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Systematics and Taxonomy of the Northern Banjo Frog (Anura: Limnodynastidae: *Limnodynastes terraereginae*) and Allied Taxa

Tom Parkin[1], Jodi J. L. Rowley[1,2], Grace L. Gillard[1,2], Jarrod Sopniewski[3], Glenn M. Shea[1,4], and Stephen C. Donnellan[5]

The Australian banjo frogs are a distinctive group of medium to large, terrestrial, and burrowing limnodynastid frogs known for their conspicuous, single-note advertisement calls which are often likened to the pluck of a banjo string. Preliminary analyses of mitochondrial DNA sequences had previously indicated that the present taxonomy of the group, based primarily on morphology and advertisement calls, may not best reflect the true evolutionary relationships among taxa. In this study, we use comprehensive geographic sampling and integrative analyses of mitochondrial DNA sequences, nuclear single-nucleotide polymorphisms, adult morphology, and advertisement call data to re-evaluate the systematics and taxonomy of the Northern Banjo Frog (*Limnodynastes terraereginae*) and allied taxa. Our study reveals the presence of three evolutionarily distinct, morphologically divergent, and narrowly allopatric lineages that replace each other in a north–south series from the tip of Cape York Peninsula to the Sydney Basin in the south. Our findings demonstrate that our understanding of the systematics and taxonomy of Australian frogs remains incomplete, even for large and apparently "well-known" species that live in densely populated areas.

THE banjo frogs or 'pobblebonks' are a distinctive and charismatic group of medium to large (34–94 mm body length) terrestrial and burrowing limnodynastid frogs endemic to Australia. Often referred to as the *Limnodynastes dorsalis* group (Martin, 1972; Roberts and Maxson, 1986; Schäuble et al., 2000), species in this group are recognizable by their conspicuous, single-note, resonant "bonk" or "tok" advertisement calls, which are often likened to the pluck of a banjo string. Eight taxa are recognized currently, including four species and five subspecies: *Limnodynastes dorsalis*, *L. interioris*, *L. terraereginae*, and *L. dumerilii*, which is further divided into the subspecies *L. dumerilii dumerilii*, *L. d. fryi*, *L. d. insularis*, *L. d. variegatus*, and *L. d. grayi*. Except for *L. dorsalis*, which is restricted to south-western Western Australia, all other taxa occur from southeastern to northeastern Australia where they share mostly parapatric distributions with some zones of sympatry (Martin, 1972). Hybrid zones are known to form at contact zones between multiple species, based on the presence of intermediate morphological and advertisement call phenotypes within these zones (Martin, 1972). The extent of hybridization between species at contact zones has been found to correspond particularly to divergence in advertisement calls: species with the most similar calls are thought to hybridize more frequently. Their distributions span a variety of mesic to semi-arid habitats, with two species, *L. terraereginae* and *L. dumerilii grayi*, even occurring in the highly acidic wallum wetlands of the eastern Australian coastline. Tadpoles of these species possess a remarkable tolerance for acidic waters and can complete their development in aquatic environments with pH levels as low as 3.0 (Hines and Meyer, 2011; Hird et al., 2022).

The phylogenetic relationships among species of the *L. dorsalis* group have been inferred previously using microcomplement fixation (Roberts and Maxson, 1986) and mitochondrial DNA sequences (Schäuble et al., 2000), with the findings of both studies suggesting the current taxonomy for the group, based primarily on morphology and advertisement call structure, may not best reflect the true evolutionary relationships among taxa. In particular, the genetic data indicate that *L. dumerilii grayi* is deeply divergent from topotypic *L. dumerilii* (Roberts and Maxson, 1986) and may be more closely related to *L. terraereginae* (Schäuble et al., 2000).

In this study, we aimed to clarify the phylogenetic relationships among taxa of the *L. dorsalis* group and re-evaluate the systematics and taxonomy of *L. terraereginae sensu lato*. We use comprehensive geographic sampling to explore divergence in mitochondrial and nuclear DNA, morphology, and advertisement calls between the taxa. Further, using targeted surveys of potential contact zones, we sought to document the interactions between taxa and quantify the extent of admixture occurring between them.

MATERIALS AND METHODS

Sampling.—We carried out targeted surveys for all eastern Australian members of the *Limnodynastes dorsalis* group in New South Wales (NSW), Queensland (QLD), Victoria (VIC), and Tasmania (TAS) between 2020–2022. Surveys were

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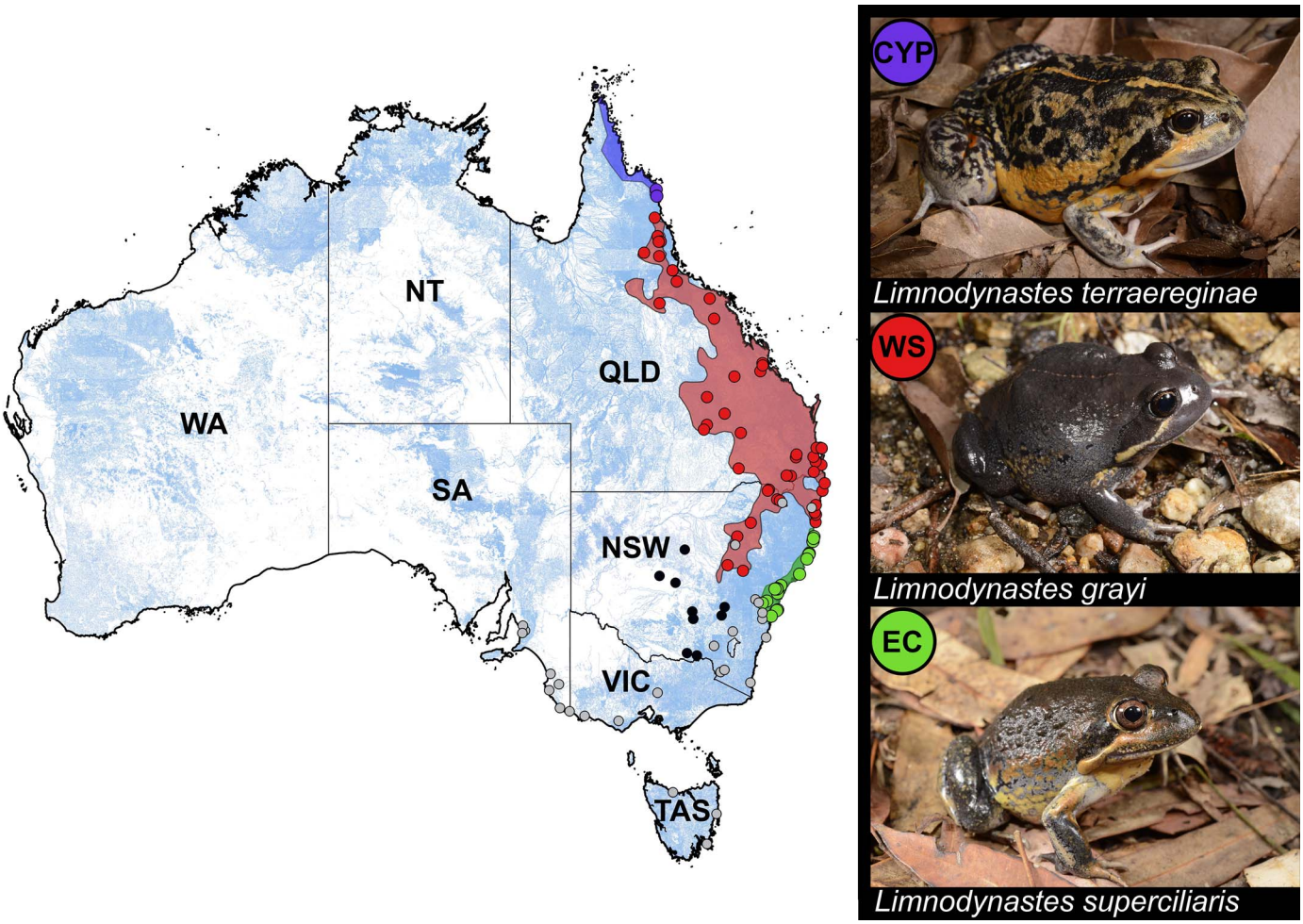

Fig. 1. Distribution of genotyped samples for the eastern Australian *Limnodynastes dorsalis* group examined in this study. Purple circles = CYP lineage; red circles = WS lineage; green circles = EC lineage; gray circles = *L. dumerilii* (including all subspecies); and black circles = *L. interioris*. Surface hydrology in blue.

conducted during spring and summer months and were timed to coincide with rainfall, when the species are most detectable. Our fieldwork focused on collecting specimens, genetic samples, and acoustic recordings of male advertisement calls to facilitate integrative taxonomic analyses. Newly collected samples were combined with a comprehensive coverage of tissues and specimens available in the collections of the Australian Museum (AMS), South Australian Museum (SAMA), Australian Biological Tissue Collection (ABTC), Queensland Museum (QM), and Museums Victoria (NMV). Collection locations of samples used in the genetic analyses are shown in Figure 1 and their details are listed in Table 1. Details of samples used for the morphological analyses are presented in Supplementary Table S1 (see Data Accessibility).

Our fieldwork focused on two primary objectives: (1) genotyping unsampled populations to confirm the distribution of lineages, including collecting topotypic samples to enable interpretation of the nomenclature, and (2) identifying and sampling areas of actual or potential contact between lineages to evaluate admixture between them. In addition to the advertisement calls recorded during fieldwork, we used call recordings obtained from the Australian Museum's national citizen science project, FrogID (Rowley et al., 2019; https://www.frogid.net.au).

Mitochondrial DNA extraction and analysis.—Nucleotide sequences of the mitochondrial NADH subunit 4 (*ND4*) gene were obtained from all members of the *Limnodynastes dorsalis* group, including *L. terraereginae* ($n = 56$), *L. interioris* ($n = 5$), *L. dorsalis* ($n = 2$), and representative topotypic samples of all subspecies of *L. dumerilii* ($n = 21$), with a focus on the eastern coastal NSW subspecies *L. dumerilii grayi* ($n = 18$). DNA was extracted from ethanol-preserved tissues (liver, muscle, or toe tip) using a DNeasy® Blood and Tissue Kit (QIAGEN GmbH, Hilden, Germany), following the manufacturer's protocols for purification of genomic DNA from animal tissues. A fragment of the *ND4* gene was PCR amplified and directly sequenced using the primers: 5′–TGA CTA CCA AAA GCT CAT GTA GAA GC–3′ and 5′–GGT YAC GAG YAA TTA GCA GTT CT–3′. PCR was carried out in 25 µL reactions with a final concentration of 2,000 ng of template DNA, 1X MyTaq™ Red Reaction Buffer, 2 pmol of each primer, 0.5 units of Bioline MyTaqTM Red DNA Polymerase, and 16.8 µL of autoclaved water. Thermocycling was performed on an Eppendorf Mastercycler EpS (Eppendorf, Hamburg, Germany) under the following cycling protocol: (1) initial denaturation at 94°C for 3 min, (2) 10 cycles involving a denaturation step of 94°C for 45 seconds, annealing at 60°C for 1 min, and extension at 72°C for 1 min, with the annealing

Table 1. *Limnodynastes dorsalis* group specimens examined for molecular genetic analyses. Institution codes: ABTC—Australian Biological Tissue Collection, South Australian Museum; AMS—Australian Museum; NMV—Museums Victoria; SAMA—South Australian Museum; QM—Queensland Museum; TMAG—Tasmanian Museum and Art Gallery. HS—homestead, NP—National Park, SF—State Forest, NR—Nature Reserve. *ND4* column refers to GenBank accession numbers.

Tissue reg/ Field num	Species	Lineage	SNP	*ND4*	Precise location	State	Latitude	Longitude	Source institution	Voucher RegNum
A003396	*L. grayi*	WS	*y*	OR542643	Couran Cove Resort, South Stradbroke Island	QLD	−27.8231	153.416897	QM	J80365
A004649	*L. grayi*	WS	—	OR542644	Loganlea	QLD	−27.67533	153.131837	QM	J87121
A009978	*L. grayi*	WS	—	OR542646	Currawarra, 52 km NNW Mitchell	QLD	−26.05194	147.744167	QM	J91633
A012080	*L. grayi*	WS	*y*	OR542647	Carnarvon Station HS	QLD	−24.81667	147.75	QM	J93772
A012089	*L. grayi*	WS	*y*	OR542648	Spine Rd, Carnarvon Stn	QLD	−24.81083	147.751111	QM	—
A018369	*L. grayi*	WS	*y*	OR542649	Comboyuro Point Campground, Moreton Island	QLD	−27.06944	153.366389	QM	J96541
ABTC109418	*L. grayi*	WS	*y*	OR542668	~7.6 km WSW Lau-Mar HS, ~38 km N Injune	QLD	−25.55393	148.625644	QM	J91692
ABTC109425	*L. grayi*	WS	*y*	OR542669	7 km N Mount Lonsdale HS, 20 km N Mungallala	QLD	−26.26604	147.59565	ABTC	—
ABTC109712	*L. grayi*	WS	*y*	—	Pikedale Rd, SW Warwick	QLD	−28.30825	151.902539	QM	J90985
ABTC109755	*L. grayi*	WS	*y*	OR542670	Kerry Church, Beaudesert Rd, Kerry	QLD	−28.128	153.042439	QM	J91013
ABTC109841	*L. grayi*	WS	*y*	OR542671	Yuleba State Forest	QLD	−26.41353	149.424065	QM	J90907
ABTC12526	*L. grayi*	WS	*y*	OR542652	Pentland	QLD	−20.52382	145.399165	ABTC	—
ABTC12527	*L. grayi*	WS	*y*	OR542653	Pentland	QLD	−20.5238	145.399509	ABTC	—
ABTC127666	*L. grayi*	WS	*y*	OR542672	Seventeen Mile Rd, N of Helidon	QLD	−27.48993	152.158807	QM	J93217
ABTC127677	*L. grayi*	WS	*y*	OR542673	Wellers Rd, Ravensbourne	QLD	−27.36779	152.18707	QM	J93228
ABTC127841	*L. grayi*	WS	*y*	OR542674	Redcliffe Tableland, N of Nebo	QLD	−21.23772	148.103471	QM	J92790
ABTC15893	*L. grayi*	WS	*y*	OR542657	6 km N of Rockhampton	QLD	−23.3	150.52	SAMA	R41987
ABTC15899	*L. grayi*	WS	*y*	—	9 km N of Rockhampton	QLD	−23.275	150.5	SAMA	R41991
ABTC33282	*L. grayi*	WS	*y*	—	Mt Morgan	QLD	−23.64362	150.396578	ABTC	—
ABTC99405	*L. grayi*	WS	*y*	OR542667	Moonie River, E St George	QLD	−27.98197	149.317384	QM	J85842
AJ2697771	*L. grayi*	WS	—	AJ2697771	Brisbane	QLD	−27.46827	153.025434	GenBank	—
AJ2697791	*L. grayi*	WS	—	AJ2697791	Princess Hills	QLD	−18.32201	145.381561	GenBank	—
AJ2697831	*L. grayi*	WS	—	AJ2697831	Rockhampton	QLD	−23.37861	150.50888	GenBank	—
EBU115671	*L. grayi*	WS	*y*	—	Gulgong	NSW	−32.36253	149.53356	AMS	—
FS35	*L. grayi*	WS	*y*	OR542716	South Mimosa Creek, Blackdown Tableland NP	QLD	−23.88376	149.108488	QM	—
HH09038	*L. grayi*	WS	*y*	OR542717	McMahon Rd, Bribie Island NP	QLD	−27.07376	153.177139	QM	—
HH13048	*L. grayi*	WS	*y*	OR542718	Blue Lagoon, Moreton Island NP, Moreton Island	QLD	−27.09417	153.431667	QM	—
HH13054	*L. grayi*	WS	*y*	OR542719	Blue Lagoon, Moreton Island NP, Moreton Island	QLD	−27.09417	153.431667	QM	—
HH16043	*L. grayi*	WS	*y*	OR542720	Durikai SF, W of Warwick	QLD	−28.28814	151.696265	QM	—
HH16047	*L. grayi*	WS	*y*	OR542721	Durikai SF, W of Warwick	QLD	−28.28814	151.696265	QM	—
R138450	*L. grayi*	WS	—	OR542680	Coffs Harbour, 2 km From Mouth of Coffs Creek	NSW	−30.3	153.13	AMS	R138450
R138478	*L. grayi*	WS	*y*	OR542681	Wardell, S of Ballina	NSW	−28.95	153.47	AMS	R138478

Table 1. Continued.

Tissue reg/ Field num	Species	Lineage	SNP	*ND4*	Precise location	State	Latitude	Longitude	Source institution	Voucher RegNum
R146728	*L. grayi*	WS	*y*	OR542682	Byron Bay	NSW	−28.6244	153.5808	AMS	R146728
R166997	*L. grayi*	WS	*y*	OR542684	Dubbo	NSW	−32.12839	148.771181	AMS	R166997
R174876	*L. grayi*	WS	*y*	OR542686	Timmallallie Dam, Pilliga NP	NSW	−30.915	149.251	AMS	R174876
R185843	*L. grayi*	WS	*y*	OR542687	4.5 km E of Yetman Post Office	NSW	−28.90221	150.817871	AMS	R185843
R188090	*L. grayi*	WS	*y*	OR542689	Mount Kaputar Rd, Narrabri	NSW	−30.32664	149.918896	AMS	R188090
R188102	*L. grayi*	WS	*y*	—	Emmaville Rd, E of Ashford	NSW	−29.32567	151.228325	AMS	R188102
R188104	*L. grayi*	WS	*y*	OR542690	Emmaville Rd, E of Ashford	NSW	−29.37709	151.359737	AMS	R188104
R188151	*L. grayi*	WS	*y*	OR542697	Dirty Creek Rd, ~45 km N of Coffs Harbour	NSW	−29.97027	153.142288	AMS	R188151
R188152	*L. grayi*	WS	*y*	OR542698	Dirty Creek Rd, ~45 km N of Coffs Harbour	NSW	−29.9822	153.14592	AMS	R188152
R188153	*L. grayi*	WS	*y*	OR542699	Bald Knob Rd, Yuraygir	NSW	−29.88476	153.08638	AMS	R188153
R188154	*L. grayi*	WS	*y*	OR542700	Bald Knob Rd, Yuraygir	NSW	−29.88671	153.093781	AMS	R188154
R188176	*L. grayi*	WS	*y*	OR542726	Watsonville, Atherton Tablelands	QLD	−17.3776	145.305893	QM	J97858
R188177	*L. grayi*	WS	*y*	OR542727	Watsonville, Atherton Tablelands	QLD	−17.38147	145.305649	QM	J97851
R188185	*L. grayi*	WS	*y*	OR542731	Ravenshoe, Atherton Tablelands	QLD	−17.63414	145.457382	QM	J97849
R188186	*L. grayi*	WS	*y*	OR542732	Ravenshoe, Atherton Tablelands	QLD	−17.63296	145.456299	QM	J97854
R188187	*L. grayi*	WS	*y*	OR542733	Kennedy Hwy, W of Ravenshoe	QLD	−17.64344	145.358139	QM	J97855
R188191	*L. grayi*	WS	*y*	OR542734	Undara Rd, Mount Surprise area	QLD	−18.15841	144.631927	QM	J97852
R188192	*L. grayi*	WS	*y*	OR542735	W side of Paluma Range	QLD	−18.9869	146.048767	QM	J97856
R188193	*L. grayi*	WS	*y*	OR542736	W side of Paluma Range	QLD	−18.9863	146.047256	QM	J97859
R188194	*L. grayi*	WS	*y*	OR542737	W side of Paluma Range	QLD	−18.98449	146.043701	QM	J97853
R188199	*L. grayi*	WS	*y*	OR542738	Strathalbyn Rd, Bogie	QLD	−20.30673	147.884735	QM	J97850
R188201	*L. grayi*	WS	*y*	OR542739	Herveys Range, W of Townsville	QLD	−19.50798	146.251892	QM	J97848
R188202	*L. grayi*	WS	*y*	OR542740	Mount Spurgeon Rd, Mount Carbine	QLD	−16.50087	145.161514	QM	J97857
R188350	*L. grayi*	WS	*y*	OR542708	Tucabia-Tyndale Rd, Tyndale	NSW	−29.56716	153.138199	AMS	R188350
R190834	*L. grayi*	WS	*y*	OR542714	37.7 km N of Coolatai	NSW	−28.94616	150.763962	AMS	R190834
ABTC1175	*L. superciliaris*	EC	*y*	—	Watagan SF	NSW	−32.975	151.412	AMS	R130080
ABTC1176	*L. superciliaris*	EC	*y*	OR542650	Watagan SF	NSW	−32.975	151.412	AMS	R130081
ABTC1361	*L. superciliaris*	EC	*y*	—	Kurnell	NSW	−34.01	151.207	AMS	—
ABTC140434	*L. superciliaris*	EC	*y*	—	Captain Cook Dve, Kurnell	NSW	−34.02971	151.16388	AMS	R149228
ABTC140435	*L. superciliaris*	EC	*y*	OR542675	1.2 km WSW North Haven	NSW	−31.633	152.816	AMS	R150172
ABTC140438	*L. superciliaris*	EC	*y*	OR542677	Watagan State Forest, 11.5 km N Kulnura	NSW	−33.12282	151.21867	AMS	R168497
ABTC140440	*L. superciliaris*	EC	*y*	—	Watagan State Forest, 11.5 km N Kulnura	NSW	−33.12282	151.21867	AMS	R168499
ABTC140441	*L. superciliaris*	EC	*y*	—	Watagan State Forest, 11.5 km N Kulnura	NSW	−33.12282	151.21867	AMS	R168575
ABTC140571	*L. superciliaris*	EC	*y*	—	Sternbeck Pond, Olney SF	NSW	−33.1331	151.2061	ABTC	—
ABTC140572	*L. superciliaris*	EC	*y*	OR542678	Sternbeck Pond, Olney SF	NSW	−33.1331	151.2061	ABTC	—

Table 1. Continued.

Tissue reg/ Field num	Species	Lineage	SNP	*ND4*	Precise location	State	Latitude	Longitude	Source institution	Voucher RegNum
ABTC140573	*L. superciliaris*	EC	*y*	—	Sternbeck Pond, Olney SF	NSW	−33.1331	151.2061	ABTC	—
ABTC14670	*L. superciliaris*	EC	*y*	OR542655	La Perouse	NSW	−33.98	151.25	SAMA	R34900
ABTC21570	*L. superciliaris*	EC	*y*	—	Watagan SF	NSW	−33.1	151.22	SAMA	R37017
ABTC25842	*L. superciliaris*	EC	*y*	OR542660	Mungo Brush, Myall Lakes NP	NSW	−32.503	152.338	ABTC	—
R149228	*L. superciliaris*	EC	—	OR542683	Kurnell	NSW	−34.01	151.207	AMS	R149228
R153993	*L. superciliaris*	EC	*y*	OR542676	Mooney Mooney Creek Ridge, ~2 km E Central Mangrove	NSW	−33.3	151.25	AMS	R153993
R168499	*L. superciliaris*	EC	*y*	OR542685	Olney SF, Inana Community Rd	NSW	−33.12283	151.218684	AMS	R168499
R188135	*L. superciliaris*	EC	*y*	OR542694	Bell Frog Track, Hat Head NP	NSW	−31.10107	153.012985	AMS	R188135
R188136	*L. superciliaris*	EC	*y*	—	Hat Head NP	NSW	−31.12656	152.995804	AMS	R188136
R188157	*L. superciliaris*	EC	*y*	—	Darkes Forest Rd, Darkes Forest	NSW	−34.242	150.935532	AMS	R188157
R188158	*L. superciliaris*	EC	*y*	OR542701	Darkes Forest Rd, Darkes Forest	NSW	−34.24169	150.937317	AMS	R188158
R188161	*L. superciliaris*	EC	*y*	OR542702	Bore Fields Trail, South West Rocks	NSW	−30.91936	153.047424	AMS	R188161
R188162	*L. superciliaris*	EC	*y*	OR542703	Bore Fields Trail, South West Rocks	NSW	−30.92033	153.049179	AMS	R188162
R188163	*L. superciliaris*	EC	*y*	OR542679	Laurieton	NSW	−31.67459	152.80123	AMS	R188163
R188164	*L. superciliaris*	EC	*y*	OR542704	Harrington	NSW	−31.86661	152.700996	AMS	R188164
R188165	*L. superciliaris*	EC	*y*	OR542705	Agnes Banks	NSW	−33.6216	150.714264	AMS	R188165
R188207	*L. superciliaris*	EC	*y*	OR542707	Linden, Blue Mountains	NSW	−33.7075	150.493988	AMS	R188207
R188357	*L. superciliaris*	EC	*y*	OR542709	Hat Head	NSW	−30.9977	153.025114	AMS	R188357
ABTC142322	*L. superciliaris*	EC	*y*	—	Yengo NP	NSW	−33.12211	151.119241	ABTC	—
A005543	*L. terraereginae*	CYP	*y*	OR542645	Gute Hill, South McIvor River mouth	QLD	−15.16667	145.233333	QM	J88032
R188178	*L. terraereginae*	CYP	*y*	OR542728	Finch Bay, Cooktown	QLD	−15.47323	145.261917	QM	J97860
R188179	*L. terraereginae*	CYP	*y*	OR542729	Finch Bay, Cooktown	QLD	−15.47318	145.261642	QM	J97861
R188184	*L. terraereginae*	CYP	*y*	OR542730	Finch Bay, Cooktown	QLD	−15.47329	145.26152	QM	J97862
AJ2697151	*L. dorsalis*	—	—	AJ2697151	Perry Lakes	WA	−31.94234	115.781557	GenBank	—
AJ2697171	*L. dorsalis*	—	—	AJ2697171	Perry Lakes	WA	−31.94234	115.781557	GenBank	—
ABTC12837	*L. dumerilii dumerilii*	—	*y*	OR542654	Adelong Creek, 19 km S of Tumut	NSW	−35.45	148.1	SAMA	R44017
ABTC1357	*L. dumerilii dumerilii*	—	*y*	—	15 km W Coonabarabran	NSW	−31.266	149.135	AMS	R133215
ABTC14767	*L. dumerilii dumerilii*	—	*y*	OR542656	Ansteys Hill	SA	−34.83	138.73	SAMA	R37019
ABTC14778	*L. dumerilii dumerilii*	—	*y*	—	Gawler River	SA	−34.63	138.63	SAMA	R34927
ABTC7207	*L. dumerilii dumerilii*	—	*y*	OR542651	Flowerdale	SA	−37.32	145.3	SAMA	R20203
AJ2697191	*L. dumerilii dumerilii*	—	—	AJ2697191	Adelaide	SA	−34.92848	138.600746	GenBank	—
EBU115629	*L. dumerilii dumerilii*	—	*y*	—	Hill Top	NSW	−34.35432	150.494215	AMS	—
EBU115727	*L. dumerilii dumerilii*	—	*y*	—	Grafton	NSW	−29.6815	152.938116	AMS	—
R133214	*L. dumerilii dumerilii*	—	*y*	—	15 km W Coonabarabran	NSW	−31.27	149.15	AMS	R133214
R147354	*L. dumerilii dumerilii*	—	*y*	—	Lett River, E side of Glenroy Bridge on Jenolan Caves Rd	NSW	−33.5511	150.1475	AMS	R147354
R171924	*L. dumerilii dumerilii*	—	*y*	—	Oakdale, Burragorang Rd	NSW	−34.1	150.5	AMS	R171924
R188105	*L. dumerilii dumerilii*	—	*y*	—	Severin River, Strathbogie Rd, E of Ashford	NSW	−29.46906	151.481984	AMS	R188105

Table 1. Continued.

Tissue reg/ Field num	Species	Lineage	SNP	*ND4*	Precise location	State	Latitude	Longitude	Source institution	Voucher RegNum
R188208	*L. dumerilii dumerilii*	—	*y*	—	Katoomba, Blue Mountains	NSW	−33.68241	150.312622	AMS	R188208
ABTC17456	*L. dumerilii fryi*	—	—	OR542658	Thredbo Valley, nr Little Thredbo River	NSW	−36.5	148.42	SAMA	R40224
ABTC17457	*L. dumerilii fryi*	—	*y*	OR542659	Thredbo Valley, nr Little Thredbo River	NSW	−36.5	148.42	SAMA	R40225
R187835	*L. dumerilii fryi*	—	*y*	OR542688	Naas River, Namadgi NP	NSW	−34.86607	149.027552	AMS	R187835
R188439	*L. dumerilii fryi*	—	*y*	OR542712	Lake Jindabyne	NSW	−36.41451	148.613571	AMS	R188439
R188440	*L. dumerilii fryi*	—	*y*	OR542713	Lake Jindabyne	NSW	−36.41451	148.613571	AMS	R188440
ABTC40835	*L. dumerilii insularis*	—	*y*	OR542664	20 km SE of Colac	VIC	−38.42	143.37	SAMA	R34665
JJLR5384	*L. dumerilii insularis*	—	*y*	OR542722	Penguin	TAS	−41.13959	146.062317	TMAG	C1522
JJLR5395	*L. dumerilii insularis*	—	*y*	OR542723	~15 km W of Eaglehawk Neck, Tasman Peninsula	TAS	−43.03736	147.747162	TMAG	C1526
JJLR5397	*L. dumerilii insularis*	—	*y*	OR542724	Bichenon	TAS	−41.93946	148.220535	TMAG	C1524
R188169	*L. dumerilii insularis*	—	*y*	OR542706	Naval College Rd, Hyams Beach	NSW	−35.10738	150.679672	AMS	R188169
R188360	*L. dumerilii insularis*	—	*y*	OR542710	Merimbula	NSW	−36.91832	149.901199	AMS	R188360
ABTC37443	*L. dumerilii variegatus*	—	*y*	OR542661	0.3 km NNE of Piccaninnie Ponds	SA	−38.0472	140.9425	SAMA	R49388
ABTC37535	*L. dumerilii variegatus*	—	*y*	OR542662	7.4 km WSW of Kongorong Telephone Exchange	SA	−37.9186	140.4639	SAMA	R49560
ABTC37678	*L. dumerilii variegatus*	—	*y*	OR542663	18 km NE of Conmurra Telephone Exchange	SA	−36.9858	140.4133	SAMA	R49511
ABTC70600	*L. dumerilii variegatus*	—	*y*	OR542665	6.5 km SSW of Bald Hill	SA	−36.5694	139.9989	SAMA	R53352
ABTC94799	*L. dumerilii variegatus*	—	*y*	OR542666	9.3 km SSE of Kangaroo Hill	SA	−37.2211	139.9314	SAMA	R53761
JJLR5905	*L. dumerilii variegatus*	—	*y*	OR542725	Mount Clay SF	VIC	−38.22529	141.686951	NMV	D76452
R141102	*L. interioris*	—	*y*	—	Buddigower NR	NSW	−34.05	147.02	AMS	R141102
R153879	*L. interioris*	—	*y*	—	Collaroy Stn, 10 km NW of Hermidale	NSW	−31.47	146.65	AMS	R153879
R156856	*L. interioris*	—	*y*	—	Yathong NP	NSW	−32.5758	145.3964	AMS	R156856
R156863	*L. interioris*	—	*y*	—	Yarra Property, 35 km from Mt Hope	NSW	−32.8622	146.1894	AMS	R156863
R174820	*L. interioris*	—	*y*	—	Dananbilla NRF, ~40 km S of Cowra	NSW	−34.21424	148.472648	AMS	R174820
R188115	*L. interioris*	—	*y*	OR542691	Urana Rd, S of Walbundrie	NSW	−35.74117	146.757965	AMS	R188115
R188120	*L. interioris*	—	*y*	OR542692	Mirrool South Rd, Mirrool	NSW	−34.35303	147.070221	AMS	R188120
R188121	*L. interioris*	—	*y*	OR542693	Mirrool South Rd, Mirrool	NSW	−34.35513	147.069839	AMS	R188121
R188142	*L. interioris*	—	*y*	OR542696	Chiverton Rd, Cowra	NSW	−33.8648	148.622955	AMS	R188142
R188374	*L. interioris*	—	*y*	OR542711	Woomagarma	NSW	−35.83213	147.251617	AMS	R188374

temperature decreased by 1°C per cycle, (3) 34 cycles of 94°C for 45 sec, 50°C for 1 min, and 72°C for 1 min, and (4) a final extension step of 72°C for 6 min with samples kept at a holding temperature of 11°C. Amplification products were visualized on 1.5% agarose gels, purified using ExoSap-ITTM (USB Corporation, Cleveland, Ohio, USA), and sequenced in both directions at Macrogen (Seoul, South Korea). Sequence chromatograms were edited and checked for quality using Geneious Prime (v. 2023.1.2; https://www.geneious.com). Sequences were deposited in GenBank (GenBank accession numbers listed in Table 1).

New sequences were combined with sequences downloaded from GenBank (originally published by Schäuble et al., 2000). The phylogeny was rooted using two sequences each for *Limnodynastes depressus*, *L. fletcheri*, *L. peronii*, *L. salmini*, and *L. tasmaniensis*. Sequences were aligned using MAFFT (Katoh et al., 2002), implemented in Geneious Prime v. 2023.1.2. A best-fit partitioning model was inferred using ModelFinder (Kalyaanamoorthy et al., 2017) using the IQ-TREE webserver (Trifinopoulos et al., 2016; http://iqtree.cibiv.univie.ac.at), using the Bayes Information Criterion (BIC). Maximum-likelihood phylogenetic analyses were also performed with IQ-TREE with branch support assessed using 1,000 ultrafast bootstrap replicates. We considered branches receiving ≥70% bootstrap support to be well supported following Hillis and Bull (1993).

Net average sequence divergence between lineages (dA) was calculated in MEGA 11 version 11.0.13 (Tamura et al., 2021) as: $d\text{A} = d\text{XY} - (d\text{X} + d\text{Y})/2$, where dXY is the average distance between groups X and Y, and dX and dY are the within-group means.

SNP data filtering.—Samples were submitted to Diversity Arrays Technology (DArT Pty Ltd, Canberra, ACT, Australia) for commercial DNA extraction and DArTseq™ 1.0 genotyping (Kilian et al., 2012). Diversity Arrays Technology uses a combination of genome complexity reduction methods and next generation sequencing platforms. DNA samples were processed in restriction enzyme digestion/ligation reactions using a combination of the *Pst*I/*Sph*I restriction enzymes, and ligated fragments were PCR amplified and sequenced as described by Kilian et al. (2012) and Mahony et al. (2021a, 2021b).

The data were converted to a matrix of SNP loci by individuals, with the contents stored as integers 0, homozygote, reference state; 1, heterozygote; and 2, homozygote for the alternate state. DNA sequences and statistics such as call rate, polymorphic information, heterozygosity, read depth, and reproducibility for all loci and individuals were also reported. Diversity Arrays Technology reports associated with this study include DFr21-6065, DLimno21-6282, and DLimno22-6847.

Due to slight differences in the methods used by Diversity Arrays Technology in the sequencing of each submission, we observed initial biases in the data correlated with each sequence submission. To account for this, we reassembled the short read sequences obtained from Diversity Arrays Technology to reduce any potential adapter contamination using Trimmomatic v0.39 (Bolger et al., 2014) and Stacks v2.62 (Catchen et al., 2013; Rochette et al., 2019). Initially, we used Stacks::process_radtags to remove barcode sequences from each file. We then used Trimmomatic to filter adapter sequences, using the following parameters: ILLUMINACLIP:TruSeq3-SE.fz:2:20:10; LEADING:5, SLIDINGWINDOW:4:5; MINLEN:68; CROP:68. To standardize read lengths among sequencing submissions, we truncated each read to 68 base pairs using the crop parameter as read lengths were far longer in the more recent sequencing submission. Following this, we completed the core Stacks pipeline *de novo*, using mostly default parameters, apart from at the 'ustacks' stage setting 'm' (minimum read depth required to make a stack) to 4, and in the 'cstacks' stage setting 'n' (the number of mismatches allowed between loci of different samples when assembling the loci catalog) to 2, based upon recommendations in Paris et al. (2017). We output a VCF file during the 'populations' process, which was then converted to be compatible with the R package dartR (Gruber et al., 2018) for further analyses.

The SNP data and associated metadata were read into a genlight object (Jombart et al., 2010) to facilitate processing with dartR. Only loci with 100% repeatability (reproducibility) were chosen for subsequent analysis. Further filtering was undertaken based on having a call rate <95% and the locus being present in at least 70% of individuals. We retained only one SNP from each locus at random. Any monomorphic loci arising because of the removal of individuals were also deleted. Given the low within-population sample sizes ($n \leq 15$), we did not filter loci for departures from Hardy-Weinberg equilibrium or linkage disequilibrium.

SNP analyses.—We used several approaches to visualize genetic similarity among individuals and detect potential admixture in the SNP dataset. First, we visualized genetic clusters using the principal coordinates analysis (PCoA) ordination method implemented in the gl.pcoa and gl.pcoa.plot functions of dartR. We used a scree plot of eigenvalues to determine the number of informative PC axes to examine using the gl.pcoa.scree function. We then constructed a phylogenetic representation of the SNP data using the neighbor-joining method (Saitou and Nei, 1987) via the gl.tree.nj function of dartR.

In instances where the SNP data appeared to cluster geographically within a lineage, we tested for isolation by distance (IBD). Most localities were represented by a single individual in our dataset, rendering interpopulation analyses using $F_{ST}/1–F_{ST}$ as the genetic distance measure unreliable. Instead, we calculated an individual-based genetic distance matrix based on the proportion of shared alleles (D_{SA}) between individuals, which has been shown to be a powerful statistic for detecting IBD (Sere et al., 2017). D_{SA} was calculated for individuals with the gl.propShared function of dartR, with log-transformed Euclidean geographic distances calculated between collection localities for individuals in the Mercator projection with the dist function of the stats package in R. We then performed a Mantel test between pairwise geographic and genetic distance matrices via the mantel.randtest function of the adegenet package (Jombart et al., 2010), assessing significance through 999 permutations.

Secondly, we used the Bayesian model-based clustering algorithm implemented in STRUCTURE (Pritchard et al., 2000) to identify population structure and detect admixture. We tested hierarchical support for the lineages identified in the mtDNA and PCoA analyses using a balanced subset of individuals from a spread of the range of each taxon. This was done to minimize bias introduced when using an uneven sample size (i.e., Puechmaille, 2016). STRUCTURE runs were implemented via the gl.run.structure

Table 2. Definition of morphometric traits measured for the *Limnodynastes dorsalis* group. Asterisks indicate characters not defined by Watters et al. (2016).

Abbreviation	Trait	Definition
SVL	Snout–vent length	Direct line distance from tip of snout to posterior margin of vent
HL	Head length	From the posterior of the jaws to the tip of snout
HW	Head width	At the widest point; angle at the jaws
HDD*	Head depth	From posterior edge of eye to directly under jaw
IOD	Interorbital distance	The shortest distance between the anterior corners of the orbits
DFE*	Frontal eye distance	Shortest distance between anterior edge of orbits, closest to snout
IND	Internarial distance	Shortest distance between anterior edge of nostrils
ED	Eye diameter	Horizontally from the anterior to the posterior corner of the eye
SL	Snout length	Distance from the tip of the snout to the anterior corner of the eye
EN	Eye–nostril distance	From anterior corner of the eye to the posterior margin of the nostril
TEY*	Tympanum–eye distance	Shortest distance from posterior corner of eye to the anterior margin of the tympanum
NS	Snout–nostril length	Distance from the center of the external nares to the tip of the snout
TIB	Tibia length	Distance from the outer surface of the flexed knee to the heel/tibiotarsal inflection
FOL*	Foot–heel length	Distance from tip of Toe 4 to heel/tibiotarsal inflection
THL	Thigh length	Distance from the vent to the knee
FL	Foot length	From base of the inner metatarsal tubercle to the tip of Toe 4
IMT	Inner metatarsal tubercle length	The greatest length of the inner metatarsal tubercle
HAL	Hand length	From the base of the outer palmar tubercle to the tip of Finger 3
LAL	Lower arm length	Distance from elbow to the tip of Finger 3
UAL	Upper arm length	From the body to the elbow
AL*	Arm length	From the elbow to the tip of Finger 3
Fin3W*	Finger 3 width	The greatest horizontal distance between edges of Finger 3, measured at the 3rd subarticular tubercle
Toe4W*	Toe 4 width	The greatest horizontal distance between edges of Toe 4, measured at the 3rd subarticular tubercle

function in dartR, using the uncorrelated allele frequency and admixture ancestry models to assess values of K from 1 to 5, performing three independent runs with 20,000 burn-in and then 50,000 MCMC iterations for each value of K. The preferred K value was determined using *L(K)* and the change in the second order of likelihood, Δ*K* (Evanno et al., 2005), obtained using the gl.evanno function. We then ran ten independent runs with the preferred K for 20,000 burnin and 100,000 MCMC iterations and summarized the individual ancestries across all ten runs in CLUMPAK (Kopelman et al., 2015) implemented via the gl.plot.structure function.

We further assessed divergence between clusters identified in the PCoA and STRUCTURE analyses by determining the number of loci showing fixed allelic differences between them. Fixed difference at a locus occurs when two populations share no alleles. When many loci are examined, and sample sizes are finite, fixed differences will occur through sampling error. We used simulations implemented in dartR (Georges et al., 2018) to estimate the expected false positive rate in pairwise comparisons using the gl.fixed.diff. We used tloc = 0.05, meaning that SNP allele frequencies of 95,5 and 5,95 percent were regarded as fixed when comparing two populations at a locus.

Finally, we used the program NewHybrids (Anderson and Thompson, 2002) to identify F_1, F_2, or backcrossed hybrid individuals in the dataset. Two parental lineages were compared per run with parental reference states identified through the PCoA and STRUCTURE clustering. We selected a subset of 200 loci that were most informative in assessing hybridization, namely loci that showed fixed differences between the parental populations, using the "AvgPic" method in the gl.nhybrids function of dartR.

Adult morphology.—We examined preserved specimens held in the AMS collection, including the type series for *Limnodynastes dorsalis* var. *terraereginae*, and all genotyped specimens in the SAMA collection. In addition, we examined the type of *Platyplectrum superciliare* at Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK) and high-resolution images of the type of *Heliorana grayi* held at the Natural History Museum Vienna, Austria (NHMW). We measured 23 morphometric characters (adapted from Watters et al., 2016) with digital calipers to the nearest 0.1 mm (Table 2) and documented variation in a range of external morphological features deemed by preliminary investigation to be potentially diagnostic (i.e., extent of webbing on the hind foot, ventral pattern, and presence/absence of a vertebral stripe), thereby extending our analysis of morphological traits to include poorly preserved specimens for which we were unable to obtain reliable morphometric measurements. Abbreviations for all morphometric traits are listed in Table 2. Sex of adults was determined by directly observing testes and darkened nuptial pads or vocal sacs in males, or ovarian follicles and distended finger spatulae in females.

To compare differences in geometric shape among taxa, we used a multivariate linear discriminant function analysis (DFA). Due to sexual size dimorphism, male and female samples were analyzed independently. Potentially confounding variation associated with differing body sizes and allometric growth was minimized by adjusting measurements to the values they would assume if they were of a mean body size for that sex using the allometric growth equation of Thorpe (1976): $Y_i^* = log_{10}Y_i - b(log_{10}SVL_i - log_{10}SVL_{mean})$, where Y_i^* is the adjusted value for character Y of the ith specimen; Y_i is the raw/unadjusted value for character Y; b is the mean of the

regression coefficients for Y_i against SVL_i estimated independently for each taxon from logarithmically transformed values of Y_i and SVL_i; SVL_i is the measured snout–vent length (SVL) of the *i*th specimen; and SVL_{mean} is the pooled mean SVL.

DFAs were conducted after the measurements had been adjusted for size/growth and log-transformed as described above using the lda function from v7.3-40 of the R package MASS (Venables and Ripley, 2002) in RStudio v 4.2.1. We allocated specimens *a priori* into three "taxa" for the DFA based on individual genotypes or, if genetic data were not available, then based on whether the collection location fell within the geographic distribution of a genetic group. The raw mensural data and DFA results are presented in Supplementary Table S1 (see Data Accessibility). Because the geographical provenance of the holotype of *Platyplectrum superciliare* is uncertain (=Australia), we assigned it to a taxon using the predict function for unknowns in lda.

Advertisement calls.—In-field recordings were made using a Zoom H5 Handy Recorder with a RODE NTG2 shotgun microphone. Acoustic recordings obtained from the FrogID dataset were 20–60 second recordings (MPEG AAC audio file) made using smartphones, with a sampling rate of 44.1 kHz.

Acoustic analyses were conducted using Raven Pro 1.6 (Center for Conservation Bioacoustics, 2019), with a fast-Fourier transformation of 512 points, and 50% overlap. We measured dominant frequency (kHz), call duration (s), and call rate (calls/min) for up to five calls per individual frog, where call rate was calculated using the formula: $\frac{\text{Number of calls } (n)-1}{\text{Sample duration } (s)} \times 60$ (e.g., Mitchell et al., 2020). To visualize the harmonics of each call more accurately, we then used a fast-Fourier transformation of 1,024 points, and 50% overlap to measure fundamental frequency (kHz). Following the definitions of Köhler et al. (2017), dominant frequency refers to the frequency of a call which contains the highest energy, while fundamental frequency refers to the base frequency of a call. We obtained mean values for each call parameter, where the unit of replication was the individual.

Ambient temperature was recorded in the field for the four acoustic recordings taken during fieldwork. As ambient temperature is not recorded in the FrogID app (Rowley et al., 2019), we estimated temperature for all FrogID recordings using historical weather data from the Australian Bureau of Meteorology (BOM). Using the package "chillR" (Luedeling, 2021), we obtained an hourly estimate of temperature based on the minimum and maximum temperatures of the 15 days before and 15 days after each recording was made (e.g., Mitchell et al., 2020). These temperature data were estimated from the BOM weather station closest to each recording. To determine whether the interaction between call parameters and taxonomic lineage was influenced by ambient temperature, we conducted linear regression models.

We assigned taxonomic group based on location and analyzed recordings from genotyped specimens and throughout the core ranges of each lineage. To determine whether call parameters differ among the lineages, we conducted one-way analysis of variance. Given the significant relationship between temperature and fundamental frequency, we conducted a one-way analysis of covariance for fundamental frequency, with ambient temperature as a factor. To test whether differences existed between groups, we conducted pairwise comparisons using Tukey *post hoc* tests of honest significant difference. All statistical analyses were conducted in R (R Core Team, 2020).

Conservation assessments.—Due to an absence of population data, we assessed the conservation status of the lineages redescribed herein using Criterion B of the IUCN Red List guidelines (IUCN Standards and Petitions Committee, 2022) by estimating the geographic range of each taxon through calculation of their area of occupancy (AOO) and extent of occurrence (EOO). Under the IUCN Red List guidelines, to qualify as threatened under Criterion B, taxa must not only meet the minimum distribution threshold (AOO: $<$2,000 km^2, EOO: $<$20,000 km^2) but also at least two of three other conditions, specifically: (a) severely fragmented or number of locations $\leq$10; (b) continuing decline observed, estimated, inferred, or projected in any of: (i) EOO, (ii) AOO, (iii) area extent and/or quality of habitat, (iv) number of locations or subpopulations, (v) number of mature individuals; or (c) extreme fluctuations in any of: (i) EOO, (ii) AOO, (iii) number of locations or subpopulations, (iv) number of mature individuals. Calculations of AOO and EOO were made using the Atlas of Living Australia (ALA) spatial portal (https://www.ala.org.au; accessed online August 2022). For the assessments, we estimated the distribution of each taxon by tracing polygons in QGIS (v. 3.10.9; QGIS.org, 2023) around occurrence records obtained from genotyped specimens, morphologically examined museum specimens, validated acoustic recordings from FrogID, and occurrence records obtained from ALA (accessed August 2022). These distribution polygons were then uploaded into the ALA spatial portal and used as the basis for assessment of AOO (2 $\times$ 2 km grid resolution) and EOO (minimum convex hull).

RESULTS

Mitochondrial DNA.—The sequences in the *ND4* alignment varied from 408 to 715 bp in length. The best-fit nucleotide-substitution model identified was TIM3+F+I+G4. The maximum-likelihood phylogenetic analyses (Fig. 2) provided strong support for two major clades within *Limnodynastes terraereginae sensu lato*, including a lineage restricted to Cape York Peninsula in Far North QLD (hereafter referred to as the CYP lineage) and a widespread lineage (hereafter the WS lineage) covering the remainder of the species range. The WS lineage was further subdivided into northern (mid to north QLD) and southern sub-clades; however, the southern sub-clade did not receive strong bootstrap support. Samples of *L. dumerilii grayi* from eastern coastal NSW (hereafter the EC lineage) formed a highly distinct and well-supported sister lineage to the CYP and WS *L. terraereginae* clades. *Limnodynastes interioris* and *L. dumerilii* (including the subspecies *dumerilii*, *fryi*, *insularis*, and *variegatus*) form a divergent ancestral clade which is closest to the EC lineage, wherein *L. interioris* is the sister sub-clade to the *L. dumerilii* subspecies *dumerilii* and *variegatus*, rendering *L. dumerilii* paraphyletic.

Net average sequence divergence between the CYP, WS, and EC lineages ranged from 4–9% (Table 3). The EC lineage was most divergent, with net sequence divergence of 7% from the WS lineage and 9% from the CYP lineage. Net sequence divergence of the CYP lineage from the northern and southern sub-clades of the WS lineage ranged from 4–5%, with the northern and southern sub-clades only 2% divergent from each other. The CYP lineage is diagnosed by

Fig. 2. Maximum likelihood phylogenetic analyses of the *Limnodynastes dorsalis* group inferred using mitochondrial *ND4* sequences. Tree is rooted with *Limnodynastes fletcheri*, *L. peronii*, *L. depressus*, *L. tasmaniensis*, and *L. salmini*. Dots at nodes indicate bootstrap support values: >95% black dots; 70–95% gray dots. Scale bar represents substitutions/nucleotide site. See Data Accessibility for tree file.

16 apomorphic nucleotide states, WS lineage by 5 diagnostic states, and EC by 17 diagnostic states (Table 4).

SNP analyses.—A total of 12,179 binary SNP loci were scored for 125 individual samples. After filtering by a call rate of 95% and locus presence in at least 70% of individuals, 1,368 SNP loci for 121 individuals remained, with a total of 2.2% missing data across the dataset. Four samples (A005543, EBU115629, EBU115671, and R171924) were removed due to not meeting the call-rate threshold.

In the initial PCoA clustering analysis involving the total SNP dataset, the proportion of variation explained by the PC axes were: 1st axis—40%, 2nd axis—20%, 3rd axis—10%, and 4th axis—4%. Three distinct genetic clusters were present in

Table 3. Net average mitochondrial *ND4* sequence divergence between species of *Limnodynastes*.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14
(1) WS lineage (south)	—													
(2) WS lineage (north)	0.02	—												
(3) CYP lineage	0.04	0.05	—											
(4) EC lineage	0.07	0.07	0.09	—										
(5) *L. d. fryi*	0.10	0.11	0.11	0.11	—									
(6) *L. interioris*	0.10	0.11	0.10	0.10	0.02	—								
(7) *L. d. dumerilii/variegatus*	0.10	0.11	0.11	0.10	0.02	0.00	—							
(8) *L. d. insularis*	0.10	0.10	0.11	0.09	0.04	0.04	0.03	—						
(9) *L. dorsalis*	0.11	0.10	0.10	0.11	0.12	0.11	0.11	0.11	—					
(10) *L. salmini*	0.13	0.12	0.13	0.15	0.15	0.15	0.15	0.15	0.13	—				
(11) *L. fletcheri*	0.17	0.17	0.17	0.18	0.21	0.19	0.19	0.19	0.17	0.13	—			
(12) *L. peronii*	0.20	0.19	0.20	0.18	0.22	0.21	0.21	0.20	0.17	0.14	0.16	—		
(13) *L. depressus*	0.20	0.19	0.21	0.20	0.24	0.23	0.23	0.21	0.21	0.17	0.17	0.18	—	
(14) *L. tasmaniensis*	0.19	0.18	0.17	0.18	0.17	0.18	0.18	0.17	0.16	0.14	0.16	0.16	0.17	—

the PCoA, including: (1) EC lineage; (2) WS/CYP lineages; and (3) *L. interioris* and the *L. dumerilii* subspecies cluster (Fig. 3A). One sample (ABTC142322) appeared to be intermediate between the EC lineage and *L. dumerilii* and was later confirmed by STRUCTURE and NewHybrids to be a backcrossed hybrid. To further examine relationships within the lineages of *L. terraereginae*, we performed a secondary PCoA clustering analysis comparing only the WS ($n = 51$) and CYP ($n = 3$) samples. In this analysis, northern and southern samples of the WS lineage clustered across a continuum which appeared to correspond with geographic distribution (possibly indicating a pattern of IBD), whereas the CYP samples were clearly separated from the WS lineage on both the 1st and 2nd axes of the PCoA (Fig. 3B). To further examine the influence of geographic distance on divergence within the WS lineage, we performed an independent IBD analysis for this group which confirmed a significant (P value = 0.001) linear correlation between geographic and genetic distances matrices for individuals. This suggests that IBD is an important driver of the divergence observed within the WS lineage.

The STRUCTURE analyses of the balanced subset including the CYP, WS, and EC lineages identified K = 3 as the optimal ancestry model. The plot of individual ancestry coefficients, based on K = 3, clustered northern and southern individuals of the WS lineage as a single clade, with the CYP and EC lineages clustering as separate distinct clades (Fig. 3C). The number of loci showing fixed allelic differences between the WS, CYP, and EC lineages ranged from 23–131 (out of 1,574 loci compared; Table 5) and comparisons between each taxa were significant after simulation ($P < 0.001$).

In the neighbor-joining (NJ) analysis of relationships among individuals (Fig. 4), WS, CYP, and EC samples each formed distinct lineages consistent with the SNP clustering findings (Fig. 3) and the relationships among their mtDNA sequences (Fig. 2). In both the mtDNA phylogenetic analysis and the SNP NJ tree, WS and CYP are sister lineages. In the SNP NJ analysis, *L. interioris* is the sister lineage to all the subspecies of *L. dumerilii* which contrasts with the relationships among their mitochondrial DNA sequences wherein *L. interioris* is the sister lineage to only the *dumerilii* and *variegatus* subspecies of *L. dumerilii*.

Admixture analyses.—Our surveys confirmed that the eastern species of the *Limnodynastes dorsalis* group variously occupy allopatric, parapatric, and sympatric distributions throughout their range, with boundaries between species corresponding with shifts in habitat and/or major biogeographic boundaries. We found the WS and CYP lineages to be allopatric over a distance of at least 110 km between the Einasleigh Uplands/Wet Tropics and Cape York Peninsula bioregions in northern QLD with no evidence of admixture between them.

Similarly, the WS and EC lineages appear to be narrowly allopatric in northern NSW. Analyses of the WS–EC subset did not detect admixture, despite inclusion of samples collected within ~70 km between South West Rocks (EC lineage) and Coffs Harbour (WS lineage). Morphologically verified museum specimens indicate that the EC lineage may occur as far north as the Nambucca River, which would reduce the gap between lineages to ~49 km. However, numerous targeted surveys conducted in 2020–2022 failed to locate either species in closer proximity than the samples available to us and so we consider the taxa to be allopatric at present.

In contrast, the WS lineage and *L. dumerilii* were found to be parapatric/sympatric in a variety of ecotonal habitats in northern and western NSW. We did not detect admixture between the subsets of WS–*L. dumerilii*, despite sampling of the lineages from close geographic proximity in north-eastern NSW (~23 km), Northern Tablelands (~15 km), and Central Tablelands region (~40 km).

Admixture was detected between the EC lineage and *L. dumerilii* in samples from an ecotone between the species in the Central Coast region of NSW (Fig. 5). The NewHybrids analyses classified ABTC142322 with 95% posterior probability for being a backcrossed hybrid (Supplementary Table S2; see Data Accessibility). This was the same individual identified in the PCoA and neighbor-joining tree (Fig. 4) as intermediate between the EC lineage and *L. dumerilii*. In addition, the STRUCTURE analyses classified the same individual as admixed and indicated potential admixture in a further six samples from the same region (ABTC140573, ABTC140438, ABTC1175, ABTC25842, ABTC140441, and ABTC140571; Fig. 5). The overall level of hybridization occurring in this area appears to be relatively low given no F_1 or F_2 hybrids were detected, and an additional seven samples collected at the same site or within 32 km of the admixed individuals were classified as pure EC lineage. We also found no further evidence of admixture between the EC lineage and *L. dumerilii* in other regions of NSW where the taxa have been

Table 4. Comparison of 36 apomorphic diagnostic nucleotide states (in bold) for the CYP, WS, and EC lineages compared with other members of the *Limnodynastes dorsalis* group. Site numbers (vertical) reflect position of the site within the *ND4* sequence alignment analyzed.

Species	115	118	120	121	130	160	163	193	205	208	222	225	239	267	274	276	303	306	367	376	388	430	436	442	451	454	475	483	516	519	529	544	623	629	643	675
CYP lineage	**G**	**T**	T	**A**	T	**T**	**T**	T	C/T	T	**C**	G	T	**T**	**A**	A	G	**T**	T	**T**	G	A	A	G	**C**	T	**A**	**A**	**A**	G	**A**	T	**A**	T	G	G
WS lineage	T	G	T	G	T	**T**	G	T	C/G	T	T	G	T	A/T	G	A	G	C/G	T	G	G	**G**	A	G	T	**C**	G	G	G	**A**	G	T	T	T	**A**	G
EC lineage	A	G	**C**	G	**C**	C	G	**C/T**	**T**	**C**	T	**A**	**C**	**C**	G	**G**	**A**	C	**C**	G	**A**	A	**C**	**A**	T	T	G	G	G	G	G	**G**	T	**C**	G	**A**
L. dumerilii (all subspecies)	A/G	G	T	G	T	C	G	T	A	T	T	G	T	T	G	G	G	A/G	T/C	G	G	A	A	G	T	T	G	G	G	G	G	T	T	T	G	G
L. interioris	G	G	T	G	T	C	G	T	A	T	T	G	T	T	G	G	G	A	T	G	G	A	A	G	T	T	G	G	G	G	G	T	T	T	G	G
L. dorsalis	—	—	—	—	—	—	G	T	C	T	T	G	T	T	G	G	G	T	C	G	G	A	G	G	T	T	G	G	G	G	G	T	—	—	—	—

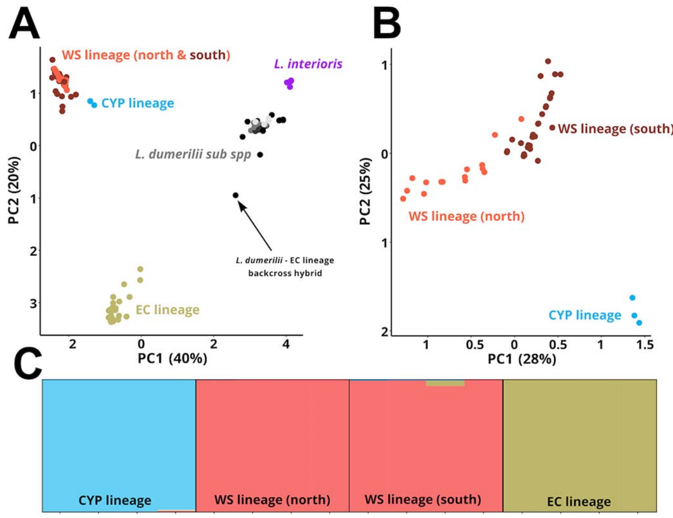

Fig. 3. Results of clustering analyses of SNP data for the eastern *Limnodynastes dorsalis* group: (A) initial PCoA ordination with representative samples of all eastern *Limnodynastes dorsalis* group members, (B) PCoA of CYP and WS lineages only, (C) STRUCTURE barplot for a balanced subset of individuals showing preference for K = 3 ancestry model.

suspected previously to hybridize (Martin, 1972). This included samples of each lineage collected within a straight-line distance of 40 km in southern Sydney, and 17 km in the Blue Mountains across an elevational transition of 404 m.

***Adult morphology*.**—There was substantial variation in overall size among the taxa (Fig. 6; Table 6), with the CYP lineage tending to be largest, EC lineage the smallest, and the WS lineage generally falling into a size class between the two (Fig. 6). We therefore relied on analyses of the SVL-corrected morphological measurements to detect variation in overall geometric shape among the taxa. The DFAs for males and females each returned two linear discriminant functions (LD), with the majority of variation explained by LD1 (88% for males and 74% for females; Fig. 7). For males ($n = 94$), the overall predictive accuracy was 0.88, while the overall predictive accuracy for females ($n = 51$) was 0.92. For males, the traits with the highest coefficients for each of the two linear discriminants were for LD1: PL, SL, and Toe4W and for LD2: SVL and TEY. For females, the traits with the highest coefficients for each of the two linear discriminants were for LD1: UAL, AL, and TEY, and for LD2: HDD and FOL. Finally, the holotype for *Platyplectrum superciliare* (ZFMK 28331) was assigned by the DFA to the EC lineage morphogroup with a posterior probability of 0.99.

Table 5. Numbers of loci with fixed allelic differences between lineages. Above diagonal: number of loci showing a fixed difference; below diagonal: expected count of false positives for each comparison, by simulation. Pairwise comparisons were based on 1,368 loci for WS and EC lineages and 1,327 for the CYP lineage. Values in bold were significant after simulation. Values in parentheses denote sample size per clade included in the pairwise comparisons.

Taxon	1	2	3	4
1. WS lineage north (18)	—	1	**35**	**90**
2. WS lineage south (32)	1.6	—	**23**	**45**
3. CYP lineage (3)	11.3	3.9	—	**131**
4. EC lineage (28)	20.2	11.6	11.1	—

Advertisement calls.—We analyzed the advertisement calls of 65 individual male banjo frogs (Table 7): WS lineage ($n = 41$), EC lineage ($n = 19$), and CYP lineage ($n = 5$). Ambient temperature was not significantly correlated with dominant frequency ($R^2 = 0.30$, $P = 0.31$), call duration ($R^2 = 0.10$, $P = 0.72$), or call rate ($R^2 = 0.01$, $P = 0.33$), although a positive relationship existed with fundamental frequency ($R^2 = 0.22$, $P = 0.02$). The advertisement calls of each species were similar, with considerable overlap in the measured call parameters (Figs. 8, 9; Table 7). While dominant frequency ($F_{2,62} = 14.44$, $P < 0.001$), call duration ($F_{2,62} = 5.78$, $P = 0.005$), and fundamental frequency ($F_{2,62} = 7.00$, $P = 0.02$) differed significantly among taxa, call rate did not differ significantly ($F_{2,62} = 1.17$, $P = 0.331$).

The advertisement call of the EC lineage was most distinct from the other taxa (Figs. 8, 9; Table 7), with both a significantly higher dominant frequency and fundamental frequency than the WS lineage (dominant frequency—$P < 0.001$; fundamental frequency—$P = 0.003$) and CYP lineage (dominant frequency—$P = 0.003$; fundamental frequency—$P = 0.030$). While both the dominant and fundamental frequencies of CYP lineage calls were marginally lower than those of the WS lineage (dominant frequency—$P = 0.784$; fundamental frequency—$P = 0.741$), these differences were not significant. Calls of the EC lineage were shorter in average duration than both the WS lineage ($P = 0.025$) and CYP lineage ($P = 0.012$). The call durations of the CYP lineage were only marginally longer than the WS lineage ($P = 0.273$). We observed no differences between the advertisement calls of the northern and southern mitochondrial sub-clades of the WS lineage, with respect to dominant frequency ($P = 0.909$), call duration ($P = 1.000$), and fundamental frequency ($P = 0.556$), although the northern clade did call at a faster rate than the southern clade ($P = 0.007$).

Systematic implications.—Based on broad congruence between our datasets, we conclude that the WS, CYP, and EC lineages warrant recognition as distinct species under the evolutionary species concept (*sensu* de Queiroz, 1998, 2007). Our evidence for lineage separation is based on the following operational criteria:

Monophyly: Our analyses of sequences of the mitochondrial *ND4* gene reveal the presence of three, well-supported, reciprocally monophyletic mitochondrial groups (Fig. 2), with a level of sequence divergence of 4–11% between lineages (Table 3), comparable to other limnodynastid and myobatrachid species groups such as *Heleioporus* (4–22%, Mahony et al., 2021b), *Philoria* (5–15%, Mahony et al., 2022), and *Assa* (6%, Mahony et al., 2021a). Our analyses of the SNP dataset revealed consistent clustering of samples in both the PCoA ordination, neighbor-joining tree, and Bayesian methods (Figs. 3, 4), with the SNP clusters corresponding fully to the lineages observed in the *ND4* phylogeny.

Reproductive isolation: Representative sampling across the range of each proposed taxon identified deep genetic breaks among the lineages across relatively short geographic distances. Interactions among the taxa can be variously characterized as allopatric, parapatric, and sympatric. Low levels of admixture were detected at an ecotone between the parapatric EC lineage and *Limnodynastes dumerilii* (Fig. 5), suggesting occasional hybridization between these non-sister species occurs. We suspect hybridization occurs due to accidental mismating following the sporadic migration of individuals between otherwise discrete habitats.

Diagnosability: The lineages are diagnosable based on a combination of: a) a range of external morphological features (i.e., adult body size, extent of foot webbing [Fig. 10] and aspects of color/pattern); b) differences in geometric shape as identified in the linear discriminant function analyses (Fig. 7); c) differences in the male advertisement call (i.e., dominant frequency, call duration), particularly between the EC lineage and other taxa; and d) 5–17 apomorphic nucleotide character states (Table 4) and fixed allelic differences at significant numbers of SNP loci (Table 5).

Nomenclatural implications.—To resolve long-standing confusion surrounding the provenance and identity of the holotypes of *Heliorana grayi* and *Platyplectrum superciliare* we examined the type specimens and GMS investigated their provenance. We briefly discuss the nomenclatural implications of our findings below and provide a more detailed summary of the provenance of the type specimens in Appendix 1.

Provenance of the *Heliorana grayi* type: The collection locality for the *Heliorana grayi* type (NHMW 4695) was initially vaguely specified by Steindachner (1867) as *Neu-Süd-Wales* (i.e., NSW). Inspection of the NHMW type catalogue and an investigation into the provenance of the type specimen (see Appendix 1) has since revealed the true collection locality for the type of *Heliorana grayi* to be Rockhampton, QLD (Häupl and Tiedemann, 1978; Gemel et al., 2019).

Without examining the type, authors of subsequent taxonomic revisions (i.e., Parker, 1940; Martin, 1972) were led to assume that the type of *Heliorana grayi* was collected in NSW and thus incorrectly referred the name *Limnodynastes* (*dorsalis*) *dumerilii grayi* to the distinctive population of frogs occurring in eastern coastal NSW (here referred to as the EC lineage). Our examination of high-resolution images of the type of *Heliorana grayi* confirmed that the specimen corresponds in morphology (medium-large size, robust build, moderate foot webbing, and aspects of dorsal color/pattern) with genotyped specimens of the WS lineage which occurs in Rockhampton, and we therefore correctly apply the name *Limnodynastes grayi* to this taxon.

The original collection locality for the type of *Platyplectrum superciliare* (ZFMK 28331) was even more vaguely stated by Keferstein (1867) as *Australien* (i.e., Australia). Based on the investigation into the provenance of the type specimen (see Appendix 1), the results of the group assignment by the DFA, and the presence of several consistent diagnostic morphological features (i.e., small size, vestigial foot webbing [Fig. 10] and aspects of dorsal and ventral color/pattern [Fig. 11]), we conclude that the type specimen of *Platyplectrum superciliare* represents the distinctive EC lineage currently incorrectly referred to as *Limnodynastes dumerilii grayi*. We hereby apply the name *Limnodynastes superciliaris* to this taxon.

Notes on the *Limnodynastes dorsalis* var. *terrae-reginae* type series: There is no conjecture over the original collection locality of the *Limnodynastes dorsalis* var. *terrae-reginae* type (AMS R.4525, Somerset, Cape York Peninsula, QLD). Our examination of the holotype confirmed it corresponds in morphology (large size, moderate foot webbing [Fig. 10]; aspects of color/pattern [Fig. 11]) with genotyped individuals

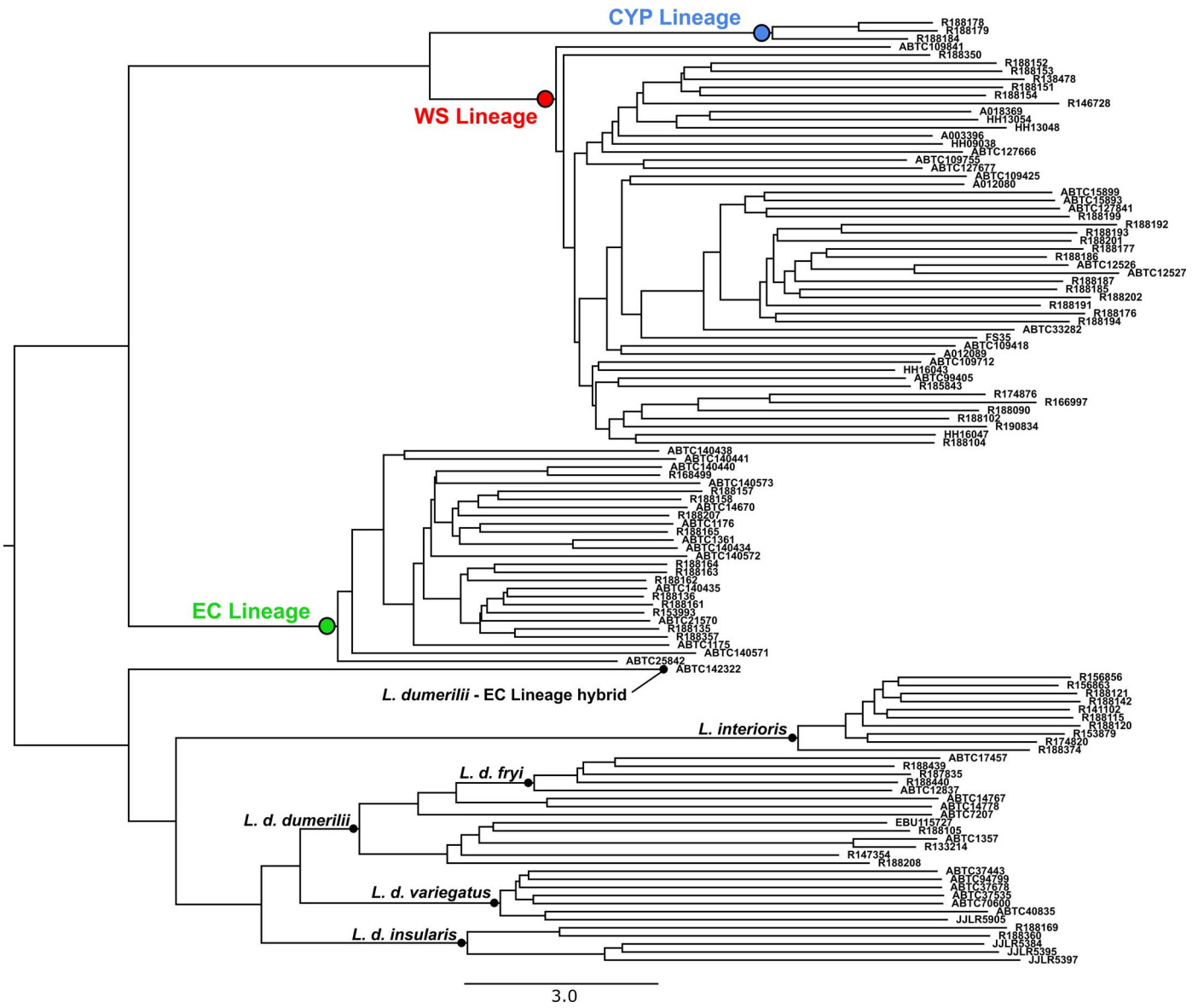

Fig. 4. Neighbor-joining tree based on analyses of the SNP dataset for the eastern *Limnodynastes dorsalis* group. Scale bar represents substitutions/site. See Data Accessibility for tree file.

of the CYP lineage and so we apply the name *Limnodynastes terraereginae* to the distinctive lineage of banjo frogs restricted to the Cape York Peninsula bioregion. Of an additional 57 paratypes held in the Australian Museum, we consider only one (AMS R.4526, Somerset, Cape York Peninsula, QLD) represents true *L. terraereginae*. The remaining paratypes, collected around Eidsvold in the Upper Burnett River region of mid-eastern QLD, can be assigned to *L. grayi* on the basis of size, aspects of color/pattern, and proximity to genotyped samples.

Taxonomy.—An updated diagnostic key to the species of the eastern Australian *Limnodynastes dorsalis* group is provided below.

KEY TO THE SPECIES OF THE EASTERN *LIMNODYNASTES DORSALIS* GROUP

1a. Scarlet or magenta patches present in inguinal region and/or legs; webbing vestigial to moderately developed (Fig. 10); ventral surface plain, unpatterned (Fig. 11, A or B) 2

1b. Scarlet or magenta patches absent from inguinal region and legs 3

2a. Large size (65–94 mm); magenta suffusions in inguinal region and/or legs; dorsal pattern usually consisting of irregular dark blotches; advertisement call with a moderately high dominant frequency (0.6–1.1 kHz, mean 0.8 kHz); restricted to Cape York Peninsula bioregion ..... ***L. terraereginae***

2b. Medium to large size (47–78 mm); scarlet suffusions in inguinal region and/or legs; dorsal surface usually dark and mostly plain, sometimes with faint irregular spots or blotches; advertisement call with a moderately high dominant frequency (0.6–1.3 kHz, mean 0.9 kHz) ..... ***L. grayi***

3a. Small size (34–63 mm); webbing vestigial (Fig. 10, C); ventral surface plain, unpatterned pearl-cream (Fig. 11, C); advertisement call of a high dominant

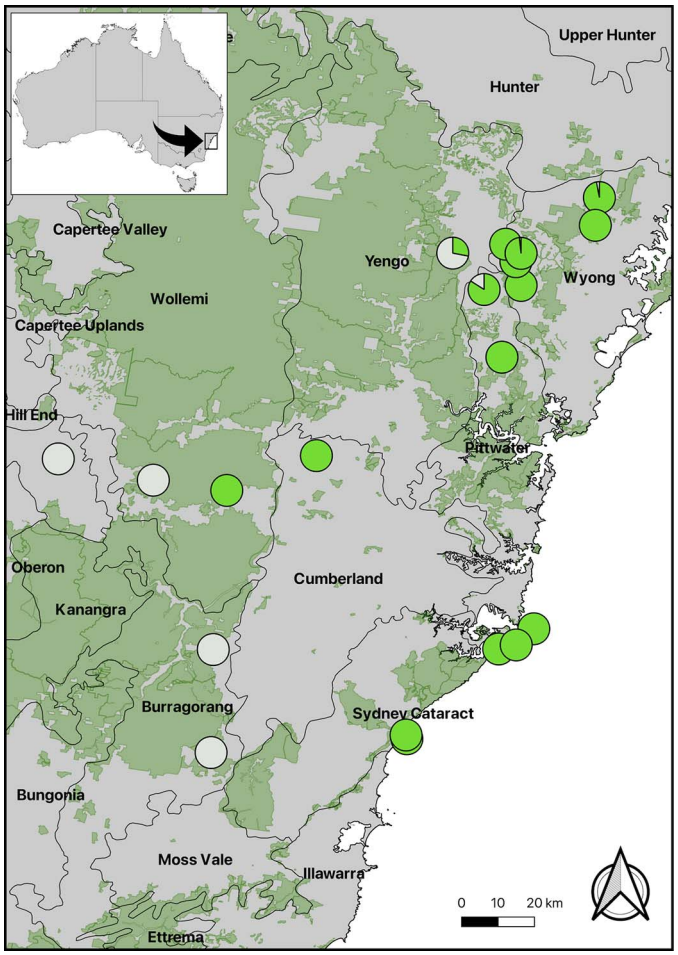

Fig. 5. Map of sampled contact zones between the EC lineage (green) and *L. dumerilii* (gray), with STRUCTURE ancestry proportions for individuals indicated in pie charts. Labeled polygons are IBRA7 major biogeographic subregions.

frequency (0.5–1.5 kHz, mean 1.2 kHz) and short duration (0.04–0.12 s, mean 0.07 s); restricted to sandy habitats of the Sydney Basin and North Coast bioregion ..... ***L. superciliaris***

3b. Medium to large size (46–92 mm); webbing moderate to well developed, rarely vestigial (Fig. 10); ventral surface with dark mottling/reticulations or is plain yellow-cream (Fig. 11, D, E, or F); advertisement call of low dominant frequency (0.2–1.2 kHz) 4

4a. Medium to large size (46–74 mm); webbing usually moderately developed (Fig. 10, B), sometimes well developed, rarely vestigial; ventral surface usually with dark mottling or reticulations (Fig. 11, D or E); dorsal surface plain and unpatterned or with weak irregular spots or blotches; advertisement call of low dominant frequency (0.4–1.2 kHz, mean 0.6 kHz) ..... ***L. dumerilii***

4b. Large size (64–92 mm); webbing well developed (Fig 10, A); ventral surface typically yellow or cream and unpatterned, sometimes lightly marked with dark spots or blotches (Fig. 11, F); dorsal pattern either consists of irregular dark spots and blotches or is plain and unpatterned; advertisement call of a very low dominant frequency (0.2–0.5 kHz, mean 0.3 kHz); restricted to the semi-arid plains of mid-western NSW to northern Victoria ..... ***L. interioris***

Limnodynastes grayi (Steindachner, 1867)

Figures 12, 13

Suggested common name: Scarlet-sided Banjo Frog

Holotype.—NHMW 4695 (adult male) collected in the vicinity of Rockhampton, Queensland (previously stated as Neu-Süd-Wales = NSW in the original description). Presumably collected by German natural history collector Eduard Dämel in 1866 (see Appendix 1).

Material examined.—*Heliorana grayi* type examined from high-resolution images. For full list of specimens examined in morphometric analyses see Supplementary Table S1 (see Data Accessibility).

Revised diagnosis.—*Limnodynastes grayi* is diagnosed from all species in the *L. dorsalis* group by a combination of: (1) medium-large adult body size (SVL for males 47–78 mm; females 55–75 mm), (2) robust build, (3) vestigial-moderate webbing trace on the feet (Fig. 10), (4) the presence of scarlet suffusions in the groin, (5) pale and immaculate ventral surface (Fig. 11B), (6) advertisement call with a moderately high dominant frequency (0.6–1.3 kHz, mean 0.9 kHz), and (7) genetically by five apomorphic nucleotide states on the *ND4* gene (Table 4).

Redescription of the holotype.—We redescribe the holotype based on high-resolution images of the preserved specimen after more than 155 years in preservative. Habitus stout and robust. Dorsum and ventral surface smooth. Head large, broadest at tympanum and wider than long. Head appears rounded from above and largely flat in profile, sloping more steeply at snout. Nostrils slightly raised and forward-facing. Tympanum indistinct. Subaural gland distinct and extending from below eye to above shoulder. Eyes large and concealed. Arms and legs relatively short and powerfully built, tibial gland prominent, oval-shaped and approximately 56% the length of tibia. Four fingers and five toes, all rounded, and tapering without terminal discs. Webbing on fingers absent but moderately developed on toes (Fig. 10). Subarticular tubercles prominent on fingers and toes, metacarpal tubercles prominent, inner-metatarsal tubercle also prominent, wedge-shaped and approximately the same length as the first toe. Soles of feet smoothly textured.

Color in preservative.—Uniform dark brown dorsally without patterning, transitioning to stippled cream-yellow laterally and completely plain cream-yellow ventrally. Prominent cream-yellow subaural gland and pale raised spots around cloaca and posterior edge of thighs.

Variation.—A summary of variation in morphometric characters for each sex is presented in Table 6 and Figure 6.

Color and pattern variation (in life).—Variation in color is described from images of genotyped specimens taken in life. Ventral surface plain, unpatterned translucent pearl to cream, sometimes edged with gray, cream, yellow, or orange. Vocal sac often darker and mottled in males. Dorsal surface plain brown to gray sometimes with dark or light blotches and

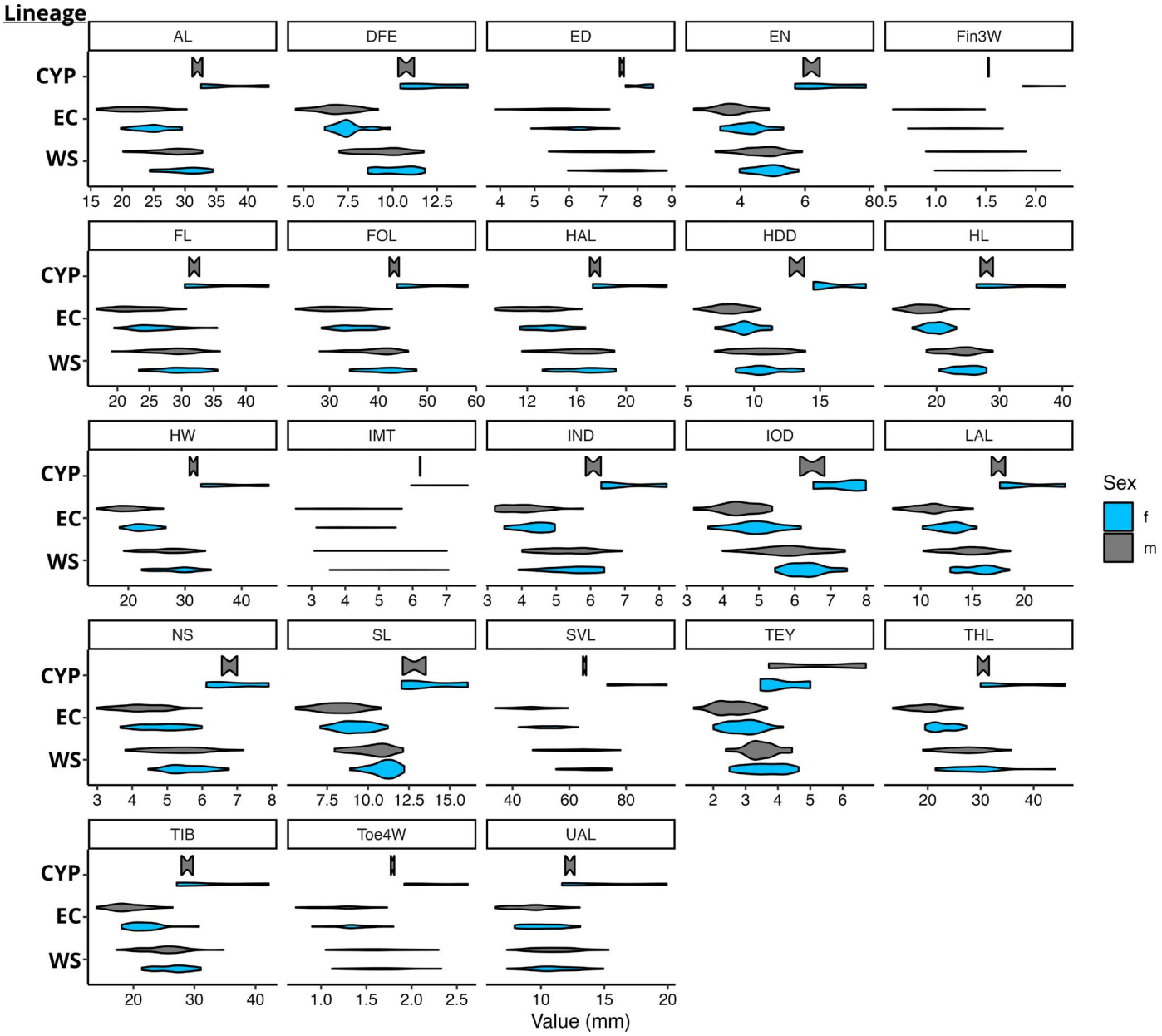

Fig. 6. Comparison of morphological measurements between adult specimens of the *Limnodynastes dorsalis* group lineages redescribed herein.

mottling. Orange-yellow vertebral stripe may be distinct, broken, faded, or absent. Lateral zone gray with yellow, orange, scarlet, black, or white mottling, reticulations, or stippling. Scarlet patches or mottling usually present in the inguinal region, upper thigh, and medial tibia. Posterior thigh flash black with gray-scarlet mottling or blotching becoming lighter toward anterior edge of thigh. Soles of feet brown-gray and with black, white, gray speckling and yellow stripe on lateral edge of foot. Shoulders with yellow-orange patch and remaining arm gray and mottled with black or white. Hands lighter white, cream, or gray. Prominent yellow-cream subaural gland with darker gray, black, or brown stripe running from rostrum, through eye to edge of subaural gland.

Advertisement calls.—The advertisement call description of *L. grayi* is based on the calls of 41 individuals sampled throughout the species' distribution, including the holotype locality (Rockhampton, QLD). The advertisement call consists of a single, resonant note. Individuals had a mean dominant frequency of 0.6–1.3 kHz, and a mean fundamental frequency of 0.4–0.7 kHz. On average, advertisement calls had a duration of 0.05–0.14 s (Table 7; Fig. 8).

Distribution.—Widely distributed across an area spanning approximately 550,000 km^2 from central western NSW to northern QLD. In the southernmost extent of its range, *L. grayi* is absent largely from higher altitude areas of the Great Dividing Range (GDR), occurring mostly on the slopes and plains to the west, as far south as Tomingley, Central West NSW. East of the GDR, *L. grayi* extends as far south as Coffs Harbour on the north coast. In QLD, *L. grayi* occurs throughout south-eastern coastal regions including several islands (i.e., Fraser, Moreton, Stradbroke, and Whitsunday Islands), extending continuously along the coast up to Bowen. In north QLD, *L. grayi* primarily occurs in upland

Table 6. Summary of metric variation (mean ± SD, and range in mm) for 23 morphometric traits between members of the *Limnodynastes dorsalis* group lineages redescribed herein. Sample size in parentheses beside sex (m or f).

	WS lineage		EC lineage		CYP lineage	
Trait	f (30)	m (63)	f (31)	m (53)	f (3)	m (2)
SVL	66.8±5.9	61.7±7.4	52.8±4.9	46.4±5.6	81.1±11.5	65.4±0.8
	55.3–74.9	47.1–78.0	42.1–63.2	33.7–59.6	73.4–94.4	64.8–66.0
AL	30.1±2.9	28.2±3.0	24.9±2.5	21.9±3.2	36.2±6.2	32.0±1.1
	24.4–34.4	20.2–32.8	19.8–29.5	15.9–30.3	32.6–43.3	31.2–32.8
DFE	10.2±1.0	9.4±1.2	7.5±0.8	6.9±1.0	12.1±1.9	10.8±0.6
	8.6–11.8	7.0–11.7	6.2–9.9	4.6–9.2	10.4–14.2	10.3–11.2
ED	7.6±0.7	7.2±0.7	6.2±0.6	5.7±0.7	8.1±0.4	7.5±0.1
	6.0–8.9	5.4–8.5	4.9–7.5	3.8–7.2	7.7–8.5	7.5–7.6
EN	4.9±0.5	4.7±0.6	4.2±0.5	3.7±0.5	6.7±1.1	6.2±0.4
	4.0–5.8	3.2–5.9	3.4–5.3	2.6–4.9	5.7–7.9	6.0–6.5
Fin3W	1.5±0.3	1.4±0.3	1.2±0.2	1.0±0.2	2.0±0.2	1.5±0.0
	1.0–2.2	0.9–1.9	0.7–1.7	0.6–1.5	1.9–2.3	1.5–1.5
FL	29.9±3.1	28.7±3.1	25.7±3.3	22.7±3.2	35.0±7.4	32.0±1.2
	23.3–35.6	19.1–36.0	19.5–35.6	16.8–30.7	30.5–43.6	31.1–32.8
FOL	41.2±3.8	39.6±3.9	35.1±3.5	31.4±4.3	48.9±8.2	43.2±1.4
	34.1–47.8	27.9–46.1	28.4–42.2	23.1–42.8	43.9–58.3	42.2–44.2
HAL	16.6±1.7	16.0±1.8	13.8±1.5	12.3±1.7	19.4±3.4	17.5±0.6
	13.2–19.2	11.6–19.1	11.4–16.7	9.4–16.4	17.3–23.3	17.1–17.9
HDD	10.8±1.5	10.5±1.6	9.3±1.1	8.2±1.1	15.9±2.3	13.3±0.8
	8.6–13.8	7.0–13.9	7.1–11.4	5.5–10.5	14.5–18.5	12.7–13.8
HL	24.8±2.0	23.5±2.7	19.8±1.7	17.8±2.3	32.1±7.4	27.9±1.4
	20.4–27.9	18.4–28.9	16.1–23.1	13.0–25.2	26.4–40.4	26.9–29.0
HW	28.6±3.2	26.9±3.3	22.5±1.9	19.7±2.5	37.7±6.3	31.5±1.0
	22.4–34.6	19.2–33.6	18.5–26.6	14.4–26.2	32.9–44.8	30.8–32.2
IMT	5.6±0.9	5.5±0.8	4.1±0.6	3.7±0.6	6.8±0.8	6.2±0.0
	3.5–7.1	3.1–7.0	3.1–5.5	2.5–5.7	6.0–7.6	6.2–6.2
IND	5.5±0.7	5.3±0.7	4.4±0.43	4.0±0.6	7.0±1.1	6.1±0.3
	3.9–6.4	4.0–6.9	3.5–5.0	3.2–5.8	6.3–8.2	5.9–6.3
IOD	6.3±0.5	5.8±0.8	4.9±0.6	4.5±0.5	7.3±0.8	6.5±0.5
	5.5–7.5	4.0–7.4	3.6–6.2	3.2–5.4	6.5–8.0	6.1–6.8
LAL	15.5±1.6	14.6±1.9	12.8±1.3	11.0±1.6	19.9±3.5	17.5±0.9
	12.9–18.6	10.3–18.7	10.2–15.4	7.3–15.1	17.7–23.9	16.8–18.2
NS	5.6±0.5	5.3±0.7	4.9±0.6	4.3±0.6	6.9±0.9	6.8±0.3
	4.5–6.8	3.8–7.2	3.7–6.0	3.0–6.0	6.1–7.9	6.6–7.0
SL	11.0±0.8	10.3±1.1	9.2±1.0	8.12±1.2	13.7±2.1	12.8±1.0
	8.9–12.2	78.0–12.1	7.1–11.2	5.6–10.8	12.1–16.1	12.1–13.5
TEY	3.6±0.6	3.5±0.5	2.9±0.5	2.6±0.5	4.1±0.8	5.2±2.1
	2.5–4.6	2.4–4.4	2.0–4.2	1.4–3.7	3.5–5.0	3.7–6.7
THL	28.6±4.5	27.0±3.5	22.9±2.3	19.9±3.1	35.4±9.1	30.5±1.5
	21.5–44.0	19.1–35.8	19.5–27.3	13.4–26.7	30.0–45.9	29.4–31.6
TIB	26.4±2.8	24.9±3.1	21.6±2.5	19.0±2.7	32.7±8.3	28.8±1.3
	21.4–31.0	17.2–34.8	18.1–30.7	14.0–26.4	27.1–42.2	27.9–29.7
Toe4W	1.6±0.3	1.6±0.3	1.4±0.2	1.2±0.2	2.2±0.4	1.8±0.0
	1.1–2.3	1.1–2.3	0.9–1.8	0.7–1.7	1.9–2.6	1.8–1.8
UAL	11.0±1.7	11.0±1.6	10.1±1.5	9.1±1.5	14.8±4.5	12.3±0.5
	7.3–14.9	7.3–15.3	7.9–13.1	6.4–13.1	11.7–19.9	11.9–12.7

areas such as the Atherton Tablelands, Hervey and Paluma Ranges, with the northernmost extent of its range appearing to be the western edge of the Carbine Uplands. The range of *L. grayi* also extends into inland QLD as far as Mungalalla in the south, and Carnarvon National Park, Torrens Creek, up to Blackbraes and Undara National Parks in the north.

Habitat.—Occurs in a variety of habitats including sclerophyll and open woodland, Melaleuca wetlands, brigalow, coastal heathland, urban, and agricultural areas. Usually found in association with sandy and sometimes granitic substrates, basalt plains, sandstone hills, and plains.

Conservation status.—Given its substantially widespread distribution (>550,000 km^2) and lack of evidence for population fragmentation or decline, *L. grayi* likely qualifies for the listing of Least Concern under the IUCN Red List Criteria (IUCN Standards and Petitions Committee, 2022).

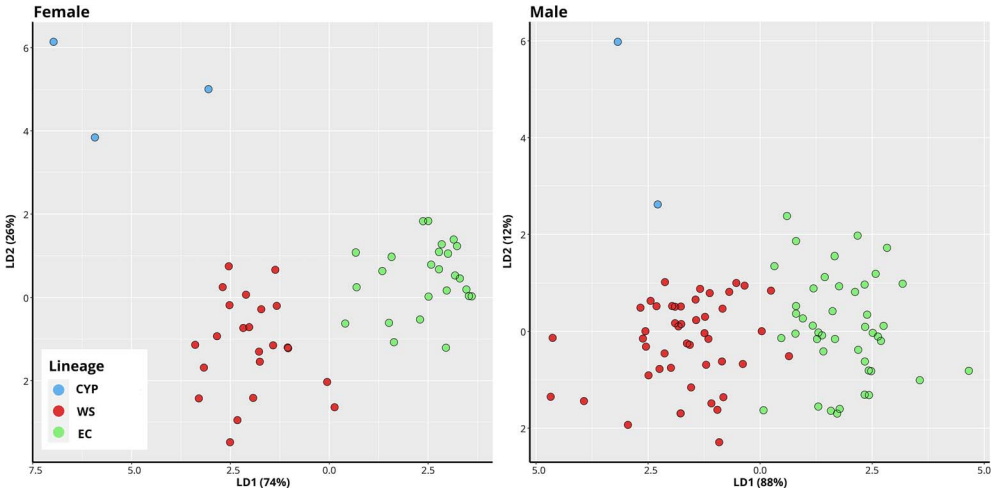

Fig. 7. Linear discriminant function analysis (DFA) scatterplot of adult morphometric characters for specimens of the *Limnodynastes dorsalis* group lineages redescribed herein.

Ecology.—Breeding occurs in static or slow-flowing aquatic habitats such as ponds, dams, road-side ditches, swamps, and wallums (Anstis, 2017; T. Parkin, pers. obs.). Males typically call from concealed positions amongst vegetation or floating in water. According to FrogID data, the species is most often recorded calling from dams, ponds, and flooded areas, particularly within rural and natural landscapes. The male calling period is from November to February, with some calling activity in September, October, and March. Tadpole development detailed by Davies (1992) and Anstis (2017). Tadpoles are highly acid-tolerant, withstanding a range from circumneutral–pH 3.0 (Hines and Meyer, 2011; Hird et al., 2022).

Limnodynastes superciliaris (Keferstein, 1867)

Figures 14, 15

Suggested common name: Coastal Banjo Frog

Holotype.—ZFMK28331 (adult male), type locality originally stated as Australien (=Australia). Most likely collected from the environs of Sydney between 1857–1862 by German natural history collector Bernhard Rudolf Schütte (see Appendix 1).

Material examined.—See Supplementary Table S1 (see Data Accessibility) for full list of specimens used in morphometric analyses.

Holotype measurements (mm).—SVL 44.9; FOL 27.8; TIB 16.9; THL 16.8; HW 19.7; IOD 4.4; DFE 6.9; IND 4.1; NS 4.3; EN 3.3; ED 5.4; HDD 8.3; SL 7.6; HL 15.9; UAL 7.6; LAL 8.4; HAL 10.3; AL 26.3; FL 20.5; IMT 3.4; TEY 1.4; Fin3W 0.9; Toe4W 1.2.

Revised diagnosis.—*Limnodynastes superciliaris* can be diagnosed from all other species in the *L. dorsalis* group by the combination of: (1) relatively small adult body size (SVL for males 34–60 mm; females 42–63 mm), (2) moderately robust build, (3) vestigial webbing trace on the hind foot (i.e., webbing does not extend beyond, or only slightly extends beyond, the first subarticular tubercle on the first toe [Fig. 10C]), (4) pale and immaculate, almost translucent, ventral surface (Fig. 11C), (5) lacks scarlet suffusions in the groin, (6) advertisement call of a high dominant frequency (0.5–1.5 kHz, mean 1.2 kHz) and short duration (0.04–0.12 s, mean 0.07 s), and (7) genetically by 17 apomorphic character states on the *ND4* gene (Table 4).

Redescription of holotype.—Described from high-resolution images of the preserved specimen after more than 158 years in preservative. Habitus moderately stout and robust. Dorsum and ventral surface smooth. Head large, broadest at tympanum and wider than long. Head appears rounded from above and largely flat in profile, sloping abruptly at the snout. Nostrils are slightly raised and outward-facing. Eyes large and concealed, tympanum indistinct. Arms and legs short and moderately slender, tibial gland prominent, oval-shaped and approximately 60% length of tibia. Four fingers and five toes, all rounded, slender and tapering without terminal discs. Webbing on fingers absent and reduced to a vestigial trace on toes (Fig. 10), no trace of a distended spatula on 2nd finger, indicating specimen is male. Subarticular tubercles prominent on fingers and toes, metacarpal tubercles prominent, inner-metatarsal tubercle also prominent, wedge-shaped and slightly longer than the first toe. Soles of feet smoothly textured. Many small, raised tubercles of varying sizes scattered on posterior edge of thighs and cloaca.

Color in preservative.—Dorsal surface medium brown with a mosaic of lighter and darker brown, cream or yellow para-

Table 7. Summary of advertisement call data for members of the *Limnodynastes dorsalis* group lineages redescribed herein, expressed as means ± standard deviation and the range of values for each taxon.

Taxon	*n*	Dominant frequency (kHz)	Call duration (s)	Call rate (calls/min)	Fundamental frequency (kHz)
CYP lineage	5	0.8±0.2 (0.6–1.1)	0.10±0.014 (0.08–0.12)	38.15±25.18 (12.72–72.06)	0.5±0 (0.5–0.6)
WS lineage	41	0.9±0.2 (0.6–1.3)	0.09±0.02 (0.05–0.14)	31.58±20.54 (4.74–89.67)	0.6±0.1 (0.4–0.7)
EC lineage	19	1.2±0.3 (0.5–1.5)	0.07±0.03 (0.04–0.12)	23.69±17.25 (5.36–75.52)	0.6±0.1 (0.5–0.8)

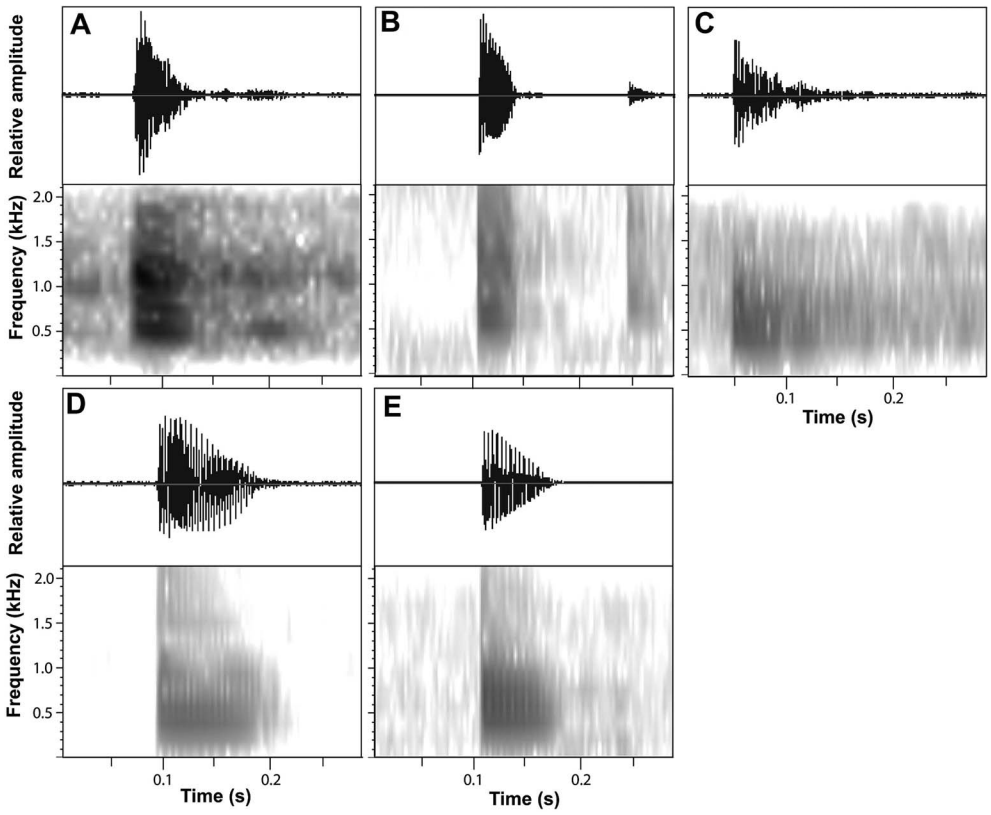

Fig. 8. Comparison of the male advertisement calls of (A) WS lineage—Rockhampton, QLD (FrogID 312613), (B) EC lineage—Harrington, NSW (AMS R.188164), (C) CYP lineage—Finch Bay, Cooktown, QLD (QM J97862), (D) *Limnodynastes dumerilii dumerilii*—Tenterfield Creek, NSW (AMS R.188096), and (E) *L. interioris*—Narrandera, NSW (FrogID 276467). Audiospectrograms and oscillograms were produced in Raven Pro 1.6 with a fast-Fourier transformation of 512 points, and 50% overlap.

vertebral lines, blotches, and spots. Distinct light cream-yellow vertebral stripe. Pattern transitions to a complex light cream-yellow and dark brown stippling on lateral surface and then completely pale cream, almost translucent on the ventral surface. Prominent cream subaural gland running from below eye to shoulder, with broad dark brown band running through eye. Upper surface of arms and legs consists of complex pattern of light and dark brown, cream-yellow blotches and spots, tending darkest inside the thigh. Posterior edge of forearm with cream stripe. Lower surface of arms and legs pale cream, almost translucent. Raised tubercles around cloaca and posterior edge of thighs, cream-yellow. Slightly darkened throat pigment indicating the specimen is male.

Variation.—Summary of variation in morphometric characters for each sex is presented in Table 6 and Figure 5.

Color and pattern variation (in life).—Variation in color is described from images of genotyped specimens taken in life. Ventral surface plain, unpatterned cream anteriorly to translucent pearl posteriorly. Vocal sac often darker yellow-brown and mottled in males. Distinct scarlet patches absent from inguinal region and legs. Dorsal surface dark to light brown with rose-gold or crimson tinge, often with longitudinally aligned paravertebral stripes blotches or mottling. Red-light brown vertebral stripe present and distinct, broken, faded, or absent. Lateral zone light brown fading to cream-white ventrally with transition often marked by a zone of gray, black, and yellow, or cream spots and mottling. Posterior thigh flash black with gray, cream, yellow or orange mottling or blotching. Soles of feet light to dark brown with gray or cream speckling. Lateral edge of foot with yellow to brown cream stripe. Shoulders with yellow, cream, brown, or gold patch, forearm darker gray or brown and usually mottled. Light brown, cream, or gold subaural gland with dark gray to black stripe above extending from rostrum through eye to edge of subaural gland.

Advertisement call.—The advertisement call description of *L. superciliaris* is based on the calls of 19 individuals from the Sydney Basin bioregion. The advertisement call consists of a single, resonant note. Individuals had a mean dominant frequency of 0.5–1.5 kHz, and a mean fundamental frequency of 0.5–0.8 kHz. On average, advertisement calls had a duration of 0.04–0.12 s (Table 7; Fig. 8).

Distribution.—Most restricted distribution of the three species (approximately 26,000 km^2). Its range is centered entirely within the Sydney Basin and North Coast bioregions, including the Wollemi, Cumberland, Pittwater, Sydney-Cataract, Wyong, Hunter, Karuah-Manning, and Macleay-Hasting subbioregions. Mostly occurs in low-lying areas; however, has been recorded up to ~600 m a.s.l. in the Blue Mountains National Park. Southerly distribution limits for this species include Stanwell Tops/Dharawal National Park. Also found throughout the Hawkesbury and Cumberland Plains region, extending to the central, mid-northern, and northern NSW coastline to at least South West Rocks and historically the Nambucca River. Does not occur on the southern coast of NSW as reported previously (i.e., Parker, 1940; Martin, 1972; Anstis, 2017). Specimens from Jervis Bay have been confirmed by our genetic analyses to represent *L. dumerilii insularis*.

Habitat.—Associated with sandy heathlands, coastal acid swamplands (wallum), and dry open sclerophyll forest. Appears to prefer remnant habitats, uncommonly recorded in urban or agricultural areas. Occurs within a variety of

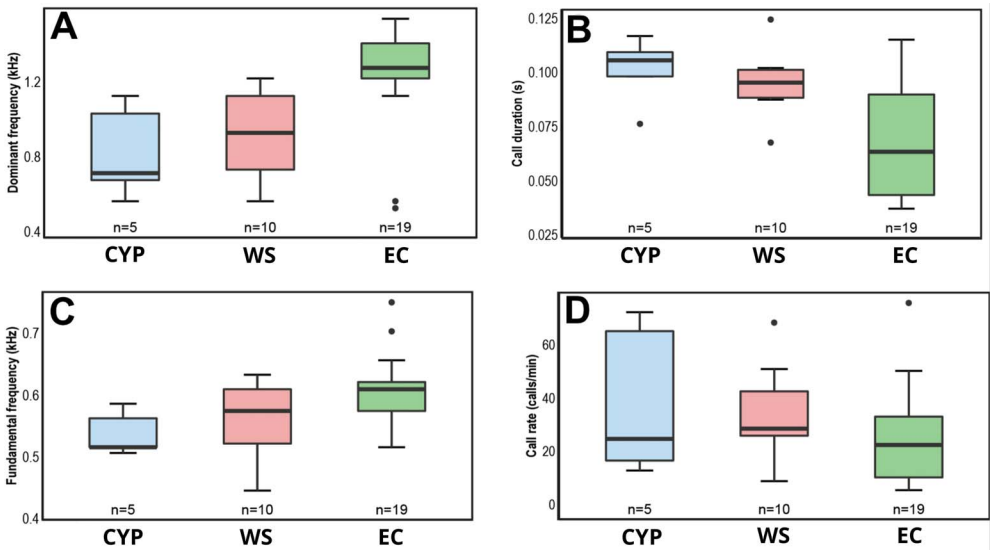

Fig. 9. Boxplot comparison of variation in the advertisement call traits between the *Limnodynastes dorsalis* group lineages redescribed herein, depicting variation in (A) dominant frequency (kHz), (B) call duration (s), (C) fundamental frequency (kHz), and (D) call rate (calls/min). Small dots represent outliers.

threatened vegetation communities, including the Castlereagh Scribbly Gum and Agnes Banks Woodlands of the Sydney Basin Bioregion (Endangered); Temperate Highland Peat Swamps on Sandstone (Endangered); River-flat eucalypt forest on coastal floodplains of southern New South Wales and eastern Victoria (Critically Endangered); Eastern Suburbs Banksia Scrub of the Sydney Region (Endangered); Coastal Upland Swamps in the Sydney Basin Bioregion (Endangered); Coastal Swamp Oak (*Casuarina glauca*) Forest of New South Wales and South East Queensland ecological community (Endangered).

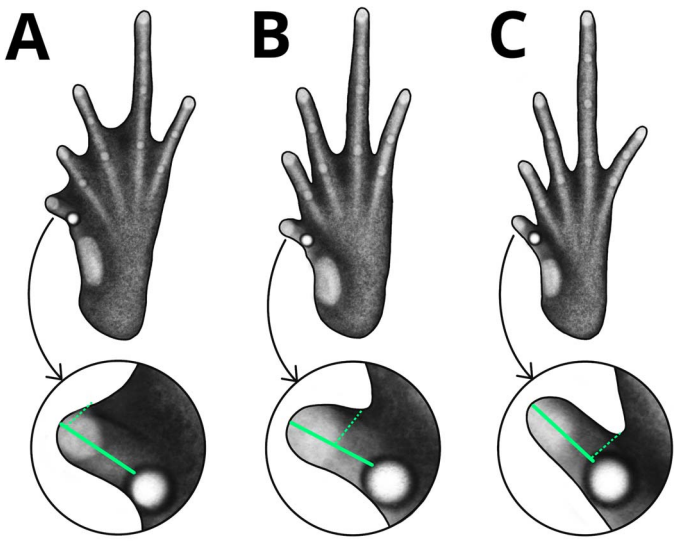

Fig. 10. Illustration of hind foot webbing extent, a useful diagnostic character for identification of the *Limnodynastes dorsalis* group. (A) Well-developed webbing (extends to beyond half-way between the 1st subarticular tubercle and tip of Toe 1), (B) moderate webbing (extends one-quarter to half-way between the 1st subarticular tubercle on Toe 1), (C) vestigial webbing (does not or only slightly extends beyond the 1st subarticular tubercle on the 1st Toe). Illustration copyright Alana de Laive.

Conservation status.—AOO and EOO were calculated at 1,928 km^2 and 37,819 km^2, respectively. The estimates for AOO potentially qualify the taxon as Vulnerable. There is lack of evidence of population fragmentation, decline, or severe fluctuation to assess *L. superciliaris* for an extinction risk category and so a listing of Least Concern is applicable. However, concern for the species conservation status is warranted given its distribution is centered largely within threatened and fragmented vegetation communities of the Sydney Basin, one of Australia's most urbanized regions.

Ecology.—Males congregate and call around static-water wetlands, wallums, swamps, and dams where they call while floating in water or secreted beneath vegetation at the water's edge. According to FrogID data, the species is most often recorded calling from streams, creeks, and dams. The peak calling period is from September to November, with some reduced calling activity from December to March. The majority of FrogID recordings of *L. superciliaris* have been recorded in natural and rural areas, with few recordings from suburban and urban landscapes. Stomach contents of museum specimens included a wide variety of invertebrate prey, including spiders, centipedes, beetles, earthworms, and ants (predominantly *Myrmecia* spp.). The species burrows into loose, sandy soils during unfavorable weather conditions and appears capable of remaining in aestivation for months at a time. For tadpole identification and development, see *L. dumerilii grayi* section in Anstis (2017).

Limnodynastes terraereginae (Fry, 1915)

Figures 16, 17
Suggested common name: Superb Banjo Frog

Holotype.—AMS R4525 (adult female) collected from Somerset, Cape York Peninsula, Far North Queensland, Australia (10.75°S, 142.58°E) by Charles Hedley and Allan Riverstone McCulloch in 1907.

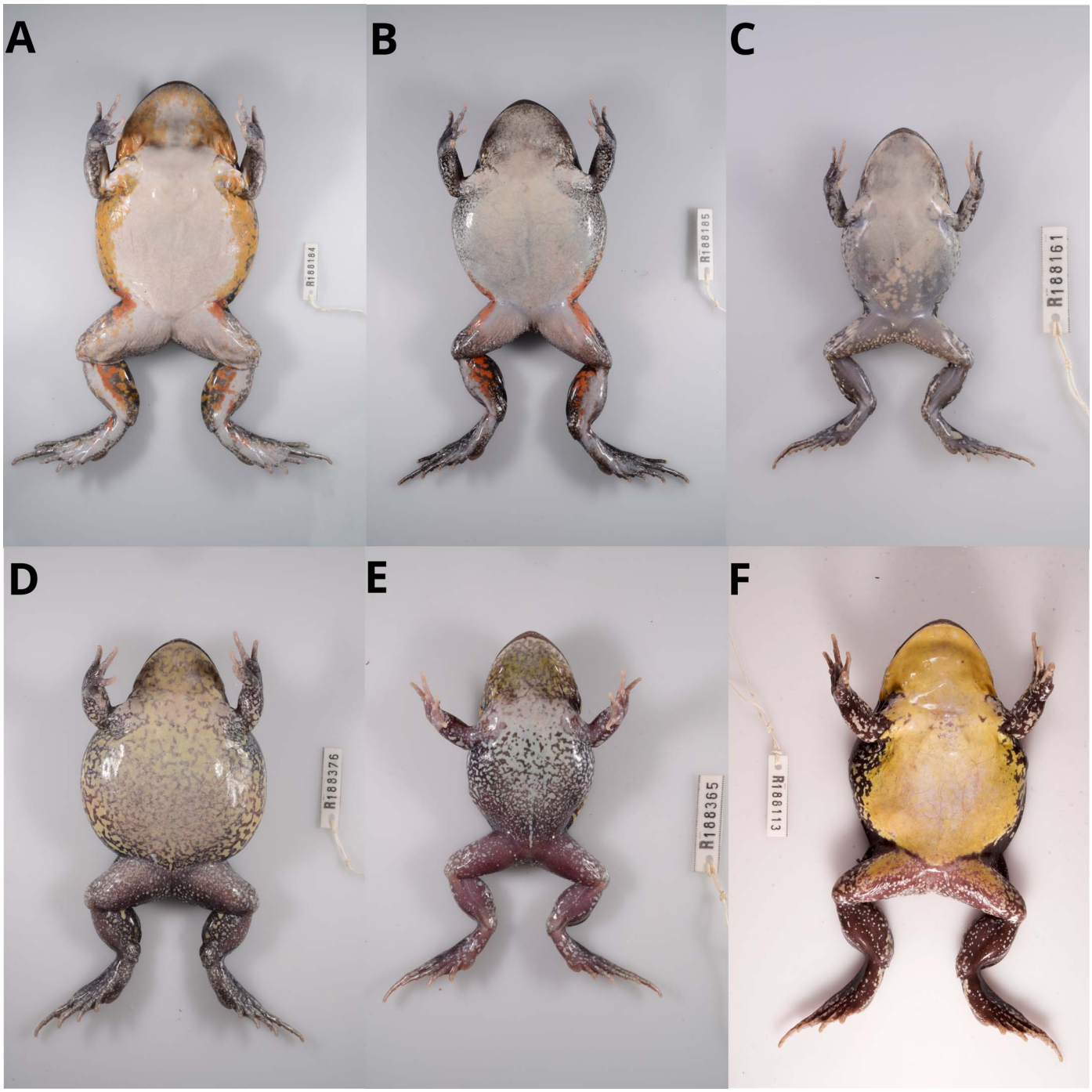

Fig. 11. Examples of typical ventral color pattern, a useful diagnostic trait between members of the eastern *Limnodynastes dorsalis* group. (A) *Limnodynastes terraereginae* (CYP lineage), (B) *L. grayi* (WS lineage), (C) *L. superciliaris* (EC lineage), (D) *L. dumerilii dumerilii*, (E) *L. dumerilii insularis*, and (F) *L. interioris.* Specimen registration labels represent 25 mm.

Material examined.—See Supplementary Table S1 (see Data Accessibility) for full list of specimens used in morphometric analyses.

Revised diagnosis.—*Limnodynastes terraereginae* can be distinguished from all species in the *L. dorsalis* group by a combination of: (1) large adult body size (SVL for males 65–66 mm; females 73–94 mm), (2) excessively robust build, (3) vestigial-moderate trace of webbing on the hind foot (Fig. 10), (4) presence of magenta suffusions in the groin, (5) pale, immaculate ventral surface, edged with yellow (Fig. 11A), (6) advertisement call with a moderately high dominant frequency (0.6–1.1 kHz, mean 0.8 kHz), and (7) genetically by 16 apomorphic nucleotide states on the *ND4* gene (Table 4).

Holotype measurements (mm).—SVL 73.4; FOL 44.5; TIB 27.1; THL 30.2; HW 32.9; IOD 6.5; DFE 11.8; IND 6.4; NS 6.7; EN 6.4; ED 8.5; HDD 14.6; SL 13.0; HL 26.4; UAL 12.7; LAL 17.7; HAL 17.3; AL 32.7; FL 31.1; IMT 6.0; TEY 3.9; Fin3W 1.9; Toe4W 2.1.

Redescription of holotype.—Habitus excessively stout. Dorsum textured with irregular tubercles, ventral surface smooth.

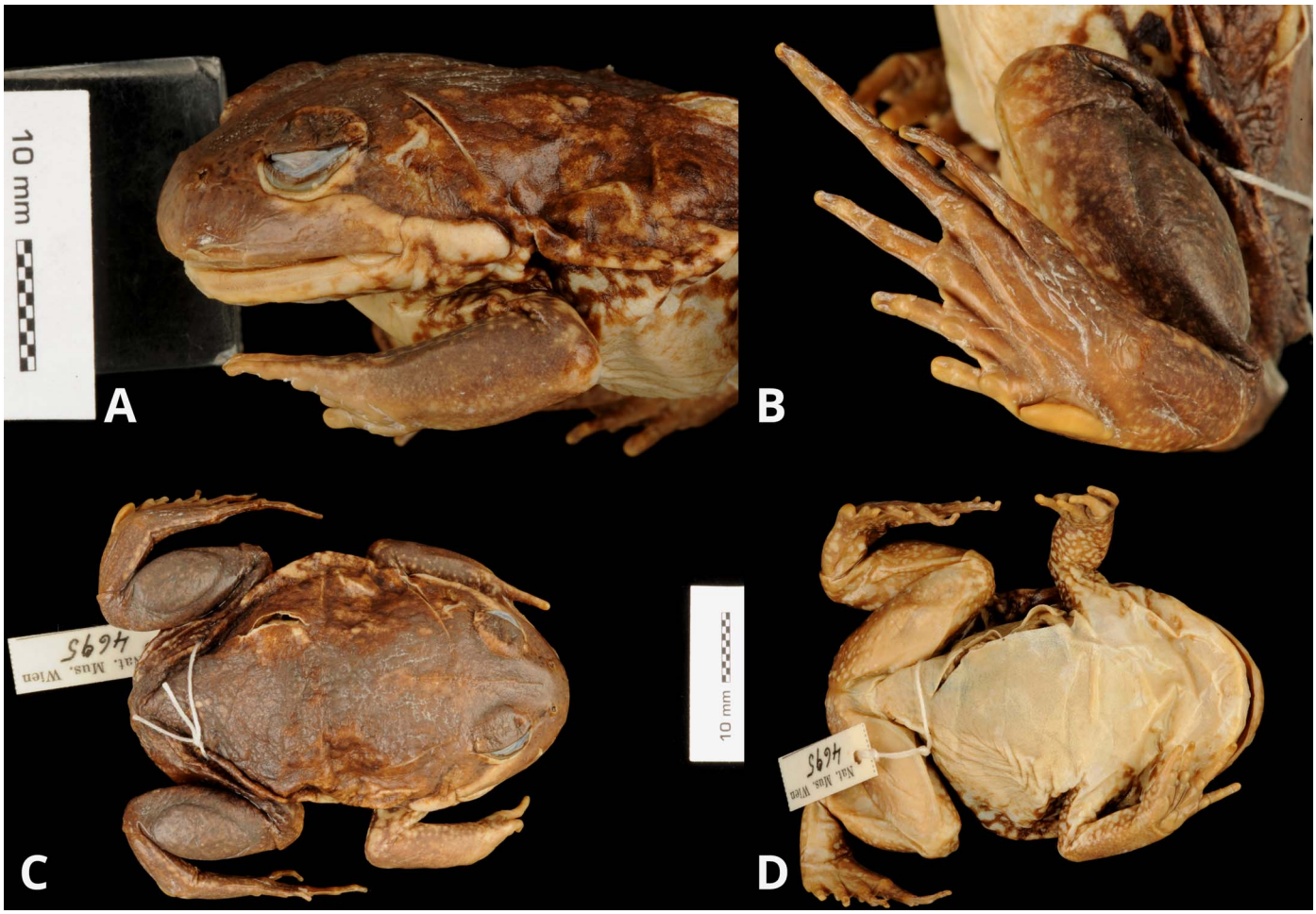

Fig. 12. Holotype of *Heliorana grayi*, NHMW 4695. (A) Left-side profile, (B) hind foot, (C) dorsal profile, (D) ventral profile. Images copyright Alice Schumacher, NHM Vienna.

Head large, broadest at tympanum, wider than long (HW/HL 1.25). Head appears rounded from above and in lateral profile. Nostrils slightly raised, outward-facing and not prominent in profile. Eyes large, bulbous and protruding, pupil round and tympanum indistinct. Arms and legs short and powerfully built, tibial gland prominent, oval-shaped and approximately 57% length of tibia. Four fingers and five toes, all rounded, thick-set and tapering without terminal discs. Webbing on fingers absent and with moderate trace on toes (Fig. 10), prominent distended finger spatulae on 2nd fingers indicating specimen is female. Subarticular tubercles prominent on fingers and toes, metacarpal tubercles prominent, inner-metatarsal tubercle also prominent, wedge-shaped and longer than the 1st toe. Soles of feet smooth. Numerous raised scattered tubercles present on posterior edge of thighs and around cloaca.

Color in preservative.—Described after more than 115 years in preservative, dorsum base color a fairly uniform cream-brown with irregularly scattered large dark brown blotches and spots, tending to become darker and denser posteriorly. Distinct yellow vertebral stripe extending from rostrum to vent. Pattern becomes more dispersed laterally and is replaced by a fairly uniform cream-yellow base which transitions to a slightly lighter and immaculate cream-yellow on the ventrum. Subaural gland cream-yellow, with darker brown banding running through eye. Upper surface of arms cream-yellow with faded mottling. Lower surface of arms and legs plain cream-yellow.

Variation.—A summary of variation in morphometric characters for each sex is presented in Table 6 and Figure 6.

Color and pattern (in life).—Ventral surface plain, unpatterned cream to pearl and edged by yellow. Vocal sac dark brown to orange and mottled in breeding males. Distinct magenta patches in inguinal region and legs. Dorsum with light brown base with strong dark brown to black blotching (Fig. 17). Yellow vertebral stripe can be distinct, broken, faded, or absent. Lateral zone with dark brown base and yellow-orange mottling or stippling. Posterior thigh flash black with scarlet to orange blotching. Soles of feet dark brown with light speckling and lateral edge of foot often with yellow stripe. Shoulder with yellow-orange patch, forearm mottled with gray, brown, white, to pearl fingers and toes. Distinct yellow to orange subaural gland with darker brown to black stripe running from rostrum, through eye and usually fading into the lateral zone.

Advertisement call.—The advertisement call description of *L. terraereginae* is based on the calls of five individuals from Cape York Peninsula. The advertisement call consists of a

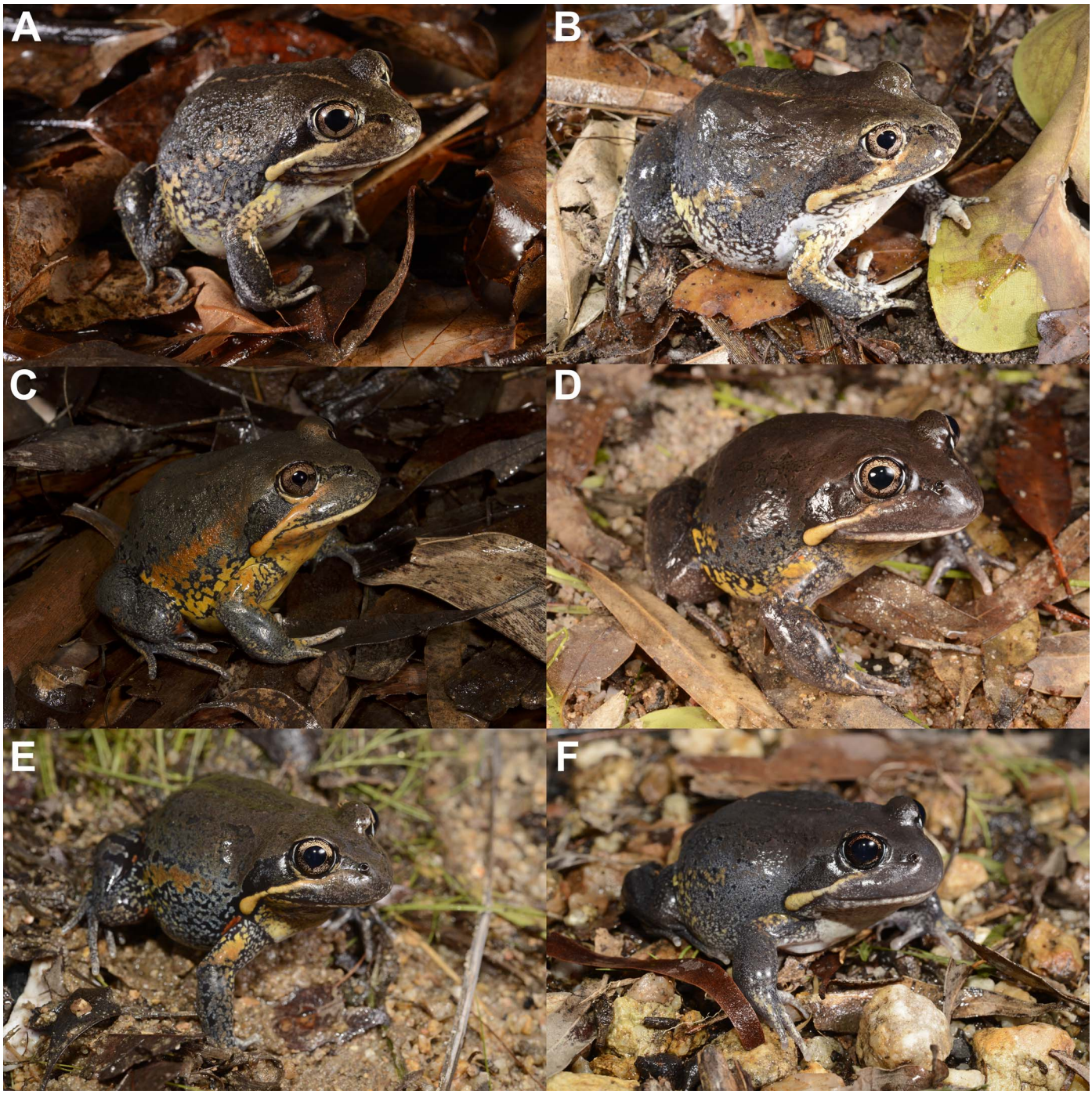

Fig. 13. Images in life of *Limnodynastes grayi*. (A) AMS R.188151, female, Dirty Creek, north coast, NSW. (B) AMS R.188350, female, Tyndale, north coast, NSW. (C) AMS R.185843, male, Yetman, Northern Tablelands, NSW. (D) QM J97851, male, Watsonville, Atherton Tablelands, Qld. (E) QM J97848, male, Hervey Range, Qld. (F) QM J97857, female, Mount Carbine, Qld.

single, resonant note. Individuals had a mean dominant frequency of 0.6–1.1 kHz, and a mean fundamental frequency of 0.5–0.6 kHz. On average, advertisement calls had a duration of 0.08–0.12 s (Table 7; Fig. 8)

Distribution.—Restricted to the eastern coast of the Cape York Peninsula Bioregion in far north QLD, from Cooktown in the south to Somerset at the tip of Cape York, encompassing an area of approximately 36,000 km^2. Recorded from Jardine-Pascoe Sandstones, Coen-Yambo Inlier, Laura Lowlands, and Starke Coastal Lowlands subregions.

Habitat.—Occurs in Melaleuca woodlands, ephemeral swamps, littoral monsoon forest, vine thicket, coastal heath, and riparian habitats with clay or sandy substrate.

Conservation status.—AOO and EOO were calculated for this taxon at 204 km^2 and 59,565 km^2, respectively. The estimate of AOO potentially qualifies the taxon for Endangered;

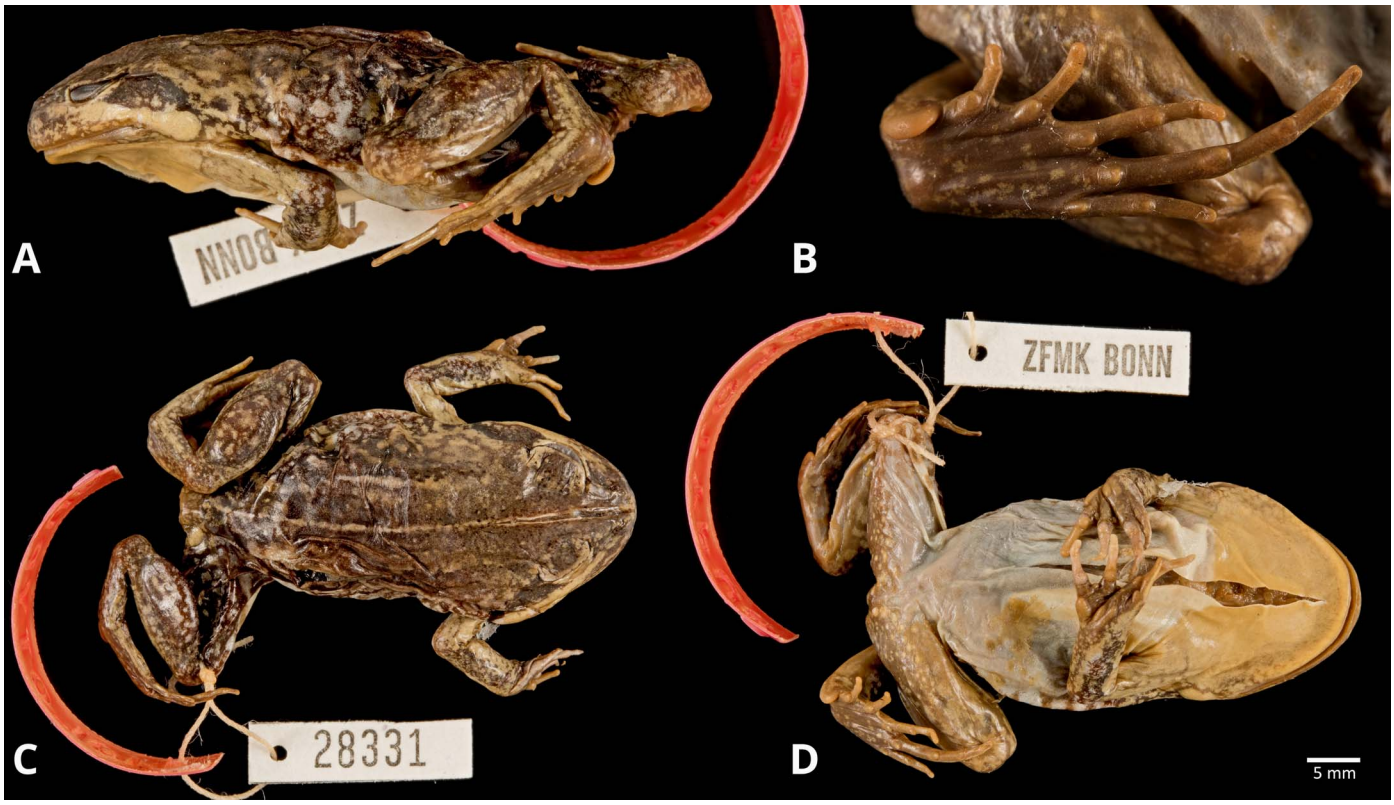

Fig. 14. Holotype of *Platyplectrum superciliare*, ZFMK 28331. (A) Left-side profile, (B) hind foot, (C) dorsal profile, (D) ventral profile. Images copyright Morris Flecks, ZFMK, Germany.

however, the EOO estimate does not meet any risk category. There is currently inadequate data available to assess whether populations of this taxon are fragmented, have declined, or have fluctuated severely and so a listing of Least Concern is appropriate until further information becomes available.

Ecology.—The peak calling period is from January to March. According to FrogID data, the species is most often recorded calling from streams, creeks, and flooded areas in natural landscapes. Males have been recorded calling in closed-canopy, flooded littoral monsoon forest near Cooktown in May 2021, elevation 12 m a.s.l. (T. Parkin, pers. obs.). Significant rainfall (>250 mm) had fallen in the region over the preceding week associated with tropical cyclone *Niran*. Several males were observed calling from exposed positions beside the water's edge, air temperature 26.5°C. Tadpoles and reproductive biology not recorded.

DISCUSSION

Our study represents the first range-wide assessment of variation in genetic diversity, morphology, and calls of *Limnodynastes terraereginae sensu lato*. Our results provide strong evidence for the recognition of three evolutionarily distinct taxa within this species group. These include the massive and superbly patterned *L. terraereginae* that is endemic to Cape York Peninsula, the medium-sized and widely distributed *L. grayi*, and a diminutive sister taxon, *L. superciliaris* (formerly *L. dumerilii grayi*), which is endemic to sandy habitats of eastern coastal NSW.

We found that the species described herein occupy narrowly allopatric ranges which replace each other in a north–south series over a distance of more than 2,800 km, extending from the Sydney Basin to the northernmost tip of Cape York Peninsula. The distributional gap between *L. grayi* and *L. terraereginae* occurs across a distance of 110 km between the Carbine Uplands and Cooktown in southern Cape York Peninsula. The intervening region is characterized as a lowland expanse of hot and humid open woodland and savannah which appears to present a barrier to dispersal between the species today. In tropical north QLD, *L. grayi* is restricted to upland sclerophyll woodlands, open forests, and heathland above 700 m a.s.l., and the data suggest that it is absent from hot and humid coastal lowlands, suggesting a physiological intolerance to elevated temperature and humidity. In contrast, *L. terraereginae* appears to be well adapted to these conditions given its distribution is entirely restricted to eastern lowland coastal habitats within Cape York Peninsula.

In northern NSW, *L. grayi* and *L. superciliaris* appear to be separated by a gap of approximately 70 km between Coffs Harbour (*L. grayi*) and South West Rocks (*L. superciliaris*). We conducted several targeted surveys within this gap and failed to locate either species within closer proximity. Of note, this region also represents a southerly distributional limit for the Wallum Sedge Frog (*Litoria olongburensis*) and gap in the distribution for the Wallum Froglet (*Crinia tinnula*), suggesting that dispersal across this zone may be restricted by an absence of suitable wallum habitat.

In contrast, *L. grayi* and *L. superciliaris* were found to occur in sympatry and/or parapatry with *L. dumerilii* in various locations throughout the species' range. The distributions of *L. dumerilii* and *L. grayi* overlap broadly in north-eastern

Fig. 15. Images in life of *Limnodynastes superciliaris*. (A) AMS R.188161, male, South West Rocks, NSW. (B) AMS R.188207, male, lower Blue Mountains, NSW. (C) AMS R.188165, male, Agnes Banks, Cumberland Plains, NSW. (D) AMS R.188164, Harrington, mid-northern coast, NSW. (E) AMS R.188163, female, Laurieton, mid-northern coast, NSW. (F) AMS R.188135, juvenile, Hat Head National Park, mid-northern coast, NSW.

NSW and south-eastern QLD where they have been found breeding side-by-side without evidence of hybridization (i.e., no morphological intermediates; Martin, 1972). The advertisement calls of each taxon are markedly distinct; however, whether this character displacement has reinforced species boundaries in sympatry remains unclear. Martin (1972) found the dominant frequency of the call of *L. dumerilii* in sympatry with *L. grayi* is significantly lower (i.e., more different from *L. grayi*) than those of allopatric populations. However, the opposite trend was seen for *L. grayi*, which has calls more similar to *L. dumerilii* in sympatry compared to allopatric populations. We found no evidence of admixture between these taxa in our SNP dataset despite sampling from close geographic proximity in north-eastern NSW (~23 km), Northern Tablelands (~15 km), and Central Tablelands region (~40 km), affirming the species maintain reproductive isolation in parapatry/sympatry.

In NSW, *L. superciliaris* is predominantly distributed along the east coast, with *L. dumerilii* occurring mainly within and west of the GDR. The presence of possible morphological

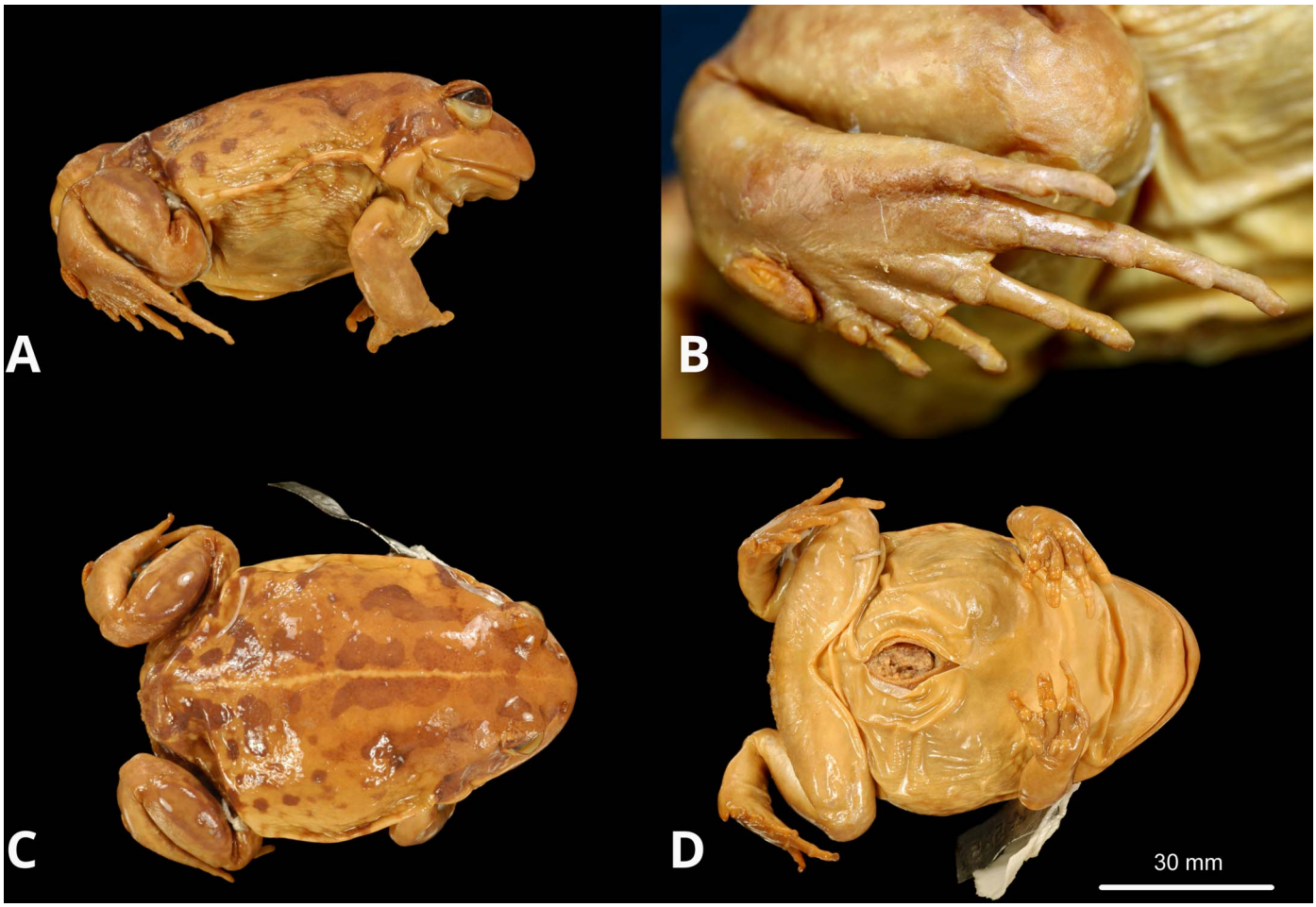

Fig. 16. Holotype of *Limnodynastes dorsalis* var. *terrae-reginae*, AMS R4525. (A) Right-side profile, (B) hind foot, (C) dorsal profile, (D) ventral profile.

intermediates between the species in southern Sydney (i.e., around Wattamolla and Stanwell Tops) previously has raised the possibility of a hybrid zone among the taxa, although insufficient data were available to conclude on the extent of hybridization (Martin, 1972). We detected admixture between *L. dumerilii* and *L. superciliaris* at an ecotonal contact zone on the Central Coast of NSW, at the junction of the Pittwater, Yengo, and Wyong sub-bioregions (Fig. 5). The overall level of admixture among the taxa was found to be relatively low given no F_1 or F_2 hybrids were detected, and an additional seven samples collected at the same site, or within 32 km of the admixed individuals, were classified as pure *L. superciliaris*. We also found no evidence of admixture between *L. dumerilii* and *L. superciliaris* in other regions of potential contact. This included samples collected within a straight-line distance of 40 km in southern Sydney, and 17 km in the Blue Mountains across an altitudinal transition of 404 m. We found the taxa to occupy distinct habitats: *L. superciliaris* occurs within lowland sandy heaths and *L. dumerilii* is associated with wet and dry sclerophyll forest, agricultural, and suburban areas on heavier soils. There is marked differentiation in morphology and advertisement calls between the taxa which likely acts as a pre-mating reproductive isolation barrier. Based on these findings, we suspect that occasional hybridization occurs as a consequence of mismating following sporadic migration of individuals between otherwise fairly discrete habitats. Further studies of the Central Coast contact zone would shed light on the reproductive compatibility of the taxa and the role of pre- and post-mating barriers in maintaining contemporary species boundaries.

DATA ACCESSIBILITY

Supplemental material is available at https://www.ichthyologyandherpetology.org/h2023025. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

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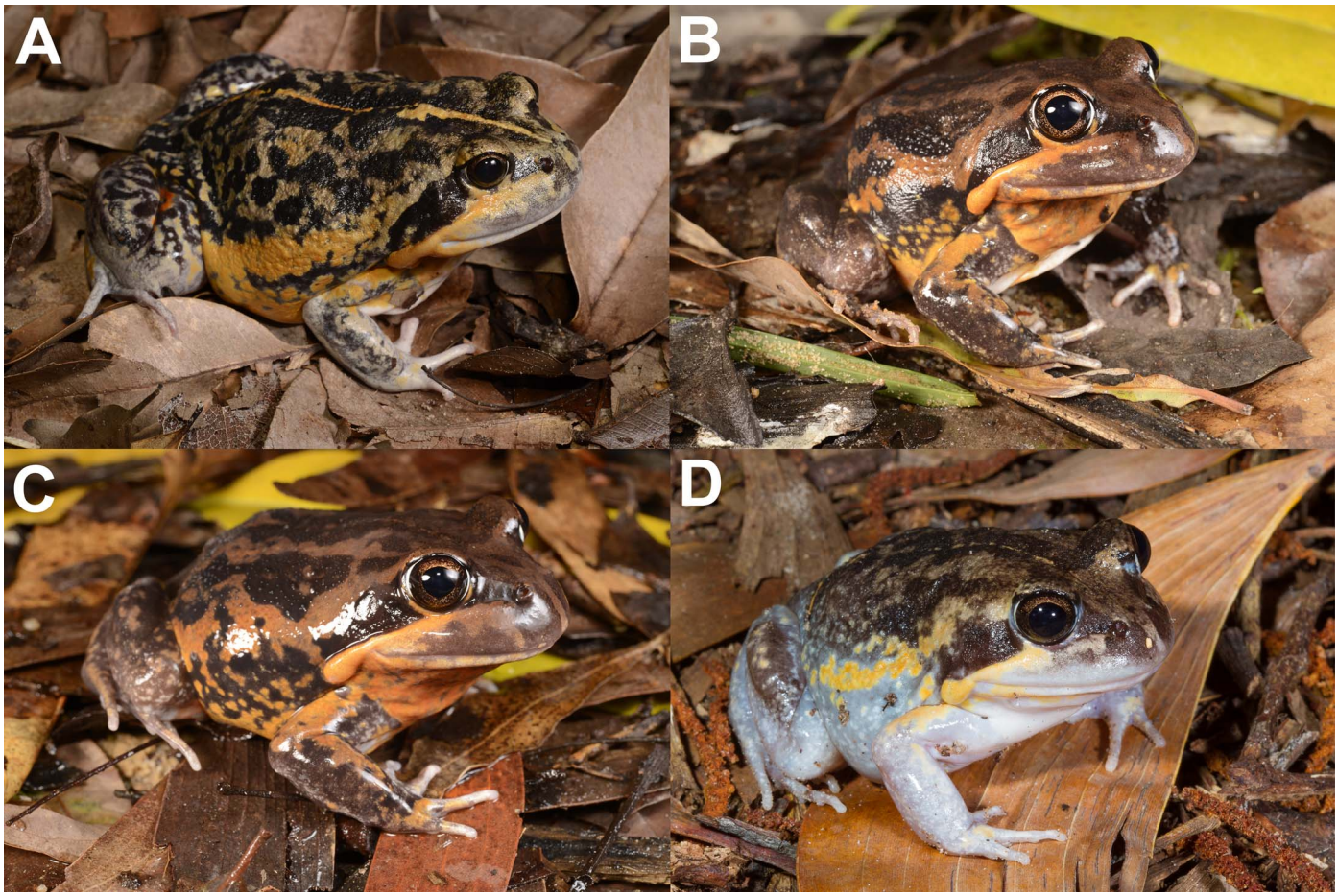

Fig. 17. Images in life of *Limnodynastes terraereginae*. (A) QM J97862, female, Cooktown, Qld. (B) QM J97860, male, Cooktown, Qld. (C) QM J97861, male, Cooktown, Qld. (D) Unvouchered individual, Kutini-Payamu (Iron Range) National Park, Qld (photo copyright: Stephen Zozaya).

providing images and measurements of the *Platyplectrum superciliare* type specimen, and Alice Schumacher of the NHM for providing images of the *Heliorana grayi* type specimen. Morris, together with Ursula Bott and Wolfgang Böhme, provided support to GMS during his visit to the ZFMK collection to examine the Schütte collection of Australian reptiles and amphibians. Michael Mahony and Harry Hines collected important tissue samples, and Jo Sumner (NMV) and Jessica Worthington-Wilmer (QM) facilitated museum tissue loans. Timothy Cutajar provided much advice and assistance with molecular techniques. Staff of the Australian Centre for Wildlife Genomics provided lab access and support. Jasmin Gray and Benjamin Parkin assisted greatly with fieldwork and descriptions of color/pattern for the taxa. Alana de Laive provided the illustration of hind foot webbing traits. Hal Cogger provided valuable insights into the taxonomy of the group and some photographs and notes on type specimens. Keith McDonald reviewed an earlier version of the manuscript and provided important comments on species ecology, distributions, and biogeography in north Queensland. Fieldwork in Tasmania was generously supported by funding from the Jayne Wilson Bequest Bursary via the Tasmanian Museum and Art Gallery. Scientific research permits were granted by each relevant state authority: NSW National Parks and Wildlife Service (SL100582); Victorian Department of Environment, Land, Water and Planning (10009662); Tasmanian Department of Primary Industries, Parks, Water and Environment (FA 21046). Ethics approval was granted by the Australian Museum Animal Research Authority under project 20-01.

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APPENDIX 1

Provenance of the holotype of* Heliorana grayi *Steindachner 1867.—The collection locality for the *Heliorana grayi* type (NHMW 4695) was initially vaguely specified by Steindachner as *Neu-Süd-Wales* (i.e., NSW). Inspection of the NHMW type catalogue has since revealed the true collection locality for the *Heliorana grayi* type to be Rockhampton, QLD (Häupl and Tiedemann, 1978; Gemel et al., 2019).

Without viewing the type, authors of subsequent taxonomic revisions (i.e., Parker, 1940; Martin, 1972) were led to assume the *Heliorana grayi* type was collected in NSW and thus incorrectly referred the name *Limnodynastes* (*dorsalis*) *dumerilii grayi* to the distinctive population of frogs occurring in eastern coastal NSW (here referred to as the EC lineage). This is likely due to the description by Steindachner (1867) being included in a report on the herpetological collections made during the Austrian *Novara* expedition, which visited Australia between 5 November to 7 December 1858, and collected there only within the area around Sydney, from as far south as Wollongong and Appin, to as far north as Ash Island on the Hunter River (Gans, 1955). However, Steindachner included in his report specimens available to him from other sources. In the case of *Heliorana grayi*, the material was obtained by Steindachner from a collector who had visited Rockhampton. Assuming this locality is correct, the most likely source of herpetological material from Rockhampton prior to 1867 is the Hamburg naturalist and natural history dealer Carl Friedrich Eduard Dämel (1821–1900), who visited Australia three times, the first between 1852–1860 (working mostly around Sydney, but with side trips to West Australia in 1859 and Port Curtis [now Gladstone] in Queensland in 1860), the second between 1865–1867, and the third (as a collector for the Godeffroy Museum in Hamburg) between 1871–1875. It is likely that the type of *Heliorana grayi* was collected by him during his second expedition, during which he collected at Rockhampton and Port Denison (now Bowen) between February to May 1866 before moving base to Somerset on Cape York between May to December of the same year before returning to Hamburg, after which time he was employed by the Godeffroy Museum (Musgrave, 1932; Weidner, 1967), although we cannot discount the possibility that it was collected on his first expedition. This is less likely, as the township of Rockhampton was only formally proclaimed in 1857 (Bird, 1904), and the region was still generally known as Port Curtis in 1860 when he first visited the region, making it unlikely that a specimen collected from there at that time would have been associated with the locality Rockhampton on receipt by Steindachner soon after Dämel returned to Germany from his first sojourn. The other significant nineteenth century collector of fauna from the Rockhampton region, Konkordie Amalie Dietrich (1821–1891), also a collector for the Godeffroy Museum, also arrived in Rockhampton in early 1866, but continued from there to Mackay in 1867, and did not return to Germany until 1873 (Sumner, 1993). Examination of the sale catalogues of the Godeffroy Museum indicates that only her herpetological material from Brisbane, her previous collecting base, had reached Hamburg by 1866 (Schmeltz, 1866), while her material from Rockhampton did not appear for sale until the following catalogue in 1869 (Schmeltz, 1869), too late for them to have been obtained by Steindachner for publication in 1867. Our examination of high-resolution images of the

Heliorana grayi type (Fig. 12) confirmed that the specimen corresponds in morphology (medium-large size, robust build, moderate foot webbing, and aspects of dorsal color/pattern) with genotyped specimens of the WS lineage which occurs in Rockhampton, and we therefore correctly apply the name *Limnodynastes grayi* to this taxon.

***Provenance of the holotype of* Platyplectrum superciliare *Keferstein 1867*.—**The original collection locality for the *Platyplectrum superciliare* type (ZFMK 28331) was even more vaguely stated by Keferstein (1867) as Australien (i.e., Australia). Keferstein's material was largely obtained from his relative Bernhard Rudolf Schütte, who visited Australia on two occasions, between 1857–1862 and 1867–1884 (Rowley et al., 2021). Keferstein's collection was originally housed in Göttingen, but the extant collections were transferred to the ZFMK collection in Bonn in 1977 (Böhme, 2014). One of us (GMS) has recently examined all of the Schütte herpetological collections in Bonn, along with scanned copies of the relevant pages from the manuscript Göttingen catalogue. There appear to have been four major lots of herpetological specimens sent from Schütte to Keferstein in Göttingen, with the years 1862, 1864, 1867, and 1868 recorded in the Göttingen catalogue entries, along with a handful of larger reptiles dated 1863 and 1865 (additional shipments dated 1870, 1874, 1877, and 1879 postdate Keferstein's death in 1870, and are not relevant). There are four entries in the Göttingen catalogue for what was then identified as *Limnodynastes dorsalis*, all obtained from Schütte: a. Sydney, 1864; b. Sydney 1867; c. Clarence River, 1867; d. Australien, 1864. The first was not present at the time of the transfer of the collection to Bonn, but the other three entries correspond to existing specimens: b. to five specimens, now ZFMK 28324–28; c. to two specimens, now ZFMK 28329–30; and d. to the holotype of *Platyplectrum superciliare*, now ZFMK 28331. Of Keferstein's two papers dealing with Schutte's collections, the first (Keferstein, 1867) only dealt with material from the 1862 and 1864 lots, while the second (Keferstein, 1868) dealt primarily with the 1867 and 1868 shipments. Of the 198 extant Schütte reptile and amphibian specimens in the ZFMK collection from the 1862 and 1864 lots, which must have been derived from his first period in Australia, almost all are recorded as from Sydney or from Sydney suburbs (Bronte, Raudwick = Randwick). The seven exceptions possessing localities are ZFMK 28274, an *Adelotus brevis* from Port Macquarie, ZFMK 28359–63, *Limnodynastes tasmaniensis* purportedly from the Clarence River, and ZFMK 28741, a *Litoria aurea* from Grafton (on the Clarence River). Schütte is not known to have traveled to the Clarence River until 1867, and hence we presume the year is wrong for the latter six specimens. The overwhelming majority of the 198 specimens with dates 1862 and 1864 are of species that are present in the Sydney area. The few exceptions are a few large and showy reptile species (ZFMK 26361–62, *Varanus gouldii*; ZFMK 26386, *Chlamydosaurus kingii*), non-Australian reptiles that are distributed in Pacific Oceania (ZFMK 20556–59, *Gehyra oceanica*) or from south-east Asia (ZFMK 27090, *Lygosoma* sp.), or species that together point to a south-west Australian origin (ZFMK 26814–15, *Egernia napoleonis*; 26909, *Cryptoblepharus buchanani*; 26979, *Ctenotus labillardieri*; 36405–07, *Elapognathus coronatus*), all of which still possess a nominal locality "Sydney," and could have been obtained by Schütte from natural history traders in Sydney or from his compatriot Gerard Krefft at the Australian Museum in Sydney (some other specimens with 1862 or 1864 dates are specifically recorded as from Krefft or the Australian Museum, and Krefft is recorded as having assisted with the shipping of Schütte's collections to Göttingen; Böhme, 2014). The holotype of *Platyplectrum superciliare* is not conspecific with *Limnodynastes dorsalis*, the only species in the *L. dumerilii* complex from south-western Australia, and hence we conclude that the most likely provenance for the specimen is the Sydney region, from where the vast majority of specimens obtained by Schütte from his first Australian visit were derived, either explicitly or by inference.

Based on the results of the group assignment by the DFA, and the presence of several consistent diagnostic morphological features (i.e., small size, vestigial foot webbing [Fig. 10], and aspects of dorsal and ventral color/pattern [Fig. 11]), we conclude the *Platyplectrum superciliare* type specimen represents the distinctive EC lineage currently incorrectly referred to as *Limnodynastes dumerilii grayi*. We hereby apply the name *Limnodynastes superciliaris* to this taxon.