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A taxonomic revision of Cheilodactylidae and Latridae (Centrarchiformes: Cirrhitoidei) using morphological and genomic characters

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Abstract

Systematic relationships within the Cirrhitoidei, a suborder of five closely related families, have been uncertain for over a century. This is particularly true in reference to the families Cheilodactylidae and Latridae, which have been revised numerous times over the past several decades. Species that have been included in these two families are found in temperate regions around the world, which has led to regionally-focused studies that have only exacerbated taxonomic confusion. Here we examine systematic relationships within the Cheilodactylidae and the Latridae using ultraconserved genomic elements with near complete taxonomic sampling, and place our results in the context of the Cirrhitoidei. Our results agree with previous findings suggesting that Cheilodactylidae is restricted to two South African species, with the type species of the family, *Cheilodactylus fasciatus* Lacépède, forming a clade with *C. pixi* Smith that together is more closely related to the Chironemidae than to other species historically associated with the genus. We also strongly resolve the relationships of species within the Latridae. As a result of our analyses we revise the taxonomy of Latridae, name a new genus, and re-elevate *Chirodactylus* and *Morwong*.

key words: morwong, trumpeter, ultraconserved elements, phylogenomics, Centrarchiformes, systematics

Introduction

The beginning of the 21st century has been marked by several large-scale molecular phylogenies for acanthomorph fishes (Chen *et al.* 2003, 2014a; Smith & Craig 2007; Near *et al.* 2012a, 2013; Betancur-R *et al.* 2013, 2017; Alfaro *et al.* 2018). These studies have produced a multitude of hypotheses for acanthomorph fish relationships based on different numbers of taxa or loci, and have questioned previous phylogenetic hypotheses based on morphology (Johnson & Paterson 1993). While the resulting molecular hypotheses differ from one another in some regards, similarities among these studies have begun to shift our thinking towards the evolutionary history of fishes (Chakrabarty 2010). One consistent finding between many of these molecular studies is a lineage not previously recognized by morphology, containing a variety of temperate freshwater and marine species now recognized as the order Centrarchiformes (Near *et al.* 2012b; Betancur-R *et al.* 2017).

Five suborders have been placed within Centrarchiformes, with taxonomic confusion regularly occurring in the suborder Cirrhitoidei — a clade containing Cirrhitidae, Chironemidae, Aplodactylidae, Cheilodactylidae and Latridae (Betancur-R *et al.* 2017). The close affinity of these families has been long recognized based on the presence of thickened and elongated unbranched pectoral-fin rays (Gill 1886), and several systematic revisions have focused on relationships within these five marine families. However, uncertainty in the relationships both between, and within, these families persists. One recurring taxonomic issue involves the Cheilodactylidae, and how it relates with the other four cirrhitoid families. Historically, the Cheilodactylidae comprised 27 species and four genera (Nelson *et al.* 2016). The majority of these species inhabit temperate regions of the Southern Hemisphere.

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Diversity is highest along the Australian coastline (Kuiter 1993), but species occur in South Africa, along both coasts of South America, around several oceanic islands in the Southern Hemisphere, and around the coasts of Japan, Korea, China, Taiwan and Hawaii in the Northern Hemisphere (Nelson *et al.* 2016). This distribution has led to regional studies with limited taxonomic sampling that have only exacerbated taxonomic confusion within the family.

Much of the confusion regarding cheilodactylid taxonomy stems from the genus *Cheilodactylus* (sensu Nelson *et al.* 2016), which is the most speciose and widely distributed group in the family. The type species of this genus (and of the family), *Cheilodactylus fasciatus* Lacépède, is quite distinct morphologically from all other species in the genus (apart from *C. pixi* Smith), which historically led to the description of various new genera. However, Allen & Heemstra (1976) noted "the differences between these various type-species [of these genera] and *C. fasciatus* are no greater than those between *C. fasciatus* and any other species of *Cheilodactylus*," and placed many of these genera in synonymy with *Cheilodactylus.* While this suggestion simplified the taxonomy of the family, it had the unintended consequence of making *Cheilodactylus* a 'catch-all' name for a variety of unique fishes, and may not accurately reflect their evolutionary history.

Recent studies have recovered a polyphyletic Cheilodactylidae, with two South African species, *Cheilodactylus fasciatus* and *C. pixi*, forming a clade distantly related to the other members of the family, which have been recovered within the Latridae (Burridge and Smolenski 2004; Sanciangco *et al.* 2016; Kimura *et al.* 2018). As the type species for *Cheilodactylus*, and the Cheilodactylidae is *C. fasciatus*, this result would restrict Cheilodactylidae *sensu stricto* to these two South African species, and the remaining cheilodactylids should be placed within the Latridae, a classification which echoes the original proposed relationships of cirrhitoid fishes (Gill 1886). However, despite these studies repeatedly finding evidence that Cheilodactylidae is polyphyletic, no formal taxonomic changes were made either due to low topological support values (Burridge and Smolenski 2004) or limited taxonomic sampling (Sanciangco *et al.* 2016), until recently by Kimura *et al.* (2018).

Using an extensive anatomical character matrix, Kimura *et al.* (2018) found support for a clade containing *Cheilodactylus fasciatus* and *C. pixi* (reclassified as Cheilodactylidae) sister to a large clade containing all Latridae plus all remaining cheilodactylids, and re-described these families accordingly. While there was strong support for this distinction (five and nine synapomorphies, respectively) there was little support for many relationships within the newly reclassified Latridae, leading these authors to follow Allen & Heemstra (1976) in synonymizing *Chirodactylus* with most of the species that had previously been in the subgenus *Goniistius* (Kimura *et al.* 2018). However, taxonomic sampling was low in that study, many of the characters used varied little across the dataset, and the resulting classification may exacerbate taxonomic confusion in this family. Here we use ultraconserved elements (UCEs) with extensive taxonomic sampling to help resolve the relationships among the cirrhitoid families, with particular focus on the complex relationships involving the Latridae and Cheilodactylidae.

Materials and methods

Museum specimens were examined for all possible species with standard meristic counts and measurements. Radiographs were taken for key-taxa to examine the arrangement of the supraneurals, which were scored following Ahlstrom *et al.* (1976). All museum specimens are reported with institutional acronyms following Sabaj (2016), and include: ANSP—The Academy of Natural Sciences, AMS—Australian Museum, Sydney, CAS—California Academy of Science, CSIRO—Commonwealth Scientific and Industrial Research Organisation, KU:KUIT—The University of Kansas, FAKU—Fish Collection at Kyoto University, FMNH—Field Museum of Natural History, LACM—Natural History Museum of Los Angeles County, LSUMZ:LSUMZ-F—LSU Museum of Natural Science, NMV—Museum Victoria, ROM—Royal Ontario Museum, SIO—Scripps Institute of Oceanography, USNM—US National Museum of Natural History, WAM—Western Australia Museum, YPM—Yale Peabody Museum. For genomic work, when possible, tissue samples from Burridge & Smolenski (2004) were used, allowing for a direct comparison between studies. However, some tissues used in that study were either exhausted, or could not render enough genomic material for the sequencing approaches used here. In these cases, and for certain key-taxa, we supplemented our dataset with tissues obtained from vouchered museum specimens. Our sampling design included species from all five cirrhitoid families, as well as outgroup taxa that have been consistently recovered within the Centrarchiformes (Near *et al.* 2012b, Betancur-R *et al.* 2013, 2017, Chen *et al.* 2014b, Lavoué *et al.* 2014).

Genomic material was extracted from tissues using a DNeasy Blood & Tissue kit (Qiagen) following manufacturer's protocols. Extracts were stored at -23ºC prior to DNA quantification and library preparations. DNA was quantified with a Qubit® 2.0 Fluorometer using a dsDNA BR assay kit following manufacturer's protocols (Life Technologies). Quality of DNA was superficially assessed by running pure genomic extracts on a 1% agarose gel with SYBR® safe DNA gel stain (Life Technologies) and 6x Blue/Orange loading dye (Promega). Approximately 0.5–1.0µg of DNA was combined with custom solid-phase reversible immobilization beads (following protocols outlined in Rohland & Reich 2012) to remove small fragments present in each extract. These were then eluted in 30µL of TE buffer, and then sonicated using an Episonic Multi-Functional Bioprocessor to an average length of 600bp. All samples were then examined on a 1% agarose gel to ensure that the sonication process was successful, and the process was repeated if necessary.

Illumina libraries were constructed using the Kapa Hyper Prep Kit (Kapa Biosystems) with dual-indexing barcodes. All reactions followed manufacturer protocols, except reaction sizes were scaled to half the volume indicated by the manufacturer. After library amplification, samples were pooled in equimolar ratios in sets of six to eight samples. Target enrichment of UCE loci was performed on each pool using the MYbaits 0.5k Actinopterygian UCE capture kit (MYcroarray), originally described in Faircloth *et al.* (2013), following manufacturer's protocols. Pools were then amplified and cleaned using 16–18 PCR cycles following procedures outlined in Faircloth *et al.* (2013). All pools were combined in equimolar proportions, and were sequenced either at the University of Georgia Genomics Institute, or the Oklahoma Medical Research Institute, using an Illumina HiSeq or MiSeq Sequencer. Sequences in demultiplexed fastq files were then trimmed of unique indexes and low quality base calls using trimmomatic (Bolger *et al.* 2014), as part of the program Illumiprocessor (Faircloth 2013). *De novo* assembly of UCE sequences was completed using Trinity v.2.0.6 (Grabherr *et al.* 2011) with default settings. Using the Phyluce v1.5.0 repository (Faircloth 2015) we constructed a 75% complete concatenated data matrix, which we analyzed using both likelihood and Bayesian phylogenetic approaches.

Prior to analysis, UCE loci in the concatenated data matrix were partitioned into three sections corresponding to their left and right flanking regions and core, using the entropy model outlined in Tagliacollo & Lanfear (2018). These partitions were then input into PartitionFinder 2 (Lanfear *et al.* 2016) to determine the optimum number of partitions based on AICc model scores using the relaxed clustering algorithm (Lanfear *et al.* 2014), and protocols outlined specifically for UCE data in Tagliacollo & Lanfear (2018). Maximum likelihood trees were constructed using RAxML v8.1.24 (Stamatakis 2014) on the CIPRES scientific gateway portal (Miller *et al.* 2010). All analyses were completed using the partitioning scheme outlined above, and a GTRGAMMA model for bootstrapping, with 1000 bootstrap iterations using the rapid bootstrapping option (-x). Bayesian topologies were constructed using the program ExaBayes (Aberer *et al.* 2014) implemented with the same partitioning scheme. By default, this program uses the same GTR+G substitution model that was used in the RAxML analysis. Four separate chains were run in parallel for 3,000,000 generations, sampling every 500 generations. Chains were then combined following a 10% burnin using LogCombiner v.1.8.2 (Drummond *et al.* 2012), and trace plots and ESS values were examined to ensure stationarity and convergence using Tracer v1.6 (Drummond *et al.* 2012). In addition to concatenated analyses, a multi-species summary coalescent method was used to take variation among gene trees into account. Gene trees were estimated independently using RAxML with the GTRGAMMA substitution model and 10 alternative runs. A species tree was then estimated with ASTRAL v5.4.4 (Mirarab & Warnow 2015) using a mapping file to specify which species had multiple individuals sequenced.

We compared results from our analyses to alternative topologies with the likelihood based approximately unbiased (AU) and Shimodaira-Hasegawa (SH) tests (Shimodaira 2002) using the program Consel v0.2 (Shimodaira & Hasegawa 2001). This enabled comparisons between our output trees and constrained topologies. Three constrained trees were constructed using the –g option in RAxML; the first enforced cheilodactylid monophyly sensu Nelson *et al.* (2016), the second constrained *Cheilodactylus* sensu Nelson et al. (2016) minus *C. fasciatus* and *C. pixi* as monophyletic (to see how robust our findings of '*Goniistius*' *nigripes* were), and the third constrained the topology to match that recovered by Kimura *et al.* (2018). Per-site log likelihood scores were then estimated using the –f g option in RAxML to create Tree-Puzzle-type input files. Consel was then used to generate 10,000 hierarchical bootstrap replicates to test between alternative topologies.

Results

Our UCE data matrix contained 439 loci, totaling 277,505bp with an average of 618bp per locus. Comparison of partitioning schemes suggest 316 partitions to be the most strongly supported (AICc 1,750,685.14). The species included, source, total number of sequencing reads, and number of UCE loci per sample can be found in Table 1. All phylogenetic analyses recovered near identical results, including a monophyletic Cirrhitoidei, and a polyphyletic Cheilodactylidae (sensu Nelson *et al.* 2016; Fig. 1, S1, S2). Concatenated data generally produced results with higher support values than the species-tree approach. Two South African species, *Cheilodactylus fasciatus* and *C. pixi*, form a clade that is the sister group to the Chironemidae. This clade in turn was recovered as the sister group to Aplodactylidae, and together, all three of these clades are the sister group to a clade comprising the Latridae and remaining cheilodactylids. The Cirrhitidae is the sister group to all other cirrhitoid families, consistent with previous analyses (Greenwood 1995; Sanciangco *et al.* 2016; Betancur-R *et al.* 2017, Kimura *et al.* 2018). The ASTRAL species-tree approach differs from the concatenated analyses only in the placement of *Goniistius vittatus* (Garrett) and *Nemadactylus gayi* (Kner); however, for both species the nodes subtending these branches were weakly supported in the ASTRAL analysis (Fig. S2).

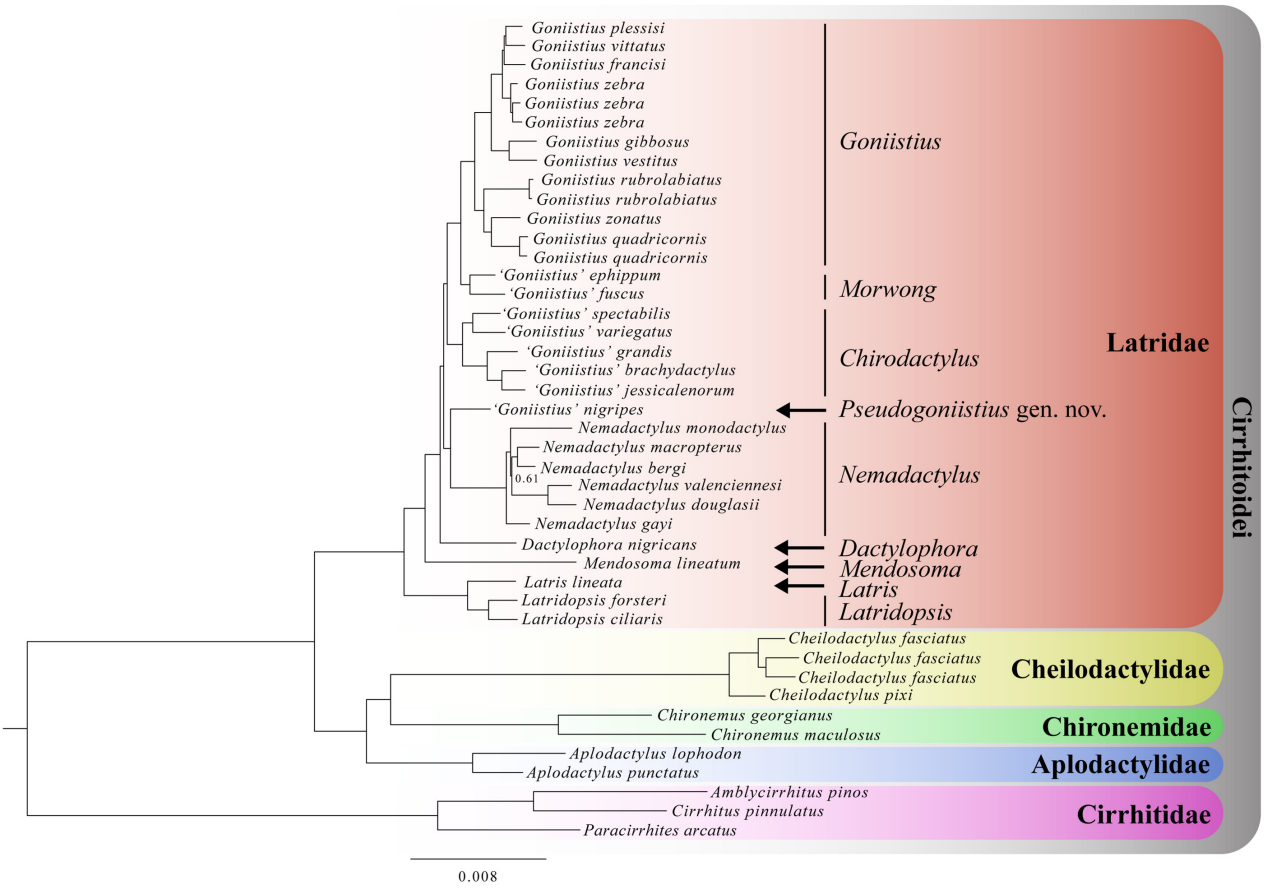

FIGURE 1. Concatenated UCE molecular phylogeny of the Cirrhitoidei, highlighting the different families with a focus on taxonomic changes within the Latridae. Topology shown was constructed in a partitioned Bayesian framework with the program Exabayes, and is identical to one constructed in a maximum likelihood framework. All nodes are strongly supported (posterior probability $\geq$ 0.99) unless otherwise noted.

Cheilodactylus sensu Nelson *et al.* (2016) as recognized here is polyphyletic. The two aforementioned South African species are distantly related to the remaining species of *Cheilodactylus*. *Goniistius* sensu Kimura *et al.* (2018) is not recovered as monophyletic, with *'Goniistius' nigripes* (Richardson) consistently recovered as the sister group to *Nemadactylus*. Furthermore, we find strong support for a clade containing *'Goniistius' spectabilis* (Hutton) and *'G.' variegatus* (Valenciennes) that is recovered as the sister group to all previously accepted species of *Chirodactylus*. Topological comparisons using AU and SH tests between our results and a tree constraining

cheilodactylid monophyly sensu Nelson *et al.* (2016), a tree constraining *Cheilodactylus* sensu Nelson et al. (2016) without *C. fasciatus* and *C. pixi* as monophyletic, and to a tree constrained to the topology found in Kimura *et al.* (2018), found statistically significant greater log likelihood values for our observed tree over all constrained trees (all p values < 0.01). All genomic data gathered for this study, including raw sequences, and assembled loci can be found on GenBank associated with NCBI BioProject PRJNA507975, and all new taxonomic names have been registered to ZooBank (LSID: urn:lsid:zoobank.org:act:B1D177BB-A145-485C-BDB5-4C2A95122EE1).

TABLE 1. Samples sequenced and summary statistics for individuals used. B&S refers to original tissues used in Burridge & Smolenski (2004).

Species	Source	Raw reads	Loci recovered
Cheilodactylidae			
Cheilodactylus fasciatus	KU:KUIT 6468	1,150,690	421
	B&S	2,308,194	444
	B&S	2,533,871	442
C. pixi	KUIT 6472	266,915	429
Latridae			
Dactylophora nigricans	B&S	382,347	452
'Goniistius' brachydactylus	KU:KUIT 6471	422,222	422
'G. ephippium'	B&S	3,642,301	440
G. francisi	B&S	2,585,692	439
'G. fuscus'	B&S	1,413,194	453
G. gibbosus	B&S	1,934,160	445
'G. grandis'	B&S	2,741,475	430
'G. jessicalenorum'	KU:KUIT 5028	4,203,003	425
'G. nigripes'	B&S	891,193	431
G. plessisi	B&S	647,246	424
G. quadricornis	B&S	938,550	438
	FMNH 121011	1,469,904	445
G. rubrolabiatus	B&S	1,657,231	411
	Peter Coulson	1,351,539	397
'G. spectabilis'	B&S	2,853,363	438
'G. variegatus'	B&S	3,563,220	449
G. vestitus	B&S	3,829,121	439
G. vittatus	B&S	209,239	415
G. zebra	FAKU 139310	1,754,289	392
	FAKU 139312	1,632,920	406
	FAKU 139313	1,639,489	398
G. zonatus	B&S	576,483	431
Latris lineata	B&S	691,644	440
Latridopsis ciliaris	B&S	312,984	430
L. forsteri	B&S	2,764,266	449
Mendosoma lineatum	B&S	352,392	440
Nemadactylus bergi	B&S	666,919	446
N. douglasii	B&S	2,405,495	448
N. gayi	B&S	249,163	434
N. macropterus	B&S	1,812,347	415
N. monodactylus	B&S	2,870,462	448

.....continued on the next page

TABLE 1. (Continued)

Species	Source	Raw reads	Loci recovered
N. valenciennesi	B&S	1,725,980	405
Aplodactylidae			
Aplodactylus lophodon	B&S	5,306,269	374
A. punctatus	B&S	796,376	436
Chironemidae			
Chironemus georgianus	B&S	958,095	392
C. maculosus	B&S	2,785,922	442
Cirrhitidae			
Amblycirrhitus pinos	YPM 24700	1,498,782	316
Cirrhitus pinnulatus	FMNH 124748	452,873	430
Paracirrhites arcatus	YPM 26776	7,074,831	213
Centrarchidae (outgroup)			
Ambloplites constellatus	YPM 15709	4,418,201	412
Lepomis macrochirus	LSUMZ-F 6271	2,738,928	439
L. megalotis	LSUMZ-F 6269	1,106,146	387
Micropterus coosae	YPM 18577	3,541,928	399
M. salmoides	LSUMZ-F 6270	3,729,082	451

Systematic accounts

Family Cheilodactylidae Regan

Diagnosis. Diagnosis follows that of Kimura *et al.* (2018) and Smith (1980) for *Cheilodactylus*. The family can be diagnosed by the following combination of characters: body compressed and ovoid, with small, terminal to sub-terminal mouth with large lips; eyes moderate size; two pairs of nostrils with cirri on the lower pair of nostrils; no bony processes on frontal bone or maxilla; teeth small, villiform in several rows, absent from vomer and palatines. Dorsal-fin elements XVII–XX, 19–25; anal-fin elements III, 9–11; pectoral-fin rays 14 with ventral 4–5 thickened and unbranched. Dorsal-fin continuous with no division between spinous and soft portions; spines increasing in length to sixth spine, and decreasing thereafter; second dorsal ray longest. Gas bladder absent; three supraneurals, with first supraneural preceding first neural spine and second and third supraneural between first and second neural spines in the arrangement of 0/0+0/2+1/1/1 (Fig. 2). Lateral-line scales 78–85; scales small and cycloid; scaly sheath present at base of dorsal and anal-fins. Cheilodactylidae can be further differentiated from Cirrhitidae by dorsal spines lacking cirri (versus present), and from both Chironemidae and Aplodactylidae by higher anal-fin ray counts and a more laterally compressed, deeper body. Cheilodactylidae can be further differentiated from Latridae by the absence of a gas bladder, by late-stage larvae lacking a 'paperfish' stage (Dudnik 1977), and by the arrangement of supraneurals with the first neural spine (see family diagnosis for Latridae below).

Genus *Cheilodactylus* Lacépède
(Fig. 3)

Cheilodactylus Lacépède, 1803:5 [Type-species: *Cheilodactylus fasciatus* Lacépède, 1803, by monotypy].
Chilodactylus Agassiz, 1846:78, 80 [unjustified emendation of *Cheilodactylus fasciatus* Lacépède, 1803].
Trichopterus Gronow, 1854:162 [Type-species: *Trichopterus indicus* Gronow, 1854, (= junior synonym of *C. fasciatus* Lacépède, 1803) by monotypy].
Pteronemus Van der Hoeven 1855:177 [Type-species: *Cheilodactylus fasciatus* Lacépède, 1803 (unneeded substitute for *Cheilodactylus* Lacépède, 1803)].

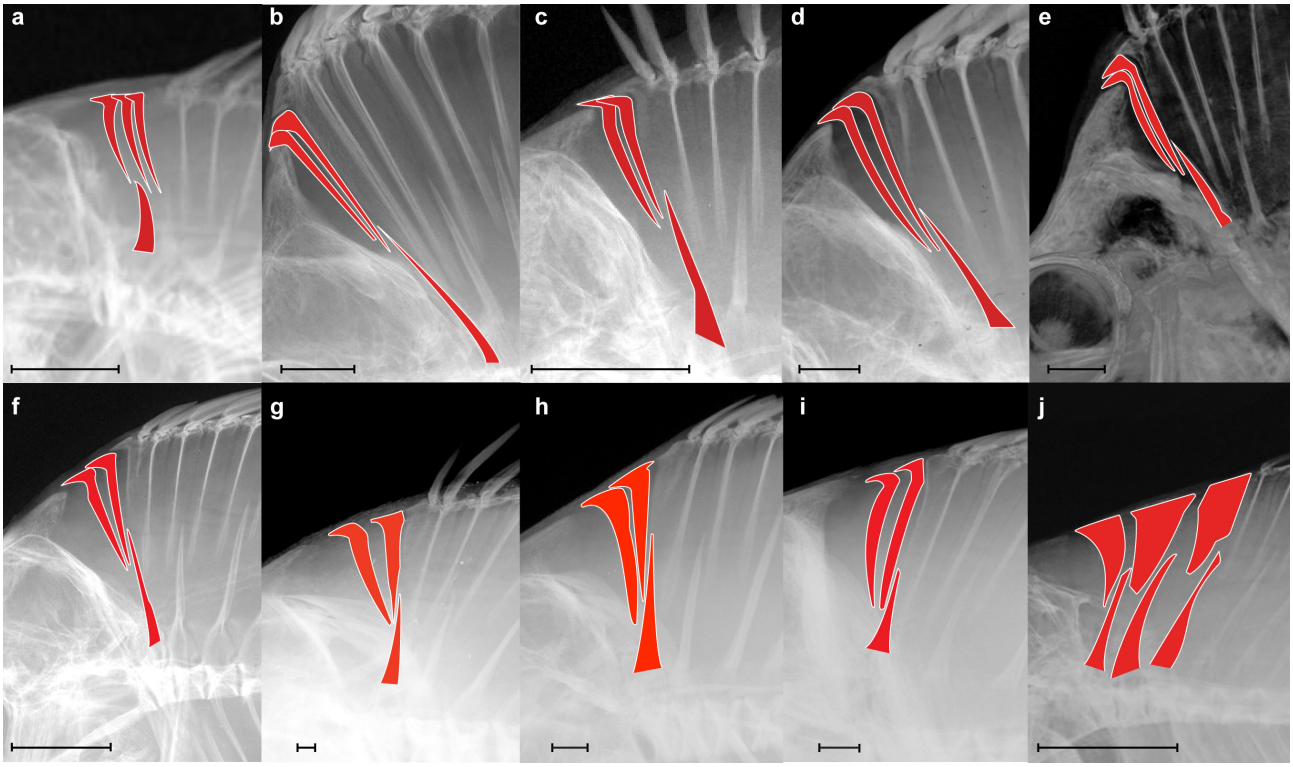

FIGURE 2. Radiographs highlighting the arrangement of supraneurals and neural spines that can differentiate the Cheilodactylidae and Latridae. All genera of these two families are shown. a) *Cheilodactylus fasciatus* ROM 50995, b) *Goniistius plessisi* USNM 226553, c) '*Goniistius*' *brachydactylus* USNM 153508, d) '*Goniistius*' *fuscus* CAS 20803, e) '*Goniistius*' *nigripes* YPM 5957, f) *Nemadactylus macropterus* USNM 39674, g) *Latris lineata* USNM 176770, h) *Latridopsis forsteri* USMN 84370, i) *Dactylophora nigricans* USNM 440480, j) *Mendosoma lineatum* CSIRO 1119. All scale bars represent 5mm.

FIGURE 3. *Cheilodactylus fasciatus,* ROM 50995, 109mm SL. Photograph by E Holm.

Etymology. Gender masculine. Derived from the Greek cheilos (lip) for the fleshy lips of these species, and daktylos (finger) for the lower, unbranched pectoral fin rays.

Inclusive species. *Cheilodactylus fasciatus* Lacépède (type species), *C. pixi* Smith

Diagnosis. As per family diagnosis.

Habitat and distribution. Both *C. fasciatus* and *C. pixi* occur in cooler waters from Namibia, to Natal, South

Africa. These species can be found in shallow, coastal rocky habitats and are common to 30m depth. However, both *C. fasciatus* and *C. pixi* have been observed at 97m and 120m, respectively (Smith & Heemstra 1986). These species generally stay close to the benthos where they hide among rocks and other rubble (Smith 1980). Tidepools are thought to be an important nursery habitat for juvenile *C. fasciatus* in South Africa (Beckley 1985).

Comments. These species range in size from 180mm for *C. pixi*, to 300mm for *C. fasciatus* (Smith 1980). Both species are primarily benthic invertivores (Smith & Heemstra 1986, Griffiths & Lechanteur 2003).

Material examined. *C. fasciatus*, ROM 050995 [n=6, South Africa: Port Alfred]; *C. pixi,* AMS I.37729 [n=5, South Africa: Tsitsikama], ANSP 97464 [n=1, Mozambique: Maputo Bay], CAS 45331 [n=1 (paratype), South Africa: Algoa Bay], USNM 221144 [n=1 (paratype), South Africa: Algoa Bay], USNM 385232 [n=6, South Africa: Tsitsikama].

Family Latridae Gill

Diagnosis. Latridae can be diagnosed by the following combination of characters: body ovoid to elongate and compressed or round in cross-section; dorsal-fin elements XV–XXV, 22–44; anal-fin elements III, 7–37; pectoral-fin rays 14 with ventral rays thick and unbranched. Gas bladder present; supraneurals never in the arrangement of Cheilodactylidae—all genera except *Mendosoma* with two supraneurals prior to first dorsal pterygiophore in arrangement of 0+0/2; no cirri on dorsal-fin elements. Latridae can be distinguished from all other cirrhitoids by having two supraneurals preceding the first neural spine, except for *Mendosoma*, which can be distinguished by having a single dorsal-fin spine articulating with the first dorsal pterygiophore (as opposed to two in all other families within Cirrhitoidei; Fig. 2). While not all larvae have been described, Latridae remains the only family in Cirrhitoidei to exhibit a late-larval 'paperfish' stage where larvae have deep bodies with a strong ventral keel adapted for pelagic life.

Genus *Chirodactylus* Gill
(Fig. 4)

Chirodactylus Gill, 1862: 119 [Type-species: *Cheilodactylus antonii* Valenciennes, 1833 (= junior synonym of *C. variegatus* Valenciennes, 1833) by original designation].
Palunolepis Barnard, 1927: 456 [Type-species: *Cheilodactylus grandis* Günther, 1860 by original designation].

Etymology. Gender masculine. Derived from the Greek cheir (hand) and daktylos (finger) for the long, unbranched lower pectoral fin rays observed in this genus.

Inclusive species. *C. variegatus* (Valenciennes) (type species), *C. brachydactylus* (Cuvier), *C. grandis* (Günther), *C. jessicalenorum* Smith, *C. spectabilis* (Hutton)

Diagnosis. *Chirodactylus* can be diagnosed by the following combination of characters: dorsal-fin elements XVII–XVIII, 22–31; anal-fin elements III, 7–10; pectoral-fin rays 14 with ventral 6–7 unbranched and thickened; lateral-line scales 46–56. Body ovoid and compressed; dorsal profile of head slight to moderate; dorsal-fin increasing gradually in length to 5th or 6th spine, decreasing thereafter; no bony processes on frontal bones medially to orbit or anterior to maxilla.

Habitat and distribution. *Chirodactylus brachydactylus, C. grandis, and C. jessicalenorum* occur off the coast of South Africa to 240m (Smith 1980). *Chirodactylus variegatus* occurs in the southeast Pacific off the coast of Chile and Peru, and *C. spectabilis* occurs in the north island of New Zealand, Tasmania, and occasionally in southern mainland Australia.

Comments. Smith (1980) noted the convoluted taxonomic history of the genus, which is briefly described here. Gill (1862) erected *Chirodactylus* to include *C. antonii* Valenciennes 1833 (type species), *C. variegatus* Valenciennes 1833, and *C. grandis* Günther 1860. Barnard (1927) later described *Palunolepis* with *P. grandis* as the type species. *Chirodactylus variegatus* was later considered a senior synonym to *C. antonii* (de Buen 1959). In a review of Australian cheilodactylids, Allen and Heemstra (1976) regarded several genera, including *Chirodactylus* (but not *Palunolepis*), as junior synonyms to *Cheilodactylus. Chirodactylus* was later resurrected in a comparison of South African morwongs by Smith (1980), who included *C. brachydactylus, C. jessicalenorum, C.*

grandis, and *C. variegatus*. However, the latter species was not recognized by all (see list of recognized species in Eschmeyer *et al.* 2019). Recently this genus was synonymized once again with *Goniistius*, similarly to the classification proposed by Allen & Heemstra (1976), due to low resolution in the topology recovered by Kimura *et al.* (2018). The genus is re-elevated and expanded here to include *C. variegatus* (senior synonym of *C. antonii*, type species) and *C. spectabilis* based on strongly supported molecular evidence and morphological characters. *Chirodactylus* is superficially similar to *Goniistius*, but can be distinguished by a shallower dorsal head profile, a lack of bony processes on the frontal bones and maxilla, and a lack of a greatly enlarged 4th dorsal-fin spine.

Material examined. *C. brachydactylus*, USNM 93652 [n=1, South Africa: Western Cape], USNM 153508 [n=2, South Africa: Western Cape], ANSP 97440 [n=1, Mozambique: Maputo Bay]; *C. jessicalenorum*, USNM 221145 [n=3, South Africa: Natal]; *C. spectabilis*, NMV A22205 [n=1, Australia: New South Wales: Green Cape], NMV A14 [n=1, Australia: Victoria], NMV A44 [n=1, Australia: Victoria: Welshpool], NMV A24816 [n=1, Australia: Victoria: Little Ram Head Point]; *C. variegatus*, CAS 8447 [n=4, Peru: Lima: Bay of Callao], USNM 77517 [n=1], USNM 128061 [n=4].

FIGURE 4. *Chirodactylus brachydactylus*, ANSP 97440, 116.9mm SL.

Genus *Dactylophora* De Vis

(Fig. 5)

Dactylophora De Vis, 1883: 284 [Type-species: *Dactylophora semimaculata* De Vis, 1883 (= junior synonym of *D. nigricans* De Vis, 1883) by monotypy].

Psilocranium Macleay, 1884: 439 [Type-species: *Psilocranium coxii* Macleay, 1884 (= junior synonym of *D. nigricans* De Vis, 1883) by monotypy].

Etymology. Gender masculine. Derived from the Greek daktylos (finger) and pherein (to carry).

Inclusive species. *Dactylophora nigricans* (Richardson) (type by monotypy)

Diagnosis. *Dactylophora* can be diagnosed by the following combination of characters: dorsal-fin elements XV–XVI, 24–26; anal-fin elements III, 9–10; pectoral-fin rays 14 with ventral 5 unbranched and thickened; lateral-line scales 45–55. Height of soft dorsal fin roughly equal to height of spinous portion. Elongate body with shallow dorsal head profile; body cylindrical in cross section; scales cycloid and large on body; eyes moderate size; no bony processes on frontal bones or maxilla.

Habitat and distribution. Found by rocky reefs, weeds and seagrasses to 30m (Kuiter 1993). Distributed along the southern coast of Australia and northern Tasmania.

Comments. Distinguished from all other latrids by a long, cylindrical body that lacks both a pointed snout and high anal-fin ray counts. Can acquire large adult sizes, reaching 1.2m TL (Kuiter 1993).

Material examined. *D. nigricans*, LACM 52122 [n=1, Australia], NMV A17775 [n=1, Australia: Victoria: Port Phillip Bay], NMV A13967 [n=1, Australia: Victoria: Port Phillip Bay], NMV A25379-001 [n=1, Australia: Victoria: Port Phillip Bay], USNM 440480 [n=1, Australia: Tasmania].

FIGURE 5. *Dactylophora nigricans*, USNM 84375, 338mm SL. Photograph by Sandra Raredon.

Genus *Goniistius* Gill

(Fig. 6)

Goniistius Gill, 1862: 120 [Type-species: *Cheilodactylus zonatus* Cuvier, 1830 by original designation].
Zeodrius Castelnau 1879: 377 [Type-species *Zeodrius vestitus* Castelnau, 1879 by subsequent designation of Jordan, 1919].
Gregoryina Fowler & Ball 1924: 270 [Type-species: *Gregoryina gygis* Fowler & Ball, 1924 (= junior synonym of *G. vittatus* Garrett, 1864) by original designation].

Etymology. Gender masculine. Derived from the Greek -gon (angled), and the Greek istion (sail) for the oblique bars found on many species.

Inclusive species. *Goniistius zonatus* (Cuvier) (type species), *G. francisi* (Burridge), *G. gibbosus* (Richardson), *G. plessisi* (Randall), *G. quadricornis* (Günther), *G. rubrolabiatus* (Allen & Heemstra), *G. vestitus* (Castelnau), *G. vittatus* (Garrett), *G. zebra* (Döderlein)

Diagnosis. Diagnosis as in Randall (1983) using the following combination of characters: dorsal-fin elements XVI–XVIII, 29–35; anal-fin elements III, 8–12; lateral-line scales 54–71; pectoral-fin rays 14 with ventral 6 thickened and unbranched; pectoral-fin rays not extending to anal-fin origin. Body ovoid and compressed; lips large and fleshy; bony processes commonly found on the frontal bone medially to the orbit or anteriorly on the maxilla except for *G. rubrolabiatus* and *G. zonatus*; dorsal profile of head steep and resulting in a deep body for all species except *G. rubrolabiatus*. All species with multiple angled bars along the body and head, which are black and white in most species (reddish brown in *G. rubrolabiatus*, and yellow in *G. zonatus*).

FIGURE 6. *Goniistius zonatus*, FMNH 58764, 161.1mm SL. Photograph by CD McMahan.

Habitat and distribution. This genus has an anti-tropical distribution in the Pacific (Randall 1983). In the Southern Hemisphere they are found in the temperate waters off eastern and western Australia and two species occur among south Pacific islands, including Easter Island. Members of this genus also occur in the Northern

Hemisphere in Japan, Korea, China, Taiwan, and Hawaii. Members of *Goniistius* are commonly found in rocky reef areas consuming invertebrates from the substrate.

Comments. In their revision of Australian morwongs, Allen and Heemstra (1976) placed several genera, including *Goniistius*, in synonymy with *Cheilodactylus* because many of these genera were erected due to morphological differences with the type species, *C. fasciatus*. Since then, *Goniistius* was treated as a valid subgenus of *Cheilodactylus* by many authors (Randall 1983, Burridge & White 2000), and several suggested re-elevating *Goniistius* (Randall 2005). Kimura *et al.* (2018) distinguished *C. fasciatus*, and *C. pixi,* as entirely distinct from all Australian morwongs, and elevated *Goniistius* as a genus within the Latridae while also expanding it to include all species historically associated with *Chirodactylus*. Of all species in this genus, *G. rubrolabiatus* appears to be the most phenotypically distinct, lacking the elevated dorsal head profile, the elongated 4th dorsal-fin spine, and the black and white coloration. However, molecular evidence strongly supports its placement within the genus.

Material examined. *G. francisi,* AMS I27139-006 [n=1, Australia: Tasman Sea: Middleton Reef], AMS I42728-001 [n=1, Australia: Lord Howe Island], AMS I27134-003 [n=1, Australia: Tasman Sea: Middleton Reef], USNM 47814 [n=1]; *G. gibbosus* WAM P25999-001 [n=1, Australia: Western Australia: Point Peron], WAM P24836 [n=1, Australia: Western Australia: Irwin Inlet], WAM P21780-001 [n=1, Australia: Western Australia: Swan River], WAM P25270-001 [n=1, Australia: Western Australia: Hardy Inlet], WAM P25072 [n=1, Australia: Western Australia: Harding River], USNM 84377 [n=1]; *G. plessisi* CAS 47908 [n=1 (paratype), French Polynesia: Easter Island], USNM 226553 [n=1 (paratype), French Polynesia: Easter Island], USNM 378135 [n=1, French Polynesia: Easter Island]; *G. rubrolabiatus* WAM 25225 [n=1 (holotype), Australia: Western Australia: Fremantle], WAM P22580 [n=1 (paratype), Australia: Western Australia: Rockingham], WAM P5562 [n=1, Australia: Western Australia: Rottnest Island], WAM P5925 [n=1, Australia: Western Australia: Trigg Island], USNM 214831 [n=1 (paratype), Australia: Western Australia: Cockburn Sound]; *G. vestitus* AMS I41831-003 [n=1, Australia: New South Wales: Iron Peg Point], AMS I4858-005 [n=1, Australia: New South Wales: Clarence River], CAS 20400 [n=1, Australia: Queensland: Moreton Bay], NMV 54113 [n=1, Australia: New South Wales: Port Jackson]; *G. vittatus* CAS 20386 [n=2, United States: Hawaii: Oahu: Honolulu], USNM 126514 [n=1, United States: Hawaii]; *G. zebra* CAS 23483 [n=1, Japan: Kanagawa Prefecture: Misaki], USNM 56431 [n=1]; *G. zonatus* CAS 13996 [n=3, China: Hong Kong: Cape D'Aguilar], USNM 71062 [n=1, Japan: Osaka Prefecture: Misaki].

Genus *Latridopsis* Gill

(Fig. 7)

Latridopsis Gill, 1862: 115 [Type-species: *Anthias ciliaris* Forster, 1801 by original designation].

Micropus Kner, 1868: 29 [Type-species: *Micropteryx polycentrus* Kner, 1868 by monotypy (objectively invalid; preoccupied four times and replaced by *Orqueta* Jordan, 1919)].

Evistias Gill, 1893:114 [Type-species: *Platystethus huttonii* Günther, 1876 (= junior synonym of *L. forsteri* Castelnau, 1872 or *L. ciliaris* Forster, 1801) by monotypy].

Orqueta Jordan, 1919:344 [Type-species: *Micropteryx polycentrus* Kner, 1868 as a replacement name for *Micropus* Kner, 1868, four times preoccupied].

Melbanella Whitley 1937: 132 [Type-species: *Micropus muelleri* Steindachner, 1879 (= junior synonym of *L. forsteri* Castelnau, 1872) by original designation].

Etymology. Gender feminine. Derived from the Greek latris (slave) and opsis (appearance).

Inclusive species. *Latridopsis ciliaris* (Forster) (type species), *Latridopsis forsteri* (Castelnau)

Diagnosis. *Latridopsis* can be diagnosed with the following combination of characters: dorsal-fin elements XVI–XVII, 37–43; anal-fin elements III, 31–37; pectoral-fin rays 16–19; pectoral-fin rays not greatly elongated, upper rays longer than lower rays, distal edges of fins rounded. Body moderately ovoid to elongate and highly compressed laterally; caudal peduncle thin; snout pointed with a terminal mouth; lips not as enlarged as other species in Latridae; strong notch between spinous and soft dorsal-fins; dorsal-fin spines not enlarged and none that are significantly longer than others; anal-fin long and reaching caudal peduncle. Body gray in appearance; scales cycloid.

Habitat and distribution. Tasmania, southeastern Australia and New Zealand. Demersal species, generally found near rocky reefs to 160m (Roberts 2015).

Comments. These species feed on a variety of benthic invertebrates. They are generally solitary, or in small groups, but migrate in large schools (Kuiter 1993). Commercially harvested in parts of their range (Roberts 2015).

Material examined. *L. ciliaris* CAS 58777 [n=1, New Zealand: Cape Wanbrow]; *L. forsteri,* AMS I17556-010 [n=1, Australia: Tasmania: Granville Harbour], USNM 226548 [n=1].

FIGURE 7. *Latridopsis forsteri*, SIO 84-299, 165mm SL. Photograph by Ben Frable.

Genus *Latris* Richardson

Latris Richardson, 1839: 98 [Type-species: *Latris hecateia* Richardson, 1839 (= junior synonym of *L. lineata* Forster, 1801) by monotypy].

Etymology. Gender masculine. Derived from the Greek word latris (slave).

Inclusive species. *Latris lineata* (Forster) (type species), *Latris pacifica* Roberts

Diagnosis. Diagnosis follows that of Roberts (2003) with the following combination of characters: elongate, compressed body; eye small; terminal mouth; caudal peduncle thin, with caudle fin strongly forked; dorsal-fin elements XVII–XX, 33-44; anal-fin elements III, 26–37; pectoral-fin rays 16–19 with 6–9 branched rays; pectoral-fin rays not reaching anal-fin origin; 98–125 lateral line scales; 37–43 vertebrae; scales small and cycloid.

Habitat and distribution. Found throughout the temperate Southern Hemisphere, with the exception of South Africa, to 300m in rocky regions (Roberts 2003).

Comments. *Latris lineata* is popular in commercial fisheries, and can live to 43 years (Roberts 2015). Less is known of *L. pacifica*, although it too may be harvested in large numbers but misidentified as *L. lineata*. Larvae are adapted to a long pelagic 'paper fish' stage that allow for long-distance dispersal. There is an extensive taxonomic history of this genus outlined in Roberts (2003).

Material examined. *L. lineata* USNM 176770 [n=1, New Zealand: Auckland], CSIRO H 4944 [n=1, Australia: Tasmania:], CSIRO H 4945 [n=1, Australia].

Genus *Mendosoma* Guinchenot

Mendosoma Guinchenot, 1848: 212 [Type-species: *Mendosoma lineata* Guinchenot, 1848 by subsequent designation of Bleeker, 1876].

Etymology. Gender neuter. Derived from Venetian mendole (fish), and the Greek soma (body).

Inclusive species. *Mendosoma lineatum* Guinchenot (type by monotypy)

Diagnosis. *Mendosoma* is diagnosed from all other latrids by having a combination of the following

characters: dorsal-fin elements XXII–XXV, 23–27; anal-fin elements III, 17–21; pectoral-fin rays 16–19; vertebrae 42–46. Body elongate with a pointed snout and terminal mouth; mouth highly protrusible; eye moderate; no teeth on lower jaw; scales small and cycloid; supraneurals arranged 0/0/0/1+1/1+1/1 (Fig. 2j).

Habitat and distribution. Found throughout the temperate waters of the Southern Hemisphere from Tasmania, southern Australia, New Zealand and southern Chile. Commonly found in tide pools and in the water column near rocky reefs to 22m (Roberts 2015).

Comments. Distinguished from all other latrids by the unique supraneural arrangement with a single dorsal-fin spine articulating with the first dorsal pterygiophore, the elongate, tubular body, and the pointed, highly protrusible mouth. Feeds on zooplankton in the water column. Five species of *Mendosoma* have been described in the literature, but here we take the conservative approach of only recognizing a single species based on the detailed results of Gon & Heemstra (1987).

Material examined. *M. lineatum,* CSIRO H 2377-01 [n=1, Australia: Tasmania], CSIRO T 1119 [n=1, Australia: Tasmania: Maria Island], NVM A19874 [n=1, Australia], NVM A11395 [n=1, Australia].

Genus *Morwong* Whitley

(Fig. 8)

Morwong Whitley, 1957: 65 [Type-species: *Cheilodactylus fuscus* Castelnau, 1879 by original designation].

Etymology. Gender masculine. Derived from an aboriginal word for fish.

Inclusive species. *Morwong fuscus* (Castelnau) (type species), *M. ephippum* (McCulloch & Waite)

Diagnosis. *Morwong* can be diagnosed by the following combination of characters: dorsal-fin elements XVI – XVIII, 30–35; anal-fin elements III, 8–9; lateral-line scales 59–66; pectoral-fin rays 13–14 with ventral 5–6 rays thickened and unbranched. Can be distinguished from *Goniistius* by a shallower dorsal head profile, and a shorter 4th dorsal-fin spine, and from *Chirodactylus* by a higher lateral-line scale count (59–66 in *Morwong* versus 46–56 in *Chirodactylus*) and higher dorsal-fin soft ray count (30–35 in *Morwong* versus 22–31 in *Chirodactylus*). Color generally brown to brownish red.

FIGURE 8. *Morwong fuscus,* ANSP 122393, 168.3mm SL.

Habitat and distribution. Occurs off the southeast coast of Australia, the northern island of New Zealand, and islands of the Tasman Sea, to 50m among rocky reef habitats.

Comments. Originally erected by Whitley (1957), *Morwong* was described as distinct from other members of *Cheilodactylus* by the number of dorsal-fin elements and lateral line scales, as well as 'transverse dark bars' on the body. These diagnostic characters remain largely valid when compared to Cheilodactylidae as recognized herein

(restricted to two species in South Africa). Both species of *Morwong* are largely brown to brownish red, a character only shared with *G. rubrolabiatus*, but absent from any other members of the family. Kimura *et al.* (2018) placed these two species within *Goniistius*, however, they are easily distinguished from other species in *Goniistius*, and have never been historically included in that subgenus (see Randall 1983).

Material examined. *M. ephippium,* AMS I20493-001 [n=1, Australia: New South Wales: Broughton Island], AMS I20255-001 [n=1, Australia: New South Wales: Norfolk Island], AMS I27891-026 [n=1, Australia: Tasman Sea: Elizabeth Reef], AMS I24294-001 [n=1, Australia: New South Wales: Montague Island]; *M. fuscus,* AMS I24982-001 [n=1, Australia: New South Wales: Manly], ANSP 122393 [n=1, Australia: Queensland: Bribie Island], CAS 20803 [n=1, Australia: New South Wales: Port Jackson], NMV 54265 [n=1, Australia: New South Wales: Port Jackson], USNM 59938 [n=1].

Genus *Nemadactylus* Richardson

(Fig. 9)

Nemadactylus Richardson, 1839: 98 [Type-species: *Nemadactylus concinnus* Richardson, 1839 (=junior synonym of *N. macropterus* Forster, 1801) by monotypy].

Dactylopagrus Gill, 1862: 114 [Type-species: *Cheilodactylus carponemus* Cuvier, 1830 (= junior synonym of *N. macropterus* Forster, 1801) by original designation].

Dactylosparus Gill, 1862: 117 [Type-species: *Cheilodactylus carponemus* Cuvier, 1830 (objective synonym of *Dactylopagrus* Gill, 1862)].

Acantholatris Gill, 1862: 119 [Type-species: *Chaetodon monodactylus* Carmichael, 1819 (= junior synonym of *N. monodactylus* Carmichael, 1819) by original designation].

Etymology. Gender masculine. Derived from the Greek nema (filament) and daktylos (finger) for the elongated pectoral fin rays.

Inclusive species. *Nemadactylus macropterus* (Forster) (type species), *N. bergi* (Norman), *N. douglasii* (Hector), *N. gayi* (Kner), *N. monodactylus* (Carmichael), *N. rex* Roberts, *N. valenciennesi* (Whitley), *N. vemae* (Penrith)

Diagnosis. *Nemadactylus* can be diagnosed by the following combination of characters: dorsal-fin elements XVI–XVIII, 24–31; anal-fin elements III, 11–19; pectoral-fin rays 14–16 with one greatly elongated ray that extends past the origin of the anal-fin; body ovoid and compressed without any greatly elongated dorsal-fin spines; dorsal head profile shallow; spinous and soft dorsal-fin portions not separated by a large notch.

FIGURE 9. *Nemadactylus macropterus*, ANSP 102720, 213.8mm SL.

Habitat and distribution. Widely distributed throughout the temperate Southern Hemisphere. Occur in Australia, New Zealand, South America, and oceanic islands within the Southern Ocean. Typically found on rocky reefs, or sandy habitat near rocky reefs to 400m (Kuiter 2003).

Comments. Feed on a variety of benthic invertebrates. Some species targeted in both recreational and commercial fisheries.

Material examined. *N. bergi*, ANSP 102720 [n=1, Argentina: Buenos Aires]; *N. douglasii,* NMV A13196 [n=5, Australia: New South Wales: Merimbula]; *N. gayi,* USNM 176401 [n=3], USNM 176402 [n=1]; *N. macropterus,* CAS 58782 [n=2, New Zealand: Wellington Harbor], NMV A21603 [n=5, Australia: Tasmania: Flinders Island], USNM 39674 [n=1]; *N. valenciennesi,* NMV A12627 [n=2, Australia: Victoria: Cape Duquesne], WAM P21896 [n=1, Australia: Western Australia: Esperance].

Genus *Pseudogon iistius* Ludt, Burridge & Chakrabarty, gen. nov.
(Fig. 10)

Etymology. Gender masculine. Named for the superficial similarity this species has with those of *Goniistius*, and for the confusion that this species has caused with morwong classification in the past (Randall 1983).

Inclusive species. *Pseudogoniistius nigripes* (Richardson)

Type-species. *Cheilodactylus nigripes* Richardson, 1850 by monotypy.

Neotype. WAM P24858.001, 127mm SL, King George's Sound, Western Australia, 35º S, 117º55' E, 23 July 1974, collected in 2–3m of water by G.R. Allen. Neotype herein designated. [Holotype, originally dried, 330.2 mm SL; type locality: King George's Sound, Western Australia, reported as never making it to the British Museum (Natural History) by A.C. Wheeler in personal comm. to J.E. Randall (Randall 1983). Recent communication with J.S. Maclaine (personal comm.) confirms that this holotype has not been found, and is still missing.]

Diagnosis. Diagnosis follows that of Randall (1983). Dorsal-fin elements XVII–XIX, 25–28; anal-fin elements III, 9–10; pectoral-fin rays 14 with ventral 5 or 6 thickened and unbranched; fifth pectoral-fin ray longest, extending past anal-fin origin; lateral line scales 63–69; scales cycloid; scaly sheath present at base of dorsal and anal fins; sheath is taller under soft portions of the dorsal-fin than under spinous portions. Dorsal-fin spines increasing in length to fifth, then decreasing slightly thereafter. Body compressed and ovoid with a steep head angle; fleshy, large lips present; two pairs of bony processes—one pair on frontal bones medial to orbit and the other pair superior to the maxilla. Body has a unique coloration for the family, with two wide, vertical dark bars intersecting the anal and pelvic fins, and a narrower dark bar intersecting the eye; caudal fin color is a reddish-brown. Only species in family that is known to rapidly change color by lightening the dark bars on the body.

FIGURE 10. *Pseudogoniistius nigripes*, YPM 5957, 242.6mm SL.

Habitat and distribution. Found on shallow rocky reefs in Southern Australia to 25m. Recorded, but rare, in northern New Zealand.

Comments. *Pseudogoniistius* has traditionally been allied with *Goniistius*. Recent osteological evidence supports this only in that relationships within *Goniistius* could not be resolved due to a lack of polymorphic characters (Kimura *et al.* 2018). However, other morphological (Randall 1983) and molecular approaches (Burridge & White 2000; this paper) clearly demonstrate that *P. nigripes* is not closely related to species of *Goniistius*. One character that was found distinguishing this species from all other taxa in Latridae is the presence of three spines on the anterior-most dorsal pterygiophore (Kimura *et al.* 2018). This character was confirmed in some of the specimens we examined, but was found to be variable in the species with some individuals only having two spines on the anterior-most dorsal pterygiophore (Fig. 2e). The ability to rapidly change color appears unique within the family.

Material examined. *P. nigripes* NMV A2569 [n=1, Australia: Victoria: Leonard Bay], NMV A20553 [n=1, Australia: Tasmania: Flinders Island], NMV A11913 [n=1, Australia], YPM 005957 [n=1, Australia: South Australia: Kangaroo Island].

Conclusions

Taxonomic confusion has persisted in cheilodactylid fishes for over a century. Here the families Cheilodactylidae and Latridae are examined with extensive taxonomic sampling, morphological characters, and strongly supported molecular data. Previous efforts to clarify the relationships of cheilodactylid fishes resulted in most genera being recognized as junior synonyms of *Cheilodactylus* (as per Allen & Heemstra 1976), or *Goniistius* (as per Kimura *et al.* 2018), both of which became a catch-all for a variety of morphologically, geographically, and behaviorally distinct fishes. These previous classifications did not reflect the evolutionary history of these fishes and seems to have aided in the confusion surrounding cheilodactylid relationships.

The overall relationships recovered here have been found by previous studies (Burridge & Smolenki 2004; Sanciangco *et al.* 2016; Kimura *et al.* 2018). The repeated recovery of Cheilodactylidae being restricted to two South African species from a variety of studies, which have used different species, molecular loci, and analytical approaches, increases the confidence that our findings accurately reflects the evolutionary history of these fishes. While this result is further corroborated by the osteological characters and larval characteristics included here, it does differ slightly from recent revisions of these families based purely on anatomical characters (Kimura *et al.* 2018).

This study agrees with Kimura *et al.* (2018) in that Cheilodactylidae is restricted to two South African species. However, our study strongly supports that these two species are distantly related to Latridae, being more closely related to Chironemidae and Aplodactylidae, which mirrors other molecular studies (Sanciangco *et al.* 2016). Kimura *et al.* (2018), on the other hand, recover Cheilodactylidae as a sister family to the newly redefined Latridae, which was supported by seven synapomorphies. Further, Kimura *et al.* (2018) re-elevated *Goniistius* from a subgenus, and expanded it to include many species that were never associated with the subgenus *Goniistius* (sensu Randall 1983), which reflects earlier studies that used *Cheilodactylus* as a 'catch-all' genus (Allen & Heemstra 1976). This generally reflects a lack of polymorphic characters in the anatomical data matrix of Kimura *et al.* (2018), which resulted in a polytomy for the genus, but could also be an artifact of limited taxonomic sampling. Our dataset has near complete taxonomic sampling and strongly supports a clade containing all species that have historically been associated with *Chirodactylus* (plus *Chirodactylus spectabilis*), and a clade containing *Morwong fuscus* and *M. ephippium*, both of which contain species that have never been associated with *Goniistius* (sensu Randall 1983). Furthermore, this study differs from Kimura *et al.* (2018) in recovering *Pseudogoniistius nigripes* as distantly related to other species of *Goniistius*, which reflects previous molecular (Burridge & White 2000) and morphological (Randall 1983) accounts.

This new classification scheme highlights clades that are sufficiently unique to be recognized as separate genera. One of our goals was to achieve a monophyletic taxonomy with the fewest number of changes that can be supported by morphology. While both *M. fuscus* and *M. ephippium* could be placed within *Goniistius* to reduce the number of genera in the Latridae, these taxa have never been associated with *Goniistius* in the past, and are quite distinct; in coloration, they are mostly red or brown while almost all *Goniistius* are striped with black and white

bars, and the length of dorsal-fin spines gradually increase to the fourth or fifth spine whereas species in *Goniistius* have a distinctly elongated fourth dorsal-fin spine compared to the preceding spines. Likewise, *P. nigripes* could be placed within *Nemadactylus* instead of a new, monotypic genus, yet this grouping would be unsatisfactory as this species lacks diagnostic characters of *Nemadactylus*, and is noticeably distinct from all other species in the Latridae. Finally, re-elevating *Chirodactylus* reflects a long-standing recognition that these species are notably distinct from other morwongs, and is strongly supported in all analyses herein.

By re-examining the families Cheilodactylidae and Latridae and re-describing the genera within Latridae, we have clarified their evolutionary history for future studies. The Cheilodactylidae is a small, but unique, family that is restricted to the temperate coastal waters of southern Africa. Conversely, the Latridae is a temperate family of 30 species that are extremely variable in diet, habitat, and body shape. This classification reflects the evolutionary history of this group and is a solid basis for future studies examining the evolutionary history of these families, and the suborder Cirrhitoidei.

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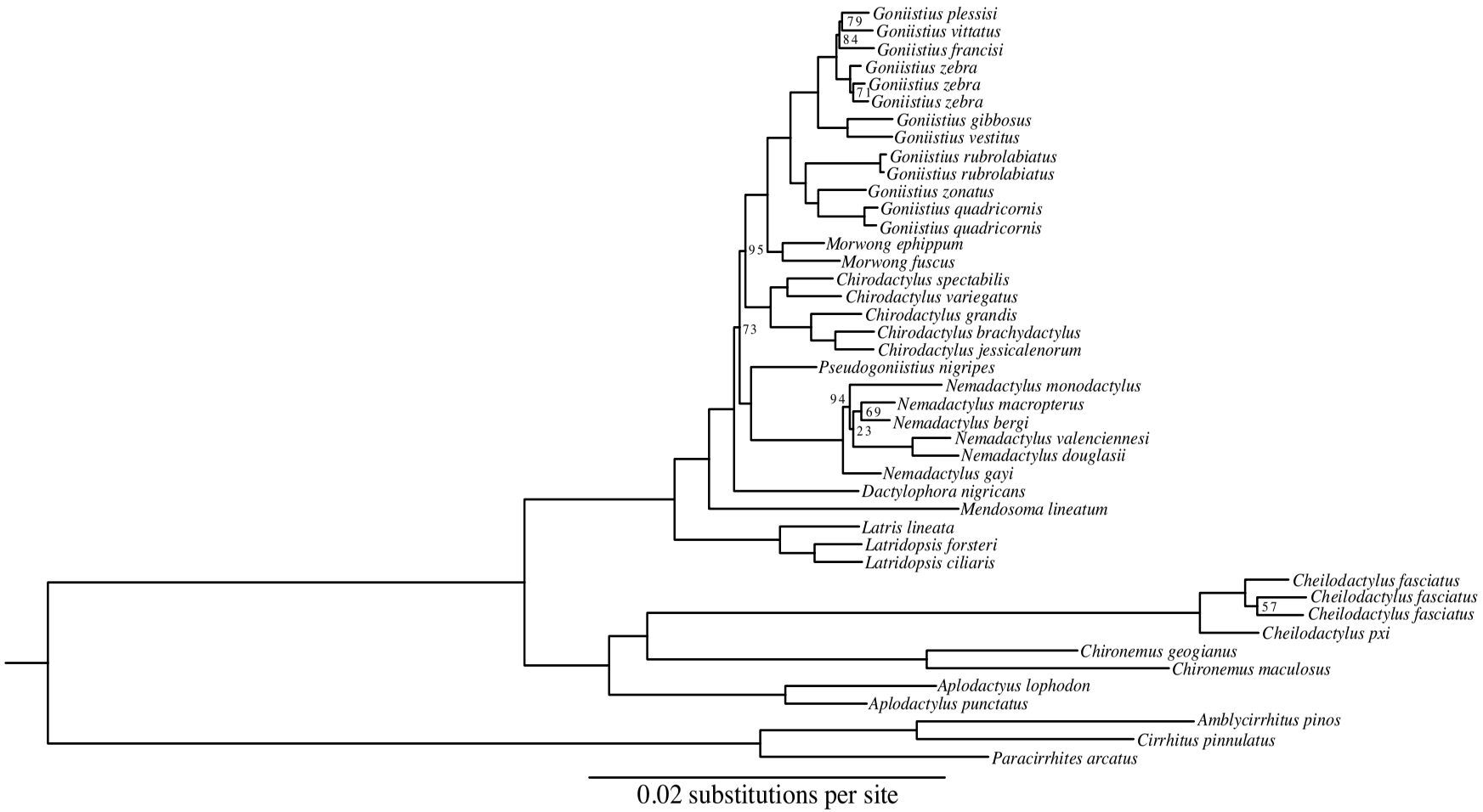

Figure S.1. Maximum likelihood phylogenomic hypothesis generated using a 75% complete concatenated data matrix with the program RAxML. Node values represent bootstrap support values, and are all 100, unless otherwise noted. Outgroups have been removed for simplicity.

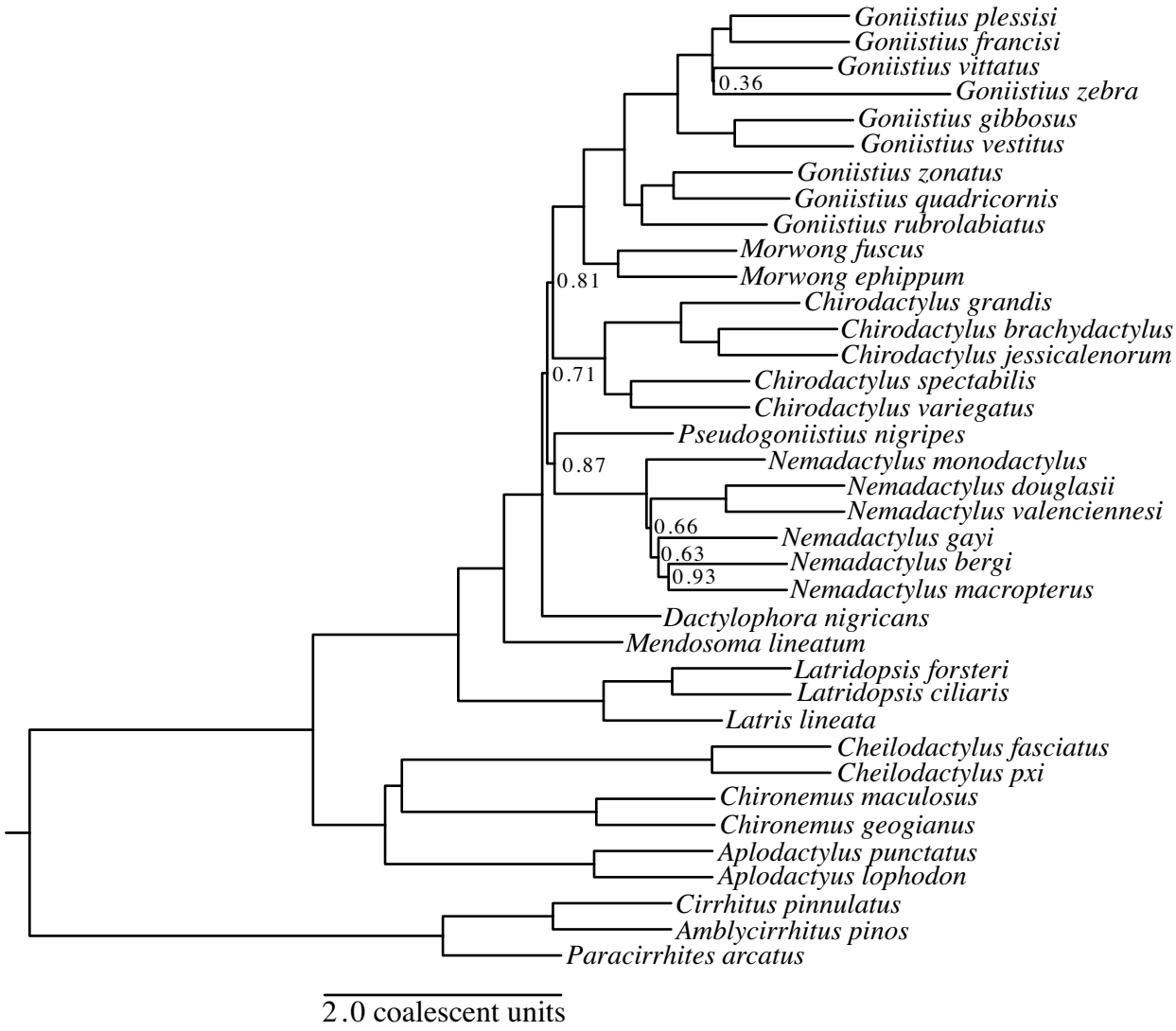

Figure S.2. Multi-species coalescent tree generated from UCE data using ASTRAL III. Local posterior probabilities are given at nodes if the values for those nodes were less than 1. Outgroups have been excluded for simplicity.