the *G. rosea* group in both mean values and ranges (Table 9). Differences between the groups were significant for body length ($r^2$= 0.76, $t_{32}$=-2.18, p=0.0366), fourth toe length ($r^2$= 0.76, $t_{32}$=-2.61, p=0.0138) and body mass ($r^2$= 0.70, $t_{32}$=-2.98, p=0.0055), and differences between all species in the *G. laevis* group and all species in the *G. rosea* group were significant for these three variables (Table 10). Adult frogs could be reliably attributed to the *G. laevis* group or *G. rosea* group on the basis of fourth toe length and body length. The *G. rosea* group species have a relatively short fourth toe, up to 6.5 mm long, while in the *G. laevis* group the fourth toe ranges from 6.4–10.4 mm long. Although there is overlap in the extreme values, it is shared by the allopatric species *G. alba* and *G. laevis*, while *G. leai*, the only *G. laevis* group species that is sympatric with the *G. rosea* group, has the longest fourth toe of all *Geocrinia* (7.8–10.4 mm), easily distinguishing it from the *G. rosea* group species. Body length also distinguishes the eastern Australian *Geocrinia* from the *G. rosea* group, ranging from 25.7–30.1 mm compared to 17.7–24.5 mm respectively. There is overlap in body size between *G. leai* and the *G. rosea* group species.

With the exception of *G. leai*, body mass of preserved male specimens was greater for the *G. laevis* group species than the *G. rosea* group species. Body mass of adult male frogs can therefore be used to distinguish *G. laevis* and *G. victoriana* from the *G. rosea* group, with a minimum body mass of 0.92 g compared to a maximum body mass of 0.69 g respectively. For females, body mass of *G. laevis* group species is consistently larger (2.12 g minimum) than the *G. rosea* group (1.40 g maximum), however of the *G. rosea* group species data was only available for *G. rosea*. Given that body mass of preserved frogs may not be reflective of mass in life, this character is unlikely to be consistently reliable for distinguishing the groups, especially when compared to fourth toe length and body length.

**TABLE 9.** Comparison of adult frog morphology between *Geocrinia* species including: testes mass (g), body mass (g), body length (i.e. snout-vent length or SVL) (mm) and fourth toe length (mm). Evidence of polyandry is indicated. Mean values for absolute testes mass and body mass are taken from Byrne *et al*. (2002) with the exception of the body mass values in parentheses which are the means of preserved female specimens taken from Vidal-García *et al*. (2014). Measures of body length and toe length are of preserved specimens from Vidal-García *et al*. (2014) with mean values presented and ranges in parentheses. Pooled mean and standard deviation (in parentheses) for all species in each group is also provided, with values taken from Vidal-García *et al*. (2014) except for testes mass taken from Byrne *et al*. (2002).

| Species | Testes Mass | Body Mass | Body Length | Toe Length | Polyandry |
|---|---|---|---|---|---|
| *G. laevis* group | 0.0087 (0.01) | 2.72 (0.63) | 27.63 (1.68) | 8.01 (1.07) | |
| *G. laevis* | 0.0024 | 0.9194 (3.06) | 28.84 (28.0–30.1) | 7.35 (6.4–8.6) | Yes |
| *G. leai* | 0.0108 | 0.6585 (2.12) | 25.96 (24.3–27.6) | 8.83 (7.8–10.4) | Yes |
| *G. victoriana* | 0.0130 | 1.5743 (2.98) | 28.08 (25.7–29.3) | 7.85 (7.2–8.7) | Yes |
| *G. rosea* group | 0.0001 (0.00) | 0.99 (0.35) | 21.18 (1.98) | 5.70 (0.36) | |
| *G. alba* | 0.0001 | 0.6465 | 22.81 (21.2–24.3) | 5.87 (5.5–6.5) | No |
| *G. lutea* | 0.0001 | 0.4712 | 19.86 (19.0–21.5) | 5.43 (5.1–5.6) | No |
| *G. rosea* | 0.0001 | 0.5654 (1.40) | 19.66 (17.7–23.5) | 5.79 (5.6–6.1) | No |
| *G. vitellina* | 0.0001 | 0.6911 | 21.78 (20.9–22.7) | 5.62 (5.0–6.0) | No |

**TABLE 10.** Results of Tukey's pairwise comparisons between *Geocrinia* species for measurements of snout-vent length (SVL), body mass (weight) and fourth toe length. P-values presented are adjusted for multiple comparisons (single-step method). Species are coded: 1 = *G. alba*, 2 = *G. laevis*, 3 = *G. leai*, 4 = *G. lutea*, 5 = *G. rosea*, 6 = *G. victoriana*, 7 = *G. vitellina*. * indicates a significant result.

| Species | | | SVL | | | Weight | | | Fourth Toe | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | t-value | P-value | | t-value | P-value | | t-value | P-value | |
| 2 | - | 1 | 7.072 | <0.001 | * | 7.744 | <0.001 | * | 3.703 | 0.01426 | * |
| 3 | - | 1 | 3.700 | 0.01428 | * | 3.865 | 0.00948 | * | 7.395 | <0.001 | * |
| 4 | - | 1 | -3.242 | 0.04264 | * | -1.968 | 0.45517 | | -1.031 | 0.94216 | |
| 5 | - | 1 | -3.696 | 0.01434 | * | -1.087 | 0.92673 | | -0.194 | 0.99999 | |
| 6 | - | 1 | 6.183 | <0.001 | * | 7.414 | <0.001 | * | 4.949 | <0.001 | * |
| 7 | - | 1 | -1.202 | 0.88733 | | -0.501 | 0.99864 | | -0.620 | 0.99558 | |
| 3 | - | 2 | -3.228 | 0.04393 | * | -3.714 | 0.01390 | * | 3.535 | 0.02137 | * |
| 4 | - | 2 | -9.504 | <0.001 | * | -8.884 | <0.001 | * | -4.334 | 0.00288 | * |
| 5 | - | 2 | -10.310 | <0.001 | * | -8.455 | <0.001 | * | -3.731 | 0.01332 | * |
| 6 | - | 2 | -0.851 | 0.97675 | | -0.316 | 0.99990 | | 1.193 | 0.89083 | |
| 7 | - | 2 | -7.992 | <0.001 | * | -7.894 | <0.001 | * | -4.139 | 0.00487 | * |
| 4 | - | 3 | -6.460 | <0.001 | * | -5.382 | <0.001 | * | -7.667 | <0.001 | * |
| 5 | - | 3 | -7.081 | <0.001 | * | -4.741 | <0.001 | * | -7.266 | <0.001 | * |
| 6 | - | 3 | 2.377 | 0.24544 | | 3.398 | 0.02985 | * | -2.342 | 0.26027 | |
| 7 | - | 3 | -4.693 | 0.00116 | * | -4.180 | 0.00433 | * | -7.674 | <0.001 | * |
| 5 | - | 4 | -0.217 | 0.99999 | | 0.913 | 0.96738 | | 0.816 | 0.98115 | |
| 6 | - | 4 | 8.701 | <0.001 | * | 8.586 | <0.001 | * | 5.459 | <0.001 | * |
| 7 | - | 4 | 2.035 | 0.41607 | | 1.442 | 0.77464 | | 0.432 | 0.99941 | |
| 6 | - | 5 | 9.458 | <0.001 | * | 8.139 | <0.001 | * | 4.924 | <0.001 | * |
| 7 | - | 5 | 2.388 | 0.24020 | | 0.561 | 0.99743 | | -0.407 | 0.99958 | |
| 7 | - | 6 | -7.070 | <0.001 | * | -7.578 | <0.001 | * | -5.331 | <0.001 | * |

Differences between the groups were also supported by the PCA of external morphology (Figure 3). The first two principal components, which were primarily loaded by snout-vent length and fourth toe length respectively, explain 76% of the variance, with 95% of the variance explained by nine principal components (Table 11). There was no overlap between the *G. laevis* group and *G. rosea* group species in the morphospace on PC2. Within the *G. laevis* group, *G. laevis* and *G. victoriana* occupied a similar area on the plot with some overlap, while *G. leai* was not closely positioned to these species on PC1, but completely overlapped with them on PC2. All species in the *G. rosea* group are much more closely positioned with overlap between *G. alba*, *G. rosea* and *G. vitellina*. *Assa darlingtoni*, a species from the sister genus to *Geocrinia*, was also included in the PCA and was distant from all *Geocrinia* species on the combination of the first two principal components. A previous study (Wardell-Johnson & Roberts 1996), that examined 11 morphometric variables of *G. rosea* group species only, found a similar result to our PCA with considerable overlap between all four species.

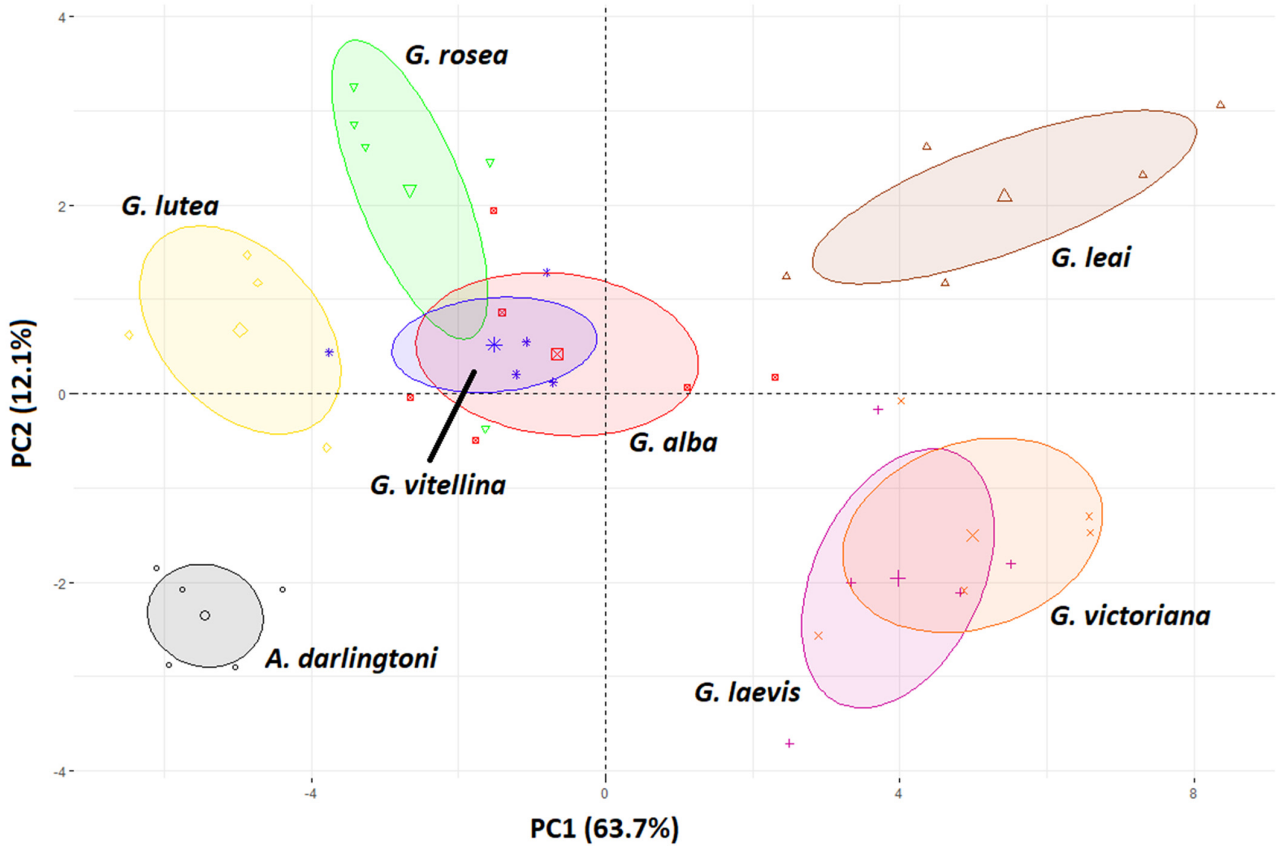


**FIGURE 3.** Principal components analysis (PCA) plot of morphological variables measured from museum specimens of *Assa darlingtoni* and all *Geocrinia* species. The y-axis represents PC1 and the x-axis represents PC2, with primary loadings respectively consisting of snout-vent length and fourth toe length. The *G. laevis* group species occupy the right side of the morphospace, with *G. leai* located away from *G. laevis* and *G. victoriana*. The *G. rosea* group species occupy the left and central sections of the morphospace with all four species closely clustered. The related species, *Assa darlingtoni*, is positioned away from the *Geocrinia,* on the left side of the plot. Confidence ellipses centred on species means are presented.

**TABLE 11.** The first nine principle components ("PC") from the principal components analysis of *Geocrinia* external morphology with the associated primary loadings ("Loading"), percentage of variance ("Variance %") explained and cumulative percentage of variance ("Cumulative %") explained. The first nine principle components explained 95% of the variance.

| PC | Loading | Variance % | Cumulative % |
|---|---|---|---|
| 1 | SVL | 63.70 | 63.70 |
| 2 | Toe 4 Length | 12.08 | 75.78 |
| 3 | Foot Length | 7.57 | 83.35 |
| 4 | Toe 2 Length | 3.50 | 86.85 |
| 5 | Mouth Width | 2.25 | 89.10 |
| 6 | Head Width | 1.83 | 90.93 |
| 7 | Finger 2 Length | 1.64 | 92.58 |
| 8 | Body Mass | 1.35 | 93.92 |
| 9 | Finger 3 Length | 1.09 | 95.01 |

Absolute testis mass also differed substantially between the groups, and all species in the *G. rosea* group have very small testes relative to the *G. laevis* group (Table 9). Within the *G. laevis* group, testes are much larger especially in *G. victoriana* and *G. leai*, which respectively have the largest testes of all *Geocrinia* species, while the testes of *G. laevis* are comparably smaller. The relatively massive testes in *G. laevis* group species correlate to mating systems which involve greater probability of male-male interactions that result in sperm competition and polyandry (Roberts & Byrne 2011). Male-male interactions are known in all *G. laevis* group species and inferably all three of these species are polyandrous to some degree, with polyandry reported in *G. leai* (Byrne *et al*. 2002, Perks 2011). Further, in both *G. laevis* and *G. victoriana*, dissected females contained on average more ova than clutches observed in the field (Anstis 2013), suggesting that they may not deposit their entire compliment of oviductal eggs in a single mating. The presence of a more complex call structure in the *G. laevis* group species is also an indication of potential polyandry (Roberts 2020). While the mating system of the *G. rosea* group species is not known, there is no evidence for polyandry, with small testes and a simple call structure suggesting the potential for at least seasonal monogamy and low instance of male-male competition (Byrne *et al*. 2002, Roberts & Byrne 2011, Roberts 2020).

**Call type.** Within *Geocrinia*, there are two advertisement call types, a simplistic monophasic rapid ticking, and a complex biphasic call with one or several introductory notes followed by a series of secondary follow up notes that are distinctly different from the introductory note. These two call types match the genetic groups. All species in the *G. laevis* group feature a biphasic call while all species in the *G. rosea* group feature a monophasic call (Littlejohn & Martin 1964, Roberts *et al*. 1995, Roberts 2020). Table 12 presents details of call properties based on available literature, and of recordings by G. Webster, M. Anstis and M. Clancy. Waveforms of advertisement calls for each species based on these recordings are presented in Figure 4.

**TABLE 12.** Averages (and ranges, where available) of call properties of *Geocrinia* species. For the *G. laevis* group frogs (biphasic calls) the duration, pulses and pulse rate are presented for an introductory note and for a secondary note (separated by a slash), but not for all notes in the entire call sequence. As frequency between introductory and secondary notes is generally similar, frequency for the entire call sequence is presented. Dissimilarly, for the *G. rosea* group frogs (monophasic call) pulses are the number of notes for the entire call sequence, and not the number of pulses per note. Greyed rows are of previously unpublished data of frogs recorded by G. Webster, M. Anstis and M. Clancy. Data for two populations of *G. leai*, Western ("W") and Southern ("S") are shown, as calls between these populations are distinctly different (Roberts 2020); note that the duration of the introductory note for the W population is the sum of the two distinct notes in the introductory call, including the short interval between them. Due to the small sample size for *G. leai* the true range of variation in the introductory note is unlikely to be presented here. NA = values not available, * indicates introductory notes are coupled if N>1, $^{R}$ indicates range of notes for entire sequence as separate values for introductory and secondary notes were not available.

| Species | Duration (s) | Notes | Pulses | Pulse Rate ($s^{-1}$) | Frequency (kHz) |
|---|---|---|---|---|---|
| *G. laevis* group | | | | | |
| *G. laevis* | 1.15/0.42 (0.59/0.21–1.77/1.00) | 3–38$^{R}$ | 21.36/24.00 (11/12–46/39) | 21.36/47.53 (9/23–35/82) | 2.66 (2.30–3.05) |
| *G. laevis* | 1.13/0.46 (0.96/0.41–1.37/0.51) | 1/4.5 (1/2–1/9) | 26.50/23.84 (14/24–32/26) | 23.38/52.61 (14/50–26/58) | 2.61 (2.58–2.67) |
| *G. leai* (W) | 0.30/0.05 | 2*/6 | NA | NA | NA |
| *G. leai* (S) | 0.09/0.05 | 1/4 | NA | NA | NA |
| *G. leai* (W) | 0.17/0.06 (0.06/0.05–0.32/0.07) | 2*/5.5 (1/4–4/6) | 33.33/21.03 (22/19–52/23) | 295.37/358.02 (248/321–355/382) | 2.99 (2.55–3.45) |
| *G. victoriana* | 0.50/0.08 (0.24/0.05–1.19/0.12) | 2/23.3 (1/5–3/53) | 62.88/35.00 (25/24–116/44) | 147.50/423.93 (52/360–250/500) | 2.72 (2.50–3.00) |
| *G. victoriana* | 0.91/0.04 (0.43/0.03–1.24/0.04) | 1.8/22.5 (1/16–2/27) | 57.13/15.64 (47/16–67/27) | 140.65/447.12 (138/439–145/456) | 2.60 (2.76–2.58) |
| *G. rosea* group | | | | | |
| *G. alba* | 1.42 | - | 14.68 (6–18) | 8.92 (8.7–9.2) | 2.43 (2.42–2.45) |
| *G. alba* | 2.02 (1.8–2.1) | - | 14.20 (13–16) | 7.04 (7.0–7.1) | 2.55 (2.24–2.76) |
| *G. lutea* | 2.88 | - | 12.00 | 4.52 (4.2–4.8) | 2.37 (2.31–2.43) |
| *G. lutea* | 3.79 (2.3–4.2) | - | 19.73 (12–25) | 5.18 (5.0–5.4) | 2.41 |
| *G. rosea* | 3.17 | - | 17.00 | 4.94 (4.6–5.4) | 2.34 (2.18–2.49) |
| *G. rosea* | 5.12 (3.9–6.6) | - | 18.33 (15–21) | 3.65 (3.2–4.0) | 2.58 |
| *G. vitellina* | 1.49 | - | 11.90 (9–15) | 7.59 (7.2–8.0) | 2.15 (2.14–2.15) |
| *G. vitellina* | 2.05 (1.5–2.5) | - | 13.82 (10–15) | 6.75 (6.1–7.1) | 2.51 (2.24–2.58) |

The call of *Geocrinia leai* has a rapid introductory note (or notes) consisting of up to four sharp coupled notes followed by four to 11 slow-paced ticks, while *G. victoriana* has one to three short upward rasping, lower introductory notes followed by an extensive, resonating series of up to 53 rapid higher ticks (Littlejohn & Martin 1964). In both of these species the introductory note resembles an "ahh" sound with the secondary notes likened to a "chik". The call of *G. laevis* resembles a strident, low-pitched rasp with an upward inflection comprised of one to three introductory notes and three to 38 notes in total (Littlejohn & Martin 1964, Harrison & Littlejohn 1985) with all notes in the call resembling an "ahh" sound.

The biphasic call of species in the *G. laevis* group can be further classified into two subgroups, Type A (*G. leai* and *G. victoriana*) and Type B (*G. laevis*). The first subgroup comprises a short introductory note or notes followed by a series of ticks while the second subgroup features a longer introductory note followed by a series of shorter notes. The biphasic call may be related to male-male competition; in *G. victoriana* the introductory note serves a territorial function and the secondary notes are attractive to females (Littlejohn & Harrison 1985). Given the similarity in call structure and relative testis size, this is likely also true for *G. leai* (D. Roberts, pers. comm.). The Type B biphasic call does not appear to serve the same function as the Type A call and possibly indicates less male-male competition in *G. laevis*, further supported by the smaller testis size (Harrison & Littlejohn 1985, Byrne *et al*. 2011, Roberts 2020).

The advertisement call of all species within the *G. rosea* group is a singular note resembling a "tik" sound repeated throughout the call and is superficially similar between species, but differs in pulse rate, call length, and audible sound quality. Compared to *G. rosea*, calls of *G. lutea* vary in pulse rate, which changes within the call (Clulow & Swan 2018, G. Webster, pers. obs.). The first note of the call of *G. rosea* tends to be softer than subsequent notes, again differing from *G. lutea* where all notes are of equal volume (G. Webster, pers. obs.). The calls of *G. alba* and *G. vitellina* differ in audible sound; the former producing a sharp 'tapping' while the latter produces a comparatively blunter 'clucking' (Clulow & Swan 2018, G. Webster, pers. obs.). Differing from *G. alba*, calls of *G. vitellina* are longer and become louder as the call progresses (G. Webster, pers. obs.). *Geocrinia lutea* and *G. rosea* may vocalise continuously with calls of over 50 notes (Roberts & Wardell-Johnson 1995). Extended calls of these species were also recorded by G. Webster including a 17.6 s call comprising 107 notes (*G. lutea*) and a 50.3 s call comprising 139 notes (*G. rosea*).

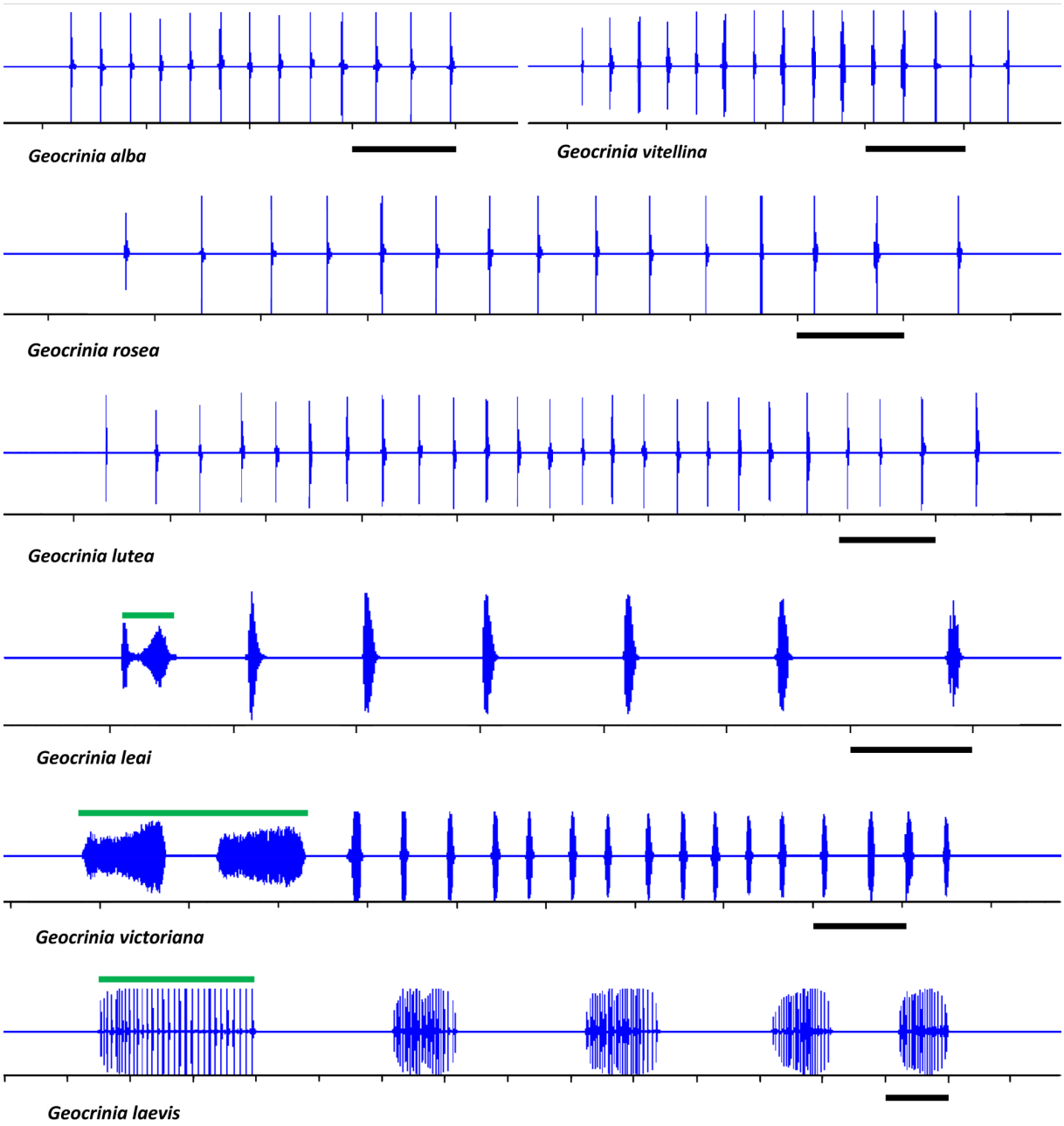


**FIGURE 4.** Single advertisement calls displayed as a waveform of relative amplitude (y-axis) over time in seconds (x-axis) for all species of *Geocrinia*, with the corresponding species labelled beneath the waveform. Black scale bar represents 0.5 seconds. For *G. laevis* group species (*G. laevis*, *G. leai* and *G. victoriana*) the introductory note is indicated by a green bar above the note(s).

**Breeding season.** The *G. laevis* group species primarily breed in autumn; but calling begins during summer and concludes in spring (Main 1957, Littlejohn & Martin 1964, Anstis 2010, Rowley & Callaghan 2020, G. Webster, pers. obs.). In the two eastern species, *G. laevis* and *G. victoriana,* calling usually commences in January or February, although *G. laevis* may being calling as early as December, peaking in March and April respectively, and generally ending by May, with *G. victoriana* continuing to call into winter in reduced numbers (Littlejohn & Martin 1964, Anstis 2013, Rowley & Callaghan 2020). For *G. leai* calling occurs between March and November, but primarily from April until October with a peak in May and June (Main 1957, Anstis 2013, Rowley & Callaghan 2020). Calling during spring is irregular and infrequent but has been noted in September and October (*G. laevis*) and as late as November (*G. victoriana/ G. leai*) (Main 1957, Littlejohn & Martin 1964, Rowley & Callaghan 2020, G. Webster, pers. obs.). The breeding strategy of the *G. laevis* group species relies on egg deposition before seasonal autumn and winter rains fall in southern Australia (Anstis 2010). These cool season rains then flood the nest site and tadpoles complete development into spring (Anstis 2010, 2013). Consequently, breeding generally concludes before spring with spring breeding events probably occurring infrequently given the importance of seasonal rains for larval development, although eggs of *G. leai* have been found in October around a permanent water body (G. Webster, pers. obs.) and this species is known to call into spring but in reduced numbers compared to autumn choruses (D. Roberts, pers. comm.). The relatively longer breeding season of *G. leai* may relate to this species' tendency, at times, to utilise more permanent water for larval development reducing its dependence on heavier rains to sufficiently inundate breeding sites (M. Anstis, pers. comm.).

Species in the *G. rosea* group however breed nearly exclusively in spring, although *G. rosea* has been observed breeding as late as mid-December (D. Roberts, pers. comm.). Contrastingly, calling activity occurs over a longer time frame and may commence in late winter and concludes in early summer (Driscoll 1998a, Anstis 2010, 2013). The earliest that calling has been reported for *G. rosea* group species is July (*G. lutea*) and August (*G. alba/G. rosea/G. vitellina*) with calling concluding in all species by December (Conroy 2001, Anstis 2013, Rowley & Callaghan 2020). Somewhat similarly to the *G. laevis* group, the breeding strategy of frogs in the *G. rosea* group appears to take advantage of abundant remnant moisture following seasonal winter rains in order for tadpoles to complete development, however reproduction does not occur before winter rains have fallen and the eggs are not dependent on flooding rain events to hatch (Anstis 2010, 2013). Rain events post-oviposition can even be detrimental to reproduction of *G. rosea* group species, as tadpoles will die if nest sites are flooded (Driscoll 1996).

**Distribution.** Frogs in the *G. laevis* group are found in south-eastern and south-western Australia (Figure 5). The south-eastern species, *G. laevis* and *G. victoriana,* occur in Victoria, Tasmania and South Australia, and Victoria and New South Wales respectively, while *G. leai* is found in the south-west of Western Australia (Atlas of Living Australia 2020a, 2020b, 2020c). All species in the *G. rosea* group are restricted to south-western Western Australia (Figure 5), and all (particularly *G. alba* and *G. vitellina*) have very restricted ranges, with *G. alba* and *G. vitellina* being confined to small areas south-east of Margaret River, while *G. rosea* and *G. lutea* are confined to regions further south, mostly around Pemberton (*G. rosea*) and Walpole (*G. lutea*) (Wardell-Johnson & Roberts 1993, Roberts & Wardell-Johnson 1995, Atlas of Living Australia 2020d, 2020e, 2020f, 2020g).

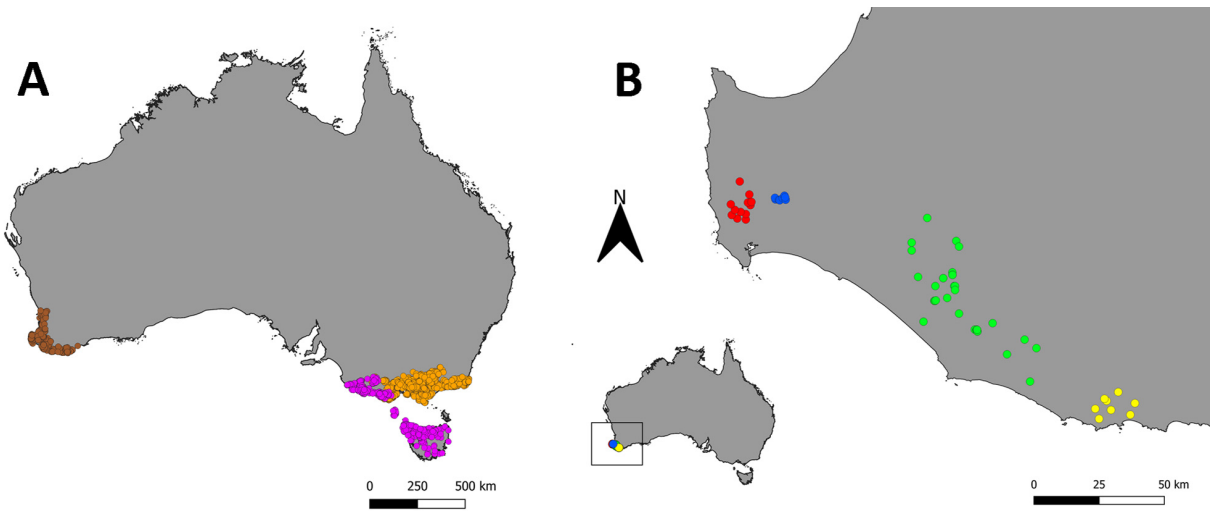


**FIGURE 5.** Geographic distribution of *Geocrinia* species: A) the *G. laevis* group—*G. laevis* (purple), *G. leai* (brown), and *G. victoriana* (orange); and B) the *G. rosea* group—*G. alba* (red), *G. lutea* (yellow), *G. rosea* (green), and *G. vitellina* (blue). Occurrence records are from Wardell-Johnson & Roberts (1993) and the Atlas of Living Australia (2020a–g).

**Taxonomy.** Given the genetic, reproductive, morphological and acoustic differences between the two groups within *Geocrinia* we believe recognition of two genera corresponding to these groups is appropriate. The type species for *Geocrinia* Blake 1973 is *Pterophrynus laevis* Günther 1864, and the name *Geocrinia* is restricted to the *G. laevis* group (Figure 6).

The name *Hesperocrinia* Wells & Wellington 1985 has formerly been applied to members of the *G. rosea* group; however this genus has *G. leai* as the type species and therefore is unavailable to be applied to the *G. rosea* group only. Given this, we propose a new generic name, *Anstisia* **gen. nov.**, for the four species in the *G. rosea* group (Figure 7). We designate *Crinia rosea* Harrison 1927, as the type species for the genus, as it is the first described of the four contained species. In line with Kaiser *et al*. (2013), and to preserve nomenclatural stability (Wüster *et al*. 2021), any recently proposed taxonomy regarding the four *Anstisia* and three *Geocrinia* species without peer review sits outside of the generally accepted practice for publishing scientific investigations and should be accordingly disregarded.

Distinction of these two genera from every other myobatrachid genus is demonstrated through phylogenetic analyses (Read *et al*. 2001, Frost *et al*. 2006, Dubois *et al*. 2021). An additional discussion of cladal relationships between the genera and close relatives is provided in the Supplementary Material.

### *Geocrinia* Blake 1973

*Geocrinia* Blake, 1973. Type species: *Pterophrynus laevis* Günther, 1864, by original designation.
*Hesperocrinia* Wells and Wellington, 1985. Type species: *Crinia leai* Fletcher, 1898, by original designation. Synonymy by acclamation.

**Definition.** Terrestrial/aquatic life history, aquatic exotrophic larvae with keratinised feeding mouthparts, larvae >20 mm in maximum length, adults <31 mm in maximum length, fourth toe length >7mm (*G. leai*/*G. victoriana*) and >6mm (*G. laevis*), testes mass >0.001 g, egg compliment >50; biphasic call, primarily autumn breeding.

**Content.** Three species: *Geocinia laevis* (Günther), *leai* (Fletcher), and *victoriana* (Boulenger).

**Distribution.** Occurring in southern Australia (south-eastern and south-western).

**Etymology.** The generic name *Geocrinia* is derived from Ancient Greek, a combination of the prefix γεω- (geô-) "earth" and verb κρῑνω (krînô) "to separate". While no etymology was provided by Blake, it presumably means "earth *Crinia*", referring to the terrestrial egg deposition and larval development of the contained species relative to the aquatic life history of the morphologically similar *Crinia*.

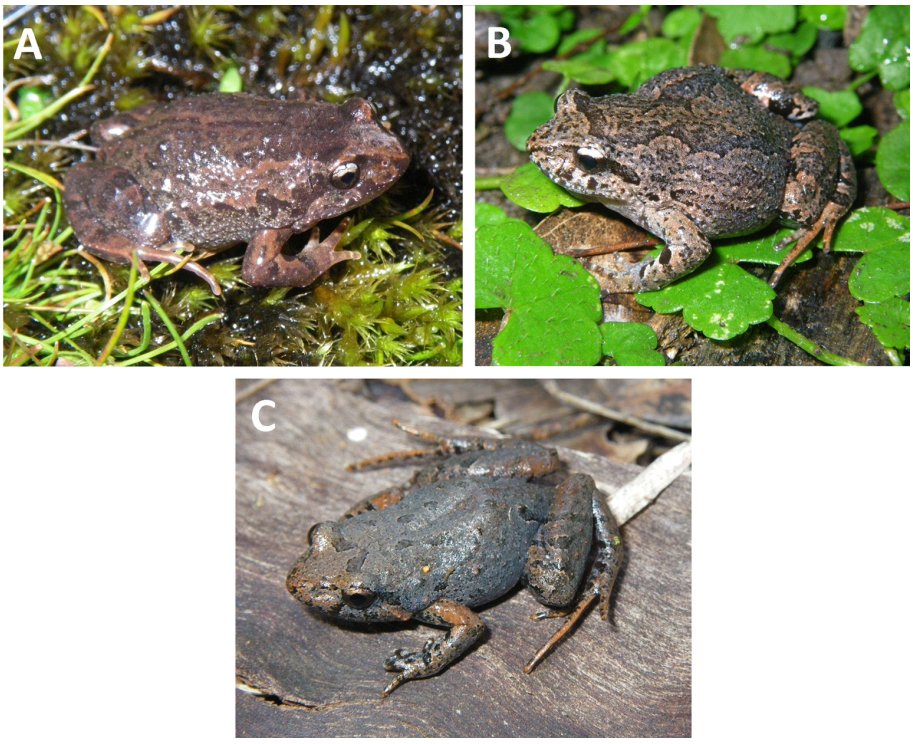


**FIGURE 6.** The species of *Geocrinia* Blake 1973 in life. A) *G. laevis*, from Cradle Mountain, Tasmania; B) *G. victoriana*, from Eden, New South Wales; and C) *G. leai*, from Pemberton, Western Australia. Photographs by G. Webster.

### *Anstisia* new genus

*Anstisia*. Type species: *Crinia rosea*, Harrison, 1927.

**Definition.** Nidicolous life history, terrestrial endotrophic larvae with vestigial non-feeding mouthparts, larvae <20 mm in maximum length, adults <25 mm in maximum length, fourth toe length <7 mm, testes mass <0.001 g, egg compliment <50, monophasic call, primarily spring breeding.

**Content.** Four species: *Anstisia alba* (Wardell-Johnson & Roberts), *lutea* (Main), *rosea* (Harrison), and *vitellina* (Wardell-Johnson & Roberts).

**Distribution.** Endemic to south-western Western Australia.

**Etymology.** The generic name *Anstisia* honours the extensive life work of Dr Marion Anstis, work that has concisely outlined the developmental differences of the three current and four former *Geocrinia* species, allowing for delineation between the two genera. Relevantly, given that her work has largely focused on the life histories of Australian anurans, in our opinion it is fitting that her name be applied to a genus that is distinguished largely on its unique life history strategy and larval morphology.


**FIGURE 7.** The species of *Anstisia* **gen. nov.** in life. A) *A. rosea*, from Pemberton, Western Australia; B) *A. lutea*, from Walpole, Western Australia; C) *A. alba*, from Witchcliffe, Western Australia; and D) *A. vitellina*, from Spearwood Creek, Western Australia. Photographs by G. Webster.

**Diagnosis.** The appearance in life of frog species within *Anstisia* and *Geocrinia* is similar (see Figures 6 and 7) although key differences exist. The three species of *Geocrinia* can be reliably distinguished from the four *Anstisia* species by ventral surface patterning in most cases. Ventral surfaces of *G. laevis* and *G. victoriana* always have some degree of marbling in the form of light grey or brown blotches. This patterning can at times be present in *G. leai*, but this species can also present a uniform ventral surface with pale yellow hues. Males of all three species can feature yellow throats. All *Anstisia* species however have distinctly individual ventral colouring. The ventral surface of *A. alba* is entirely uniform white; almost entirely coloured anteriorly with yolk orange in *A. vitellina*; rose with pink to orange hues in *A. rosea*; and off-white or cream usually with a dark yellow or lemon-yellow wash in *A. lutea*. Males of the latter two species are known to have dark grey or black throats, with females having pink and yellow throats respectively. Dorsally, *Geocrinia* species are highly variable but frequently feature a broad darker central marking.

The dorsal pattern of *A. rosea* and *A. lutea* can resemble that of *Geocrinia* but these species are reliably less variable, with the dorsal marking forming an inverted "V" on the lower back. Both *A. alba* and *A. vitellina* are similar in dorsal appearance with broken streaks of scattered darker spots.

In life, the appearance of tadpoles differs noticeably and cannot be confused, as *Geocrinia* tadpoles have a kertinised oral disc with feeding mouthparts, while *Anstisia* tadpoles do not. Tadpoles of the three *Geocrinia* species are uniformly brown on the dorsum, with patchy lighter colouration on the sides of the body and venter. In *G. laevis* and *G. victoriana* the tail muscle is very light brown and fins mostly clear, while the tail muscle in *G. leai* is pigmented with dark and light blotches with some irregular markings across the fins. Tadpoles of all *Anstisia* species possess vibrant light blue flecks across the body and tail, which are most apparent when viewed laterally, against a pigmentation of deep red-brown (*A. alba*/*A. vitellina*) to dark yellow-brown (*A. lutea*/*A. rosea*). In the *Anstisia* species, this pigmentation is lighter on the tail muscle than body, and fins are opaque. Metamorph frogs of both genera resemble the adults, although *Anstisia* species possess the vibrant blue flecking typical of the tadpoles.

In terms of distinguishing the two genera by advertisement call, *Geocrinia* species can be identified by a call consisting of two distinct note types (biphasic), compared to a singular note type (monophasic) in *Anstisia*. The introductory note alone, present in *Geocrinia*, is sufficient to distinguish this genus from all *Anstisia* species. The closely related genus, *Assa*, shares a similar monophasic ticking call to *Anstisia*; however these genera are entirely allopatric, with *Assa* occurring in northern New South Wales and southern Queensland.

## Discussion

The recognition of the new genus *Anstisia* reflects our understanding of the biology and phylogenetic relationships within the Myobatrachidae. It provides more resolved classification acknowledging the variation in diagnostic traits and the differing levels of relatedness between species within the former *Geocrinia* sensu lato, justifying the recognition of two genera. It also creates internal uniformity in life history strategies across 13 of the 14 myobatrachid genera.

Anstis (2010, 2013) provides specific synthesised accounts of differences in larval morphology and development of *Geocrinia* and *Anstisia*, empirically distinguishing the two genera, which were previously referred to as the *G. laevis* and *G. rosea* groups. The distinction of a third group containing only *G. leai*, as suggested by Blake, is not directly supported by Anstis, given the obvious similarity of life history between *G. leai*, *G. laevis,* and *G. victoriana* documented therein. Perhaps the only slight larval difference between *G. leai* and the eastern *Geocrinia* noted by Anstis is the Type 15 oral disc (very wide gap in posterior papillae and longer posterior tooth rows all of similar length) in *G. leai* and Type 14 oral disc (shorter posterior medial gap in papillae and shorter $P^3$ posterior tooth row) in *G. laevis* and *G. victoriana*. Should these differences prove to be consistent, and considering the morphologic, immunological and phylogenetic differences between *G. leai* and the eastern species, and if further genetic studies confirm *G. leai* as the basal *Geocrinia* species, this may justify subgeneric recognition of *G. leai*.

The new genus *Anstisia*, with its four species restricted to south-western Western Australia, draws more attention to the significance of the South Western Australian Ecoregion (SWAE), in particular the importance of this region to Myobatrachidae itself. The SWAE is an internationally recognised biodiversity hotspot (Wardell-Johnson *et al*. 2016), sometimes referred to as the South-western Australian Global Biodiversity Hotspot, and covers up to 48.9 million hectares (WWF 2020). It is an extremely biodiverse region with significant endemism, notably almost half of all the 6,700+ plant species from the region are found nowhere else (Harms *et al*. 2019, WWF 2020). In terms of frogs, 82%, or 28 of the 34 species there are thought to be endemic, with the exception being the more arid-adapted species. The biodiversity of this region has been attributed to endemic speciation rather than colonisation, being supported by genetic relationships between species of *Heleioporus* (Morgan *et al*. 2007). Formerly seven, and now eight, myobatrachid genera are known from the SWAE, with five of these being endemic, although derived from two separate radiations (Read *et al.* 2001, Frost *et al*. 2006, Pyron & Wiens 2011, Vidal-García & Keogh 2017, Dubois *et al*. 2021). All of the direct developing and four of the five nidicolous myobatrachid species are confined to this region (Anstis 2013).

The isolation of the SWAE and implications for diversification and speciation of biota, particularly between eastern and western Australia, is evident in many taxonomic groups and spans over millions of years (Roberts & Maxson 1985, Morgan *et al*. 2007, Rix *et al*. 2015, Wardell-Johnson *et al*. 2016, Harms *et al*. 2019). Distributions

of some plant genera, such as *Lambertia*, closely match the distribution of amphibian clades occurring in the SWAE and eastern Australia (Shearer & Crane 2012, Rix *et al*. 2015). The divergence between the eastern Australian *Geocrinia* species and the Western Australian *G. leai* may have occurred as long as 28 million years ago, while the *Heleioporus* species likely diverged about 25.6 million years ago (Roberts & Maxson 1985, Morgan *et al*. 2007). Similarly, very long divergence times between the SWAE endemic frogs, *Spicospina flammocaerulea* and *Litoria adelaidensis*, and their closest relatives from eastern and northern Australia have been suggested, respectively estimated at 25.7 and 30.8 million years (Catullo & Keogh 2014, Duellman *et al*. 2016). Even within the SWAE there is a long history of diversification, based on estimates provided by Roberts & Maxson (1985), *Geocrinia* and *Anstisia* are likely to have diverged 29.8–40.4 million years ago.

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**Supplementary material**

**TABLE S1.** The taxonomic history, previous nomenclature and synonyms of the *Geocrinia* species, with proposed names following this review in bold.

| Species | Nomenclatural History |
|---|---|
| *Geocrinia alba* Wardell-Johnson and Roberts, 1989 | *Geocrinia alba* Wardell-Johnson and Roberts, 1989 |
| | *Anstisia alba*: this paper |
| | **=*Anstisia alba* (Wardell-Johnson and Roberts, 1989)** |
| *Geocrinia laevis* (Günther, 1864) | *Pterophrynus laevis* Günther, 1864 |
| | *Crinia laevis*: Keferstein, 1868 |
| | *Crinia laevis laevis*: Loveridge, 1935 |
| | *Crinia laevis*: Littlejohn and Martin, 1964 |
| | *Geocrinia laevis*: Blake, 1973 |
| | *Geocrinia laevis* this paper |
| | **=*Geocrinia laevis* (Günther, 1864)** |
| *Geocrinia leai* (Fletcher, 1898) | *Crinia leai* Fletcher, 1898 |
| | *Crinia michaelseni*: Werner, 1914 |
| | *Crinia leai*: Harrison, 1927 |
| | *Geocrinia leai*: Blake, 1973 |
| | *Hesperocrinia leai*: Wells and Wellington, 1985 |
| | *Geocrinia leai*: Cogger, 1988 |
| | *Geocrinia leai*: this paper |
| | **=*Geocrinia leai* (Fletcher, 1898)** |
| *Geocrinia lutea* (Main, 1963) | *Crinia lutea* Main, 1963 |
| | *Geocrinia lutea*: Blake, 1973 |
| | *Geocrinia rosea*: Tyler, Smith, and Johnstone, 1984 |
| | *Hesperocrinia lutea*: Wells and Wellington, 1985 |
| | *Geocrinia rosea*: Cogger, 1988 |
| | *Geocrinia lutea*: Roberts, Wardell-Johnson, and Barendse, 1990 |
| | *Anstisia lutea*: this paper |
| | **=*Anstisia lutea* (Main, 1963)** |

*.....continued on the next page*

**TABLE S1. (Continued)**

| Species | Nomenclatural History |
|---|---|
| *Geocrinia rosea* (Harrison, 1927) | *Crinia rosea* Harrison, 1927 |
| | *Geocrinia rosea*: Blake, 1973 |
| | *Hesperocrinia rosea*: Wells and Wellington, 1985 |
| | *Geocrinia rosea*: Cogger, 1988 |
| | *Anstisia rosea*: this paper |
| | **=*Anstisia rosea* (Harrison, 1927)** |
| *Geocrinia victoriana* (Boulenger, 1888) | *Crinia victoriana* Boulenger, 1888 |
| | *Crinia froggatti*: Fletcher, 1891 |
| | *Crinia laevis froggatti*: Loveridge, 1935 |
| | *Crinia laevis victoriana*: Parker, 1940 |
| | *Crinia victoriana*: Littlejohn and Martin, 1964 |
| | *Geocrinia victoriana*: Blake, 1973 |
| | *Geocrinia victoriana*: this paper |
| | **=*Geocrinia victoriana* (Boulenger, 1888)** |
| *Geocrinia vitellina* Wardell-Johnson and Roberts, 1989 | *Geocrinia vitellina* Wardell-Johnson and Roberts, 1989 |
| | *Anstisia vitellina*: this paper |
| | **=*Anstisia vitellina* (Wardell-Johnson and Roberts, 1989)** |

**Proposed clade names.** In line with recent nomenclature proposals by Dubois *et al*. (2021), our placement of the *Anstisia* species into a genus distinct from *Geocrinia* creates a division within the myobatrachid clade Assinoa. We therefore recognise that further nested clades within Assinoa are available to be named, with one clade solely containing the genus *Assa* and another clade containing the sister-genera *Geocrinia* and *Anstisia*. We propose that the taxon names Assites **nov.** and Nidicolites **nov.** be adopted for these clades respectively. Under the current paradigm, the clades represent the rank of 'clanus' following Dubois (2006), positioned above the rank of genus.

**Etymology.** Our first proposed clanus name, Assites, refers to its single contained genus, *Assa*. The second proposed clanus name, Nidicolites, meaning "nest inhabiting" refers to the reproductive behaviour of the species within the two contained genera. Originating from Latin "nidi" the genitive singular of "nidus" (nest) and the suffix "-colus" (inhabiting). The suffix "-ites", used in both names, is a Latin word derived from the Ancient Greek "-ίτης" (those belonging to).

**Justification.** While cladal appraoches to taxonomy, where names are applied to clades positioned outside of the standardised framework of species, genus, family, etc., are not currently widely practiced or even proposed, perhaps due in part to lack of consensus or the difficulties of fitting a stable and effective model to a complex and dynamic system, we see merit in attempting this approach.

Naming clades that sit above or below the ranks of genus and family is a useful and practical means for understanding and communicating close relationships between groups of taxa, especially in an evolutionary or ecological context. Cladal recognition allows for effective discourse while promoting rapid comprehension of similarities or differences between species groups.

In our example *Anstisia* and *Geocrinia* are sister taxa, and together the sister to *Assa*, all three of these genera share affinites in modified life history as well as call structure. It is therefore helpful to talk about Assinoa or Nidicolites in this context, as it communicates the relatedness between the contained species. Refering to these three genera by the family name Myobatrachidae does not provide specific information on closeness of relationships and naively implies other myobatrachid genera may be equally closely related to genera within Assinoa and Nidicolites, despite substantional ecological and genetic differences.