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Systematics of Damselfishes

Kevin L. Tang[1], Melanie L. J. Stiassny[2], Richard L. Mayden[3], and Robert DeSalle[4]

The family Pomacentridae is a species-rich group of primarily marine fishes. The phylogenetic relationships of the damselfishes are examined herein using sequence data from five mitochondrial (12S, 16S, ATP synthase subunits 8/6, cytochrome *b*, and cytochrome *c* oxidase I) and three nuclear (histone H3, recombination activating gene 1 exon 3, and Tmo-4C4) loci. A combined data matrix of 6,865 base pairs was compiled for 462 taxa, representing 322 damselfish species, and used to reconstruct the phylogeny of pomacentrids via maximum likelihood. The resulting topology supports the monophyly of the family and some groups within it, corroborating some conclusions drawn by recent studies but contradicting others. We find that the family is composed of four major lineages, recognized herein as the subfamilies Chrominae, Glyphisodontinae, Microspathodontinae, and Pomacentrinae. The subfamily Microspathodontinae is sister to a clade of the other three subfamilies, and the subfamily Glyphisodontinae is sister to a clade of Chrominae and Pomacentrinae. The monotypic subfamily Lepidozyginae is recovered within Microspathodontinae and placed in the synonymy of Microspathodontinae. Species of *Plectroglyphidodon* and *Stegastes* are reassigned to maintain the monophyly of both genera. In Chrominae, the generic limits of *Azurina* and *Chromis* are revised to reflect monophyletic groups. The genus-group name *Pycnochromis* is resurrected to accommodate a group of former *Chromis* sister to *Dascyllus*. In Pomacentrinae, the genus *Premnas* is recovered within *Amphiprion* and placed in the synonymy of *Amphiprion*. The genus *Chrysiptera* is broadly polyphyletic within Pomacentrinae. The genus *Amblypomacentrus* is revised to accommodate some species formerly classified as *Chrysiptera*.

DAMSELFISHES (Teleostei: Pomacentridae) are a diverse and widespread family of primarily marine fishes found throughout the tropical oceans where they form a major component of reef communities (Hiatt and Strasburg, 1960; Randall, 1963; Brock et al., 1979; Allen and Werner, 2002; Bellwood and Wainwright, 2002). Currently, there are over 400 recognized damselfish species, classified in a single family, Pomacentridae, and divided among 29 genera (Fricke et al., 2020), with new species regularly being described (e.g., Allen and Erdmann, 2020; Habib et al., 2020; Shepherd et al., 2020). The oldest record of a pomacentrid is from the Paleocene (Cantalice et al., 2020), but members of the family are relatively uncommon in the fossil record (Bellwood, 1996; Bellwood and Sorbini, 1996; Bannikov and Bellwood, 2014; Cooper and Santini, 2016). Pomacentrids are generally small- to medium-sized, with most species rarely exceeding 100–150 mm standard length (SL), though some genera (e.g., *Hypsypops*, *Nexilosus*) can grow larger in size (>250 mm SL; Allen, 1991). Although the bulk of pomacentrid diversity is concentrated in the shallow waters of tropical coastal regions, some species of Indo-Pacific *Chromis* have been recorded at depths greater than 100 m (e.g., *C. abyssicola*, *C. abyssus*, *C. bowesi*, *C. gunting*, *C. hangganan*, *C. mamatapara*, *C. struhsakeri*, *C. verater*; Randall and Swerdloff, 1973; Allen and Randall, 1985; Pyle et al., 2008; Arango et al., 2019; Shepherd et al., 2020), a few genera occur in subtropical and temperate waters (e.g., *Hypsypops*, *Parma*; Allen and Hoese, 1975), and a few species are known from freshwater and brackish environments (e.g., *Neopomacentrus aquadulcis*, *N. taeniurus*, *Pomacentrus taeniometopon*, *Stegastes otophorus*; Emery, 1972; Allen, 1989, 1991; Jenkins and Allen, 2002).

Damselfishes are highly variable in their diets and trophic strategies, though most are omnivorous, feeding on an array of plankton, benthic algae, and benthic invertebrates (Hiatt and Strasburg, 1960; Randall, 1967; Allen, 1975a, 1991; Williams and Hatcher, 1983; Sano et al., 1984a). Some species are primarily herbivorous (e.g., *Stegastes* spp.), consuming different kinds of benthic and pelagic algae (Randall, 1967; Emery, 1973; Hobson, 1974; Lobel, 1980; Horn, 1989), including "farming" or cultivation of specific algal species as primary food sources (Vine, 1974; Brawley and Adey, 1977; Lassuy, 1980; Montgomery, 1980; Ferreira et al., 1998; Hata and Kato, 2002, 2004, 2006; Ceccarelli et al., 2005a, 2005b). Others are planktivorous (e.g., *Chromis* spp., *Neopomacentrus* spp.), deriving most of their diet from a variety of pelagic organisms, e.g., invertebrates (primarily copepods), vertebrates (primarily fish eggs and larvae), and algae (Randall, 1967; Emery, 1973; Hobson, 1974; Kuo and Shao, 1991). Two species (*Cheiloprion labiatus* and *Plectroglyphidodon johnstonianus*) have specialized to feed on coral polyps (Hobson, 1974; Allen, 1975a; Masuda et al., 1975, 1984; Sano et al., 1984a, 1984b; Cole et al., 2008).

Pomacentrids show a range of mating behaviors, reproductive strategies, and social structures (Breder and Rosen, 1966; Thresher, 1984; Petersen, 1995; Fishelson, 1998; Erisman et al., 2013). Pomacentrids are all oviparous, typically laying adhesive eggs on the substrate, and they display varying levels of parental care (e.g., nest building, egg guarding, brooding) by either the male alone or both parents, depending on species (Breder and Rosen, 1966; Wickler,

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1967; Robertson, 1973; Blumer, 1979, 1982). Like many marine fishes, the larvae of almost all damselfish species go through a dispersive, pelagic phase (Thresher et al., 1989; Leis, 1991; Murphy et al., 2007). The planktonic stage of their life history varies greatly in duration, depending on the species (Thresher et al., 1989; Wellington and Victor, 1989). This pelagic step is completely absent in the species of *Acanthochromis* and *Altrichthys*, which makes them unique among pomacentrids (Robertson, 1973; Allen, 1999a; Bernardi et al., 2017a). Because of that life history, they are also the only damselfishes to exhibit brooding behavior, where the parents care for and defend the young through the recruitment stage (Robertson, 1973; Allen, 1975a, 1999a; Nakazono, 1993; Kavanagh, 1998, 2000; Bernardi, 2011). This may have given rise to inter- and intraspecific brood parasitism in species of *Altrichthys* (Tariel et al., 2019).

Among damselfishes, the anemonefishes possess the most well-known life histories. All anemonefishes share an obligate symbiotic relationship with sea anemones (Collingwood, 1868; de Crespigny, 1869; Verwey, 1930; Gudger, 1946; Mariscal, 1970; Allen, 1972; Fautin, 1991; Fautin and Allen, 1997). This unique life history likely contributed to their distinctive reproductive biology and social structure: anemonefishes are protandrous serial hermaphrodites that form long-term monogamous pairs (Fricke, 1974, 1979; Fricke and Fricke, 1977; Moyer and Nakazono, 1978; Ross, 1978). When more than two fish inhabit an anemone, there is an established size-dependent dominance hierarchy, where the largest fish is the breeding female, the next largest fish is the breeding male, and any remaining fish are non-breeding individuals (Fricke, 1974, 1979; Fricke and Fricke, 1977; Moyer and Nakazono, 1978; Buston, 2004).

Taxonomic history.—Following the appearance of four pomacentrid species (*Abudefduf saxatilis*, *Amphiprion polymnus*, *Chromis chromis*, *Dascyllus aruanus*) in Linnaeus (1758), contributions to pomacentrid taxonomy were made by numerous ichthyologists: Cuvier and Valenciennes (1830); Günther (1862); Gill (1863); Bleeker (1877); Jordan and Evermann (1898); Fowler and Bean (1928); Montalban (1928); McCulloch (1929); Whitley (1929); de Beaufort (1940); Aoyagi (1941); Norman (1957); Smith (1960); Marshall (1964); Munro (1967); Allen (1975a, 1991). The oldest available name for the family is Glyphisodia, originally described as a subfamily of Rafinesque's (1815) family Chetodonia [= Chaetodontidae]. However, as noted by van der Laan et al. (2014), it does not take precedence over Pomacentridae Bonaparte, 1831 because such names do not displace a name in prevailing usage at a higher rank within the same family group (ICZN, 1999: Art. 35.5). The family-group name is therefore Pomacentridae and attributed to Bonaparte (1831), who recognized Pomacentrini as one of two subfamilies within his family Sciaenidae. Bonaparte (1831) also erected the subfamily Chromidini, one of three in his Labridae, but he did not associate that group with his Pomacentrini. The correct formation for a family-group name based on *Chromis* should be Chrominae (Steyskal, 1980). Gill (1859) established the subfamily Amphiprioninae for the anemonefishes (Table 1).

Allen (1975a) devised the last of the traditional classifications, which divided the family into four subfamilies: Amphiprioninae, Chrominae, Lepidozyginae, and Pomacentrinae. His scheme was influenced by Norman's (1957) work (Allen, 1975a: 34). Both recognized the subfamilies Amphiprioninae, Chrominae, and Pomacentrinae. Allen's (1975a) classification differed in establishing the monotypic Lepidozyginae and combining Premninae with Amphiprioninae. In a refinement of his earlier work, Allen (1991) expanded his classification to include all recognized damselfish genera. He credited parts of the expanded classification to Bleeker's (1877) organizational structure, even though the modern names and ranks often bore little resemblance to those used by Bleeker. Allen's Amphiprioninae included all of the anemonefishes, making the subfamily equivalent to Bleeker's phalanx Prochilini; Allen's Chrominae included all of the genera in Bleeker's subphalanx Chromidi except for *Actinochromis* [= *Parma*], which Allen referred to his Pomacentrinae; and Allen's Pomacentrinae included all of the genera of Bleeker's subphalanx Pomacentri (phalanx Glyphidodontini [= Glyphisodontini]) except *Lepidozygus*, for which Allen erected its own subfamily. Allen's (1975a, 1991) classification was widely adopted: e.g., Hensley (1986); Thresher et al. (1989); Nelson (1994, 2006); Sin et al. (1994); Koh et al. (1997, 2006); Elliott et al. (1999); Tang (2001); Jang-Liaw et al. (2002); McCafferty et al. (2002); Molina and Galetti (2004a, 2004b); Quenouille et al. (2004); Tang et al. (2004); Parmentier et al. (2006).

The first classification based explicitly on a phylogeny was proposed by Cooper et al. (2009), who reconstructed their tree using molecular sequence data. In revising and updating the classification to more accurately reflect the relationships within the family, major changes were necessary because of the non-monophyly of several of Allen's (1975a) subfamilies. Cooper et al. (2009) restricted the subfamily Pomacentrinae to the clade including *Pomacentrus* and its nearest relatives: *Acanthochromis*, *Altrichthys*, *Amblyglyphidodon*, *Amblypomacentrus*, *Amphiprion*, *Cheiloprion*, *Chrysiptera*, *Dischistodus*, *Hemiglyphidodon*, *Neoglyphidodon*, *Neopomacentrus*, *Pomachromis*, *Premnas*, *Pristotis*, and *Teixeirichthys*. That action displaced a number of genera (*Hypsypops*, *Microspathodon*, *Nexilosus*, *Parma*, *Plectroglyphidodon*, *Similiparma*, and *Stegastes*) from Pomacentrinae. Those taxa were referred to a newly erected subfamily, Stegastinae. The anemonefishes were not recognized as a distinct subfamily because of their close relationship to *Pomacentrus*; instead they were treated as a tribe, Amphiprionini, within Pomacentrinae. It was the only tribe recognized in their classification. Cooper et al. (2009) restricted Chrominae to the clade comprising *Chromis* and its nearest relatives, *Azurina* and *Dascyllus*, both of which rendered *Chromis* polyphyletic. They placed *Azurina* in the synonymy of *Chromis* but retained *Dascyllus*, leaving *Chromis* non-monophyletic. *Acanthochromis*, *Altrichthys*, and *Mecaenichthys* were excluded from Chrominae, with *Acanthochromis* and *Altrichthys* referred to Pomacentrinae *sensu stricto*, and *Mecaenichthys* referred to Stegastinae. They retained the monotypic Lepidozyginae, with *Lepidozygus tapeinosoma* as its sole representative. It was recovered as the sister group to all damselfishes excluding Stegastinae. The species of *Abudefduf*, minus "*Abudefduf*" *luridus*, were resolved as a monophyletic group, separate from the other subfamilies. They referred "*Abudefduf*" *luridus* to their Stegastinae and recognized Abudefdufinae for the species of *Abudefduf sensu stricto*. Cooper et al. (2014) subsequently assigned *luridus* to *Similiparma* as *S. lurida*.

In recognizing the subfamily Abudefdufinae, Cooper et al. (2009) overlooked the existence of an older available name

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Table 1. Historical classifications of the damselfishes.

Gill (1859)
Family Pomacentroidae
  Subfamily Amphiprioninae
  Subfamily Pomacentrinae
Bleeker (1877)
Order Chromides
  Family Pomacentroidei
    Phalanx Glyphidodontini
      Subphalanx Chromidi
      Subphalanx Pomacentri
    Phalanx Prochilini
Jordan and Evermann (1898)
Order Acanthopteri
  Suborder Chromides
    Family Pomacentridae
      Subfamily Pomacentrinae
      Subfamily Microspathodontinae
Fowler and Bean (1928)
Family Pomacentridae
  Subfamily Chrominae
  Subfamily Pomacentrinae
  Subfamily Premninae
McCulloch (1929)
Order Amphiprioniformes
  Family Amphiprionidae
  Family Chromidae
  Family Pomacentridae
    Subfamily Glyphisodontinae
    Subfamily Parmidae
  Family Premnidae
Whitley (1929)
Order Amphiprioniformes
  Family Amphiprionidae
  Family Chromidae
  Family Pomacentridae
    Subfamily Cheiloprioninae
    Subfamily Glyphisodontinae
    Subfamily Hemiglyphidodontinae
    Subfamily Parminae
    Subfamily Pomacentrinae
  Family Premnidae
Aoyagi (1941)
Family Pomacentridae
  Subfamily Amphiprionidae
  Subfamily Chromidae
  Subfamily Pomacentrinae
  Subfamily Glyphisodontinae
  Subfamily Hemiglyphidodontinae
Smith (1949)
Order Chromides
  Family Abudefdufidae
  Family Amphiprionidae
Norman (1957)
Order Percomorphi
  Suborder Percoidea
    Division Pomacentriformes
      Family Pomacentridae
        Subfamily Amphiprioninae
        Subfamily Chrominae
        Subfamily Pomacentrinae
        Subfamily Premninae

Table 1. Continued.

Fowler (1959)
Order Chromides
  Family Pomacentridae
    Subfamily Chrominae
    Subfamily Pomacentrinae
Marshall (1964)
Order Percomorphi
  Suborder Percoidea
    Division Amphiprioniformes
      Family Amphiprionidae
      Family Chromidae
      Family Pomacentridae
        Subfamily Cheiloprioninae
        Subfamily Glyphisodontinae
        Subfamily Parminae
        Subfamily Pomacentrinae
Munro (1967)
Order Perciformes
  Suborder Percoidei
    Family Abudefdufidae
    Family Amphiprionidae
    Family Pomacentridae
    Family Premnidae
Allen (1975a, 1991)
Family Pomacentridae
  Subfamily Amphiprioninae
  Subfamily Chrominae
  Subfamily Lepidozyginae
  Subfamily Pomacentrinae
Nelson (1994, 2006)
Order Perciformes
  Suborder Labroidei
    Family Pomacentridae
      Subfamily Amphiprioninae
      Subfamily Chrominae
      Subfamily Lepidozyginae
      Subfamily Pomacentrinae
Cooper et al. (2009)
Family Pomacentridae
  Subfamily Abudefdufinae
  Subfamily Chrominae
  Subfamily Lepidozyginae
  Subfamily Pomacentrinae
    Tribe Amphiprionini
  Subfamily Stegastinae
Cooper and Santini (2016)
Family Pomacentridae
  Subfamily Chrominae
  Subfamily Glyphisodontinae
  Subfamily Lepidozyginae
  Subfamily Microspathodontinae
    Tribe Microspathodontini
  Subfamily Pomacentrinae
    Tribe Amphiprionini
Nelson et al. (2016)
Subseries Ovalentaria
  Family Pomacentridae
    Subfamily Amphiprioninae
    Subfamily Chrominae
    Subfamily Lepidozyginae
    Subfamily Pomacentrinae

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for this group. As mentioned above, Rafinesque (1815) based the subfamily Glyphisodia on *Glyphisodon*, which is now considered a junior synonym of *Abudefduf*. Therefore, Glyphisodontinae has seniority over Abudefdufidae Whitley, 1929 and is the correct name for the pomacentrid subfamily that includes members of the genus *Abudefduf sensu stricto*. Cooper and Santini (2016) identified Glyphisodontinae as the appropriate name for this subfamily, but incorrectly attributed authorship of Glyphisodontinae to Richardson (1844), who was the first to use the formation Glyphisodontinae (van der Laan et al., 2014). Prior to Cooper and Santini (2016), the family-group name Glyphisodontinae rarely saw use (e.g., McCulloch, 1929; Whitley, 1929; Aoyagi, 1941; Marshall, 1964; Masuda et al., 1975; Ojima and Kashiwagi, 1981). When erecting their Stegastinae, Cooper et al. (2009) overlooked more senior available family-group names that could apply. *Microspathodon* and *Parma* were recovered as members of the clade, and they are the type genera of Microspathodontinae Jordan and Evermann, 1898 and Parmidae Whitley, 1929, respectively. Therefore, Microspathodontinae is the oldest available family-group name for this taxon. Cooper and Santini (2016) acknowledged this oversight and indicated that Microspathodontinae is the appropriate name for this subfamily. Unfortunately, Abudefdufinae and Stegastinae have been used extensively in many recent works: Barneche et al. (2009); Lobel et al. (2010: 321); Aguilar-Medrano et al. (2011, 2013); Cowman and Bellwood (2011, 2013); Hubert et al. (2011); Allen and Erdmann (2012); Baldwin (2013); Frédérich et al. (2013, 2014); Oka and Miyamoto (2015); Olivier et al. (2015); Aguilar-Medrano and Barber (2016); Gajdzik et al. (2016); Getlekha et al. (2016a, 2016b). Their usage persists despite Cooper and Santini's (2016) corrections: Aguilar-Medrano (2017); Stieb et al. (2017); Campbell et al. (2018); Gaboriau et al. (2018); Gajdzik et al. (2018); Getlekha et al. (2018); Merilaita and Kelley (2018); Tenggardjaja et al. (2018); Delrieu-Trottin et al. (2019: fig. S16); Muñoz-Cordovez et al. (2019); Olivier et al. (2019).

Previous phylogenetic analyses.—Pomacentrids have long posed a challenge to systematists because of their diversity and intraspecific variation (Woods and Schultz, 1960; Allen, 1975a; Nelson, 1994). The earliest phylogenies, employing morphological evidence, found support for the monophyly of Pomacentridae based on five synapomorphies: (1) a strong sheet of connective tissue originating from the medial face of the lower jaw that merges with a cylindrical ligament and inserts onto the ceratohyal (Stiassny, 1981); (2) a pair of nipple-like processes on the ventral surface of the lower pharyngeal jaw that act as insertion sites for the pharyngohyoideus muscle (Kaufman and Liem, 1982; Lauder and Liem, 1983); (3) a pharyngo-cleithral articulation between the cleithra and the muscular processes of the lower pharyngeal jaw (Kaufman and Liem, 1982; Lauder and Liem, 1983); (4) a prominent obliquus posterior muscle that is separated from the fourth levator externus muscle by a distinct aponeurosis (Kaufman and Liem, 1982; Lauder and Liem, 1983); and (5) presence of two anal-fin spines (Fitzpatrick, 1992). The first character, also called the ceratomandibular ligament, has been proposed as a "key innovation" that has contributed to the evolutionary success of the Pomacentridae (Olivier et al., 2014, 2016). The presence of only two anal-fin spines (i.e., first anal-fin pterygiophore with two supernumerary spines and one serially associated soft ray) has a long history in the literature as a diagnostic character for the family: Bleeker (1877); Jordan and Evermann (1898); Fowler and Bean (1928); de Beaufort (1940); Smith (1960); Woods and Schultz (1960); Taylor (1964); Munro (1967); Allen (1975a, 1991); Nelson (1994, 2006); Bellwood and Sorbini (1996); Bannikov and Bellwood (2014); Cooper and Santini (2016); Nelson et al. (2016).

Although there have been a few phylogenetic analyses based on morphological characters since then (e.g., Tang, 2002; Aguilar-Medrano et al., 2011, 2013; Aguilar-Medrano, 2013), with the rise of molecular techniques, most recent pomacentrid phylogenies have employed DNA sequence data. Species descriptions have often placed the newly described species in phylogenetic context (e.g., Allen et al., 2008, 2010a, 2010b, 2012a, 2012b, 2015a, 2015b, 2017a, 2017b, 2017c, 2017d, 2018a; Liu et al., 2013; Randall and DiBattista, 2013; Bernardi et al., 2017b; Motomura et al., 2017; Wibowo et al., 2018; Frable and Tea, 2019; Tea et al., 2019; Habib et al., 2020). Some studies focused on individual genera (e.g., Lacson and Bassler, 1992; Godwin, 1995; Lessios et al., 1995; Bernardi and Crane, 1999; McCafferty et al., 2002; Bernardi, 2011; Sorenson et al., 2014; Vella et al., 2016; Bertrand et al., 2017; Campbell et al., 2018). Several examined the anemonefishes (Elliott et al., 1999; Santini and Polacco, 2006; Timm et al., 2008; Litsios et al., 2012a, 2014; Litsios and Salamin, 2014; Thongtam na Ayudhaya et al., 2017, 2019; Rolland et al., 2018; Nguyen et al., 2020). Many studies have explored relationships across the whole family (e.g., Tang, 2001; Jang-Liaw et al., 2002; Quenouille et al., 2004; Tang et al., 2004; Koh et al., 2006; Cooper et al., 2009; Cowman and Bellwood, 2011; Hubert et al., 2011; Hofmann et al., 2012; Litsios et al., 2012b; Frédérich et al., 2013; Lobato et al., 2014; DiBattista et al., 2016; Stieb et al., 2017; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). Others included pomacentrids in massive surveys of major fish groups (e.g., Near et al., 2012, 2013; Wainwright et al., 2012; Betancur-R. et al., 2013a, 2015, 2017; Rabosky et al., 2013, 2018; Mirande, 2016; Sanciangco et al., 2016). Despite differences in taxa and loci used, these studies have mostly agreed on a basic framework for relationships within the family, where four major clades are consistently recovered. These four groups are reflected in the current classification as the subfamilies Chrominae, Glyphisodontinae, Microspathodontinae, and Pomacentrinae (Cooper et al., 2009; Cooper and Santini, 2016). The status of the fifth subfamily, the monotypic Lepidozyginae, remains unsettled (Cooper and Santini, 2016), with different studies finding conflicting results despite using many of the same sequences for *Lepidozygus tapeinosoma* (Cooper et al., 2009; Cowman and Bellwood, 2011; Hofmann et al., 2012; Litsios et al., 2012a, 2012b; Betancur-R. et al., 2013a, 2015, 2017; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Sanciangco et al., 2016; Stieb et al., 2017; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019).

Higher-level relationships.—The Pomacentridae have a long history of being associated with other pharyngognathous families like Cichlidae, Embiotocidae, and/or Labridae (e.g., Müller, 1843, 1845; Günther, 1862; Jordan and Evermann, 1898: 1543–1544; Jordan and Snyder, 1902; Nelson, 1967;

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Masuda et al., 1975). Liem and Greenwood (1981) identified a monophyletic assemblage composed of Cichlidae, Embiotocidae, and Labridae (then divided into Labridae *sensu stricto*, Odacidae, and Scaridae) based on shared pharyngognathous specializations. Kaufman and Liem (1982) expanded the Labroidei to include those three groups plus Pomacentridae and diagnosed the suborder on the basis of three synapomorphies of the pharyngeal jaw structure. Stiassny and Jensen (1987) discovered additional synapomorphies, also of the branchial region, supporting the group's monophyly. This composition of Labroidei saw widespread use (e.g., Lauder and Liem, 1983; Richards and Leis, 1984; Liem, 1986; Potthoff et al., 1987; Nelson, 1994). Springer and Orrell (2004), on the basis of dorsal gill-arch characters, found a monophyletic Labroidei (Cichlidae, Embiotocidae, Labridae *sensu stricto*, and Pomacentridae) that also included Pholidichthyidae (their Clade A 5). However, numerous other studies have demonstrated that Labroidei is not monophyletic (e.g., Streelman and Karl, 1997; Sparks and Smith, 2004; Dettaï and Lecointre, 2005, 2008; Westneat and Alfaro, 2005; Smith and Wheeler, 2006; Chen et al., 2007; Mabuchi et al., 2007; Smith and Craig, 2007; Azuma et al., 2008; Setiamarga et al., 2008; Li et al., 2009; Santini et al., 2009; Matschiner et al., 2011; Meynard et al., 2012; Wainwright et al., 2012).

Despite not supporting a monophyletic Labroidei, there was a consensus among those phylogenies that damselfishes are part of a larger clade that also includes Cichlidae and Embiotocidae but excludes Labridae (Smith and Wheeler, 2006; Chen et al., 2007; Mabuchi et al., 2007; Setiamarga et al., 2008; Santini et al., 2009; Meynard et al., 2012; Wainwright et al., 2012). This group was formally recognized in Wainwright et al. (2012) as Ovalentaria and included, in addition to the three former labroid families (Cichlidae, Embiotocidae, Pomacentridae), two other major assemblages (Atherinomorpha, Blennioidei) and a series of previously unaffiliated percomorph families (Ambassidae, Gobiesocidae, Grammatidae, Mugilidae, Opistognathidae, Pholidichthyidae, Plesiopidae, Polycentridae, Pseudochromidae [including Congrogadidae]). This sprawling lineage is united by the possession of adhesive, demersal eggs with chorionic filaments, though not all members display this feature (Wainwright et al., 2012: 1027). Smith and Wheeler (2004: 641) first suggested this as a character that may unite what was then considered a disparate array of seemingly unrelated taxa (Atherinomorpha, Blennioidei, Cichlidae, Gobiesocidae, Grammatidae, Opistognathidae, and Pomacentridae). Springer and Orrell (2004: fig. 6) recovered a large group (their Clade A) similar to Ovalentaria that included Atherinomorpha, Cichlidae, Embiotocidae, Grammatidae, Mugilidae, Opistognathidae, Pholidichthyidae, Pomacentridae, and Pseudochromidae. Most subsequent authors have followed Wainwright et al. (2012) in adopting the name Ovalentaria for the group (e.g., Near et al., 2012, 2013; Betancur-R. et al., 2013a, 2015, 2017; Friedman et al., 2013; Lin and Hastings, 2013; Chen et al., 2014; Campanella et al., 2015; Collins et al., 2015; Cortesi et al., 2015; Longo and Bernardi, 2015; Mirande, 2016; Nelson et al., 2016; Sanciangco et al., 2016; Conway et al., 2017; Dornburg et al., 2017; Alfaro et al., 2018; Hughes et al., 2018; Rabosky et al., 2018; Verma et al., 2019). Li et al. (2009) used Stiassnyiformes for a similar group composed of Atherinomorpha, Blennioidei, Gobiesocidae, Mugilidae, Plesiopidae, and Pomacentridae. However, that name did not gain much traction, with only passing mention by a few authors (e.g., Betancur-R. et al., 2013a, 2017; Collins et al., 2015; Nelson et al., 2016). Hastings et al. (2014) recognized the clade containing Cichlidae, Embiotocidae, and Pomacentridae as the "Chromides," a name used intermittantly in the literature for some or all of these fishes (e.g., Müller, 1843, 1845; Günther, 1862; Bleeker, 1877; Jordan and Evermann, 1898; Jordan, 1923; Smith, 1949; Fowler, 1959; Rosen and Patterson, 1990; Wainwright et al., 2012).

Despite the recent flurry of large-scale fish phylogenies, there has been little agreement on the closest relatives of Pomacentridae. Some studies have identified familiar families as the sister group: Cichlidae (Springer and Orrell, 2004; Azuma et al., 2008; Setiamarga et al., 2008; Miya et al., 2013), Embiotocidae (Streelman and Karl, 1997; Sparks and Smith, 2004; Westneat and Alfaro, 2005; McMahan et al., 2013), or both (Mabuchi et al., 2007). However, many other taxa have been resolved as the sister group: Blennioidei (Near et al., 2012; Davis et al., 2016), Congrogadidae (Betancur-R. et al., 2015, 2017; Sanciangco et al., 2016), Gobiesocidae (Smith and Wheeler, 2006), Mugilidae (Chen et al., 2007; Santini et al., 2009; Collins et al., 2015), Plesiopidae (Wainwright et al., 2012; Near et al., 2013; Rabosky et al., 2013), and Pseudochromidae (Hughes et al., 2018). Other phylogenies have inferred Pomacentridae as the sister group to mixed assemblages (Meynard et al., 2012; Betancur-R. et al., 2013a; Friedman, et al., 2013; Cortesi et al., 2015; Mirande, 2016; Alfaro et al., 2018; Rabosky et al., 2018). Olivier et al. (2016) reported that among eight groups of Ovalentaria they examined (Blennioidei, Cichlidae, Embiotocidae, Grammatidae, Opistognathidae, Plesiopidae, Pomacentridae, Pseudochromidae), only pomacentrids and pseudochromids share the presence of a ceratomandibular ligament (i.e., strong sheet of connective tissue originating from lower jaw and merging with ligament that inserts onto ceratohyal; Stiassny, 1981). However, they observed that its insertion on the lower jaw differs between the two groups, which indicated to them that the function also differs (closing the jaw in pomacentrids vs. opening in pseudochromids). Eytan et al. (2015) explored relationships within Ovalentaria and found limited resolution for pomacentrid relatives, with weak support for various possible sister groups, including Atherinomorpha, Polycentridae, Pseudochromidae, or different clades of mixed Ovalentaria. In these various studies, the putative sister groups are consistently members of Ovalentaria, but there is no consensus as to which one is most closely related to Pomacentridae.

Objectives.—First, we intend to infer the phylogenetic relationships among representative species of the family Pomacentridae using molecular evidence from both nuclear and mitochondrial loci. In doing so, we will test the monophyly of the genera and subfamilies within the family. Second, based on that phylogeny, we will provide a revised classification of the Pomacentridae, one that more accurately reflects the current understanding of pomacentrid relationships. Third, we will assess the family's higher-level relationships to other major fish groups and identify a possible sister group. In producing a molecular phylogeny of this species-rich group and a revised classification to accompany it, we hope to give better insight into the relationships within the

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family and among its constituent taxa, as well as highlight areas of the tree that require further study.

MATERIALS AND METHODS

Taxon sampling.—A total of 462 taxa were examined, consisting of 333 pomacentrids, representing all genera, 322 species, and 129 outgroup species (Supplemental Table 1; see Data Accessibility). The coverage is a little more than 75% of all 422 currently recognized species (Fricke et al., 2020). Novel sequence data were collected from 160 pomacentrid taxa representing 151 different species and 58 outgroup species. They were submitted to GenBank and assigned the following accession numbers: MW630140–MW631728 (Supplemental Table 1; see Data Accessibility). In an effort to include as many damselfish species as possible, taxon sampling was supplemented by sequences published in the Barcode of Life Data System (BOLD) and GenBank databases, primarily from large-scale damselfish phylogenies (Quenouille et al., 2004; Cooper et al., 2009; Frédérich et al., 2013), with additional data drawn from relevant publications (e.g., Santini and Polacco, 2006; Litsios et al., 2014). The outgroups include 129 non-pomacentrid taxa. They were chosen to represent a broad cross section of percomorph diversity, with particular emphasis on putative close relatives of Pomacentridae. A full list of taxa examined along with their corresponding BOLD or GenBank accession numbers is provided in Supplemental Table 1 (see Data Accessibility). Nomenclature, including type information and synonymies, follows Fricke et al. (2020) and van der Laan et al. (2014) unless otherwise noted. Meristic counts, morphometric measurements, and geographic distributions follow Allen (1991) unless otherwise noted. Institutional abbreviations follow Sabaj (2020).

Closer examination of material used in Tang (2001) revealed that five species were misidentified or mislabeled: *Amblyglyphidodon aureus*, *Amphiprion percula*, *Pomacentrus brachialis*, *Stegastes dorsopunicans* [= *S. adustus*], and *S. variabilis*. Those sequences appeared again in Jang-Liaw et al. (2002) and Tang et al. (2004). The specimen originally identified as *Amblyglyphidodon aureus* (USNM 336462; KU T773) has been reidentified as *A. melanopterus* (J. T. Williams, pers. comm.). *Amblyglyphidodon melanopterus* was described after the original publication of the DNA sequence. This change affects GenBank sequences AF285922 and AF285944. Originally identified as *A. percula*, KU 27120 (KU T2928) is actually a specimen of *A. ocellaris*. This change affects GenBank sequences AF285924 and AF285946. Previously identified as *P. brachialis*, USNM 334307 (KU T763) appears to be an undescribed species (labeled as *Pomacentrus* cf. *microspilus* herein; Supplemental Table 1; see Data Accessibility). This change affects GenBank sequences AF285934 and AF285956. Additionally, the following published sequences orginated from that same specimen: JQ937575, JQ937708, JQ937856, JQ938374, JQ938680, JQ938830, JQ938989, JQ939282, JQ939822, JQ939985, JQ940140 (Betancur-R. et al., 2013b: table S1), KC826191, KC826482, KC827370, KC828518, KC829263, KC830142, KC830640, KC831171 (Betancur-R. et al., 2013a: table S1). *Stegastes dorsopunicans*, the name used in Tang (2001), is a junior synonym of *S. adustus*. However, that specimen, USNM 327593 (KU T86), is actually *S. diencaeus*. This change affects GenBank sequences AF285937 and AF285959. Furthermore, there are published sequences derived from that specimen labeled as *Stegastes fuscus*: JQ707061, JQ707096, JQ707129, JQ707164, JQ707186, JQ707219, JQ707255, JQ707289 (Frédérich et al., 2013: table S1); KC826243, KC826479, KC827380, KC827940, KC828201, KC828463, KC829313, KC830499, KC831203 (Betancur-R. et al., 2013a: table S1). Although the specific barcode sample was not identified, Souza et al. (2016) were likely referring to this specimen when they mentioned a "single record in the BOLD database identified as *S. fuscus*" that "matches sequences of *S. diencaeus* and appears to be a misidentification." *Stegastes fuscus* has been restricted to the coast of Brazil and USNM 327593 was collected in Belize where the name *S. adustus* would apply (Longley and Hildebrand, 1941; Greenfield and Woods, 1974; Smith-Vaniz et al., 1999). Changes in nomenclature mean that the specimen previously identified as *Stegastes variabilis* (USNM 327596; KU T188) is now treated as *S. xanthurus*. *Stegastes variabilis* has also been restricted to Brazil, and the widespread species that occurs elsewhere in the western Atlantic is now recognized as *S. xanthurus* (Robertson and Van Tassell, 2012; Smith-Vaniz and Jelks, 2014). Souza et al. (2016) confirmed a genetic divergence between the two populations. Our specimen was collected off the coast of Belize (16°48′11″N, 88°13′58″W). This change affects GenBank sequences AF285938 and AF285960. Further examination of material used in Tang et al. (2004) indicated that KU T3517, originally identified as *Neopomacentrus cyanomos*, appears to be a specimen of *N. azysron*. This affects GenBank sequences AY098626 and AY098631.

DNA amplification and sequencing.—A total of eight loci (three nuclear and five mitochondrial), spanning nine genes, were targeted for amplification and sequencing based on their perceived suitability to resolve the phylogenetic relationships of this family. The three nuclear loci encompassed histone H3 (H3), recombination activating gene 1 exon 3 (RAG1), and an anonymous, titin-like protein (Tmo-4C4). Even though no pomacentrid-focused phylogeny has employed H3 prior to this study, sequences from this histone gene have been used to good effect in phylogenies of other percomorph groups (e.g., Smith and Wheeler, 2004, 2006; Sparks and Smith, 2004; Lin and Hastings, 2011, 2013; McMahan et al., 2013; Smith and Busby, 2014; Ghedotti et al., 2018; Smith et al., 2018). The nuclear gene RAG1 was chosen because it is widely used in fish systematics, including several studies of pomacentrids (e.g., Quenouille et al., 2004; Cooper et al., 2009; Frédérich et al., 2013; Lobato et al., 2014; Souza et al., 2016; Bertrand et al., 2017; Delrieu-Trottin et al., 2019). Tmo-4C4 has been used sparingly to investigate damselfishes (Allen et al., 2012a; DiBattista et al., 2015; He et al., 2018, 2019a), but it has proven to be phylogenetically informative for putative close relatives of Pomacentridae (e.g., Streelman and Karl, 1997; Streelman et al., 1998; Farias et al., 2000; Sparks and Smith, 2004; Chakrabarty, 2006; Smith et al., 2008; McMahan et al., 2013; Xia et al., 2016).

The five mitochondrial regions comprised two ribosomal RNA genes (12S and 16S), a contiguous segment of two overlapping ATP synthase subunits (ATPase 8/6), and two cytochrome genes, cytochrome *b* (cyt *b*) and cytochrome *c* oxidase I (COI). Both separately and in conjunction, 12S and 16S have seen widespread use in fish phylogenies, especially within Pomacentridae (e.g., Bernardi and Crane, 1999; Elliott

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et al., 1999; Tang, 2001; Jang-Liaw et al., 2002; Tang et al., 2004; Koh et al., 2006; Santini and Polacco, 2006; Cooper et al., 2009; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Litsios and Salamin, 2014; Lobato et al., 2014; Delrieu-Trottin et al., 2019; Nguyen et al., 2020). The ATPase 8/6 region has not been used as extensively as the other four mitochondrial loci, but it has been effective in resolving phylogenetic relationships within Pomacentridae (McCafferty et al., 2002; Quenouille et al., 2004; Litsios et al., 2012a, 2012b; Litsios and Salamin, 2014). The two cytochrome loci are likely the most popular genes for elucidating fish phylogenies. Cyt *b* has been cited as the most widely used locus in fish phylogenetics (Lydeard and Roe, 1997), and COI enjoyed rapid, widespread adoption since it was designated as the primary gene for the Barcode of Life Initiative (Hebert et al., 2003; Ward et al., 2005, 2009). Both loci have demonstrated their value for determining the relationships among damselfishes (e.g., Elliott et al., 1999; Santini and Polacco, 2006; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Liu et al., 2013; Randall and DiBattista, 2013; Litsios and Salamin, 2014; Sorenson et al., 2014; Allen et al., 2017b, 2017c, 2017d; Bernardi et al., 2017b; Motomura et al., 2017; Wibowo et al., 2018; Delrieu-Trottin et al., 2019; Frable and Tea, 2019; Tea et al., 2019; Habib et al., 2020; Nguyen et al., 2020).

Genomic DNA was extracted from fin clips or muscle tissue (stored at –70°C or in 95–99% ethanol) with a DNeasy Blood & Tissue Kit (Qiagen), following the manufacturer's protocol. Amplification of genomic DNA was accomplished via PCR in 25–50 μl volumes using variations of the following thermal cycling settings: 94–95°C denaturing (40–60 sec), 40–55°C annealing (40–60 sec), and 72°C extension (60–120 sec), for 35–40 cycles; an initial heating step at 94–95°C (30 sec–4 min) preceded cycling in some profiles and a final extension step at 72°C (7 min) followed cycling in some profiles. Two-step nested PCR protocols were used for some samples that proved difficult to amplify. Some RAG1 sequences were amplified using a touchdown procedure similar to the one described in Quenouille et al. (2004). TaKaRa Ex Taq (TAKARA Bio) was used for some PCR amplifications of the more sensitive nuclear loci. Primers were drawn from the following sources: Folmer et al. (1994); Palumbi (1996); Streelman and Karl (1997); Colgan et al. (1998); Wiley et al. (1998); Tang (2001); López et al. (2004); Near et al. (2004); Chen et al. (2007); Li and Ortí (2007); Tang et al. (2010). New primers had to be designed to amplify and sequence certain loci successfully. A complete list of primers is provided in Supplemental Table 2 (see Data Accessibility). Amplified PCR products were purified using one of several methods: AMPure (Agencourt Bioscience), ArrayIt (TeleChem International), ExoSAP-IT (USB/Affymetrix), QIAquick Gel Extraction Kits (Qiagen), and outsourced commercial purification using ExoSAP-IT. Sequencing was performed on Applied Biosystems 3700 and 3730xl automated sequencers housed in the Sackler Institute for Comparative Genomics at the American Museum of Natural History (AMNH). Additional DNA sequencing was conducted by three core facilities: htSEQ High-Throughput Genomics Unit (University of Washington, USA), Macrogen (Korea), and the University of Michigan DNA Sequencing Core (USA). Complementary fragments for each locus were spliced together and edited to produce a consensus sequence for analysis. Contig sequences were assembled with one of the following software applications: BioEdit 7.09 (Hall, 1999), Geneious 6.1.8 (BioMatters; Kearse et al., 2012), Sequence Navigator 1.01 (Applied Biosystems), and Sequencher 3.1 (Gene Codes). All novel sequences generated for this study were deposited in GenBank (Supplemental Table 1; see Data Accessibility).

Phylogenetic analyses.—Sequences were aligned by MAFFT 7.453 (Katoh et al., 2002; Katoh and Standley, 2013), with 1,000 iterations (--maxiterate 1000), gap extension penalty = 0.123 (--ep 0.123), and gap open penalty = 1.53 (--op 1.53). The E-INS-i (genafpair) alignment algorithm was used for ribosomal genes and L-INS-i (localpair) was used for protein-coding genes. The aligned output was read by Mesquite 3.61 (Maddison and Maddison, 2019) and converted into PHYLIP format for analysis. Maximum-likelihood analyses were conducted by IQ-TREE 1.6.12 (Nguyen et al., 2015) with the following settings: stopping rule (-numstop) = 100; perturbation strength (-pers) = 0.5; partition model = edge-proportional (-spp). The data matrix was partitioned by gene and optimal models for each partition (Chernomor et al., 2016) were selected by ModelFinder (Kalyaanamoorthy et al., 2017), as implemented in IQ-TREE (-m TEST). The topology with the best likelihood score was retained from ten independent searches. Bootstrap values were calculated from 1,000 ultrafast replicates (-bb 1000; Hoang et al., 2018). Phylogenies were visualized with FigTree 1.4.4 (Rambaut, 2018).

RESULTS

The final aligned data matrix used for analysis consisted of 6,865 nucleotide bases (with 3,708 parsimony-informative sites) for 462 taxa (Supplemental File: Data Matrix; see Data Accessibility). Alignment of the sequences produced a 1150 bp fragment of 12S, a 670 bp fragment of 16S, a complete 845 bp sequence of ATPase 8/6, a complete 1,140 bp sequence for cyt *b*, a 658 bp fragment of COI, a 331 bp fragment of H3, a 1,509 bp fragment of RAG1, and a 562 bp fragment of Tmo-4C4. Alignment produced no indels in the cyt *b*, COI, and H3 sequences. A single-codon insertion near the 3′ end of ATPase 8 was observed for *Chrysiptera biocellata* and *C. brownriggii*. *Embiotoca jacksoni* displayed a unique 3 bp gap downstream, before the region of overlap with ATPase 6. Alignment of RAG1 produced single-codon deletions in *Caranx hippos*, *Pholidichthys leucotaenia*, and *Takifugu rubripes*, none of which overlapped with each other. Among pomacentrids, only *Chromis lepidolepis* possessed such a gap, which it shared with *Caranx hippos*. *Himantolophus albinares* and *Trichopodus trichopterus* each had contiguous two-codon deletions which were not homologous. The one-codon gap in *Pholidichthys* overlapped with the gap seen in *Trichopodus*. In Tmo-4C4, *Nothobranchius furzeri* and *Plesiops coeruleolineatus* shared a single-codon insertion. *Haplochromis burtoni* and *Oryzias latipes* each possessed unique single-codon deletions. ModelFinder via IQ-TREE selected the following models: GTR+F+I+G4 for 12S, 16S, cyt *b*, and COI; TIM2+F+G4 for H3; and TIM2+F+I+G4 for ATPase 8/6 and RAG1; TIM3e+I+G4 for Tmo-4C4 (Lanave et al., 1984; Tavaré, 1986; Rodríguez et al., 1990; Posada, 2003).

Phylogenetic analyses employing maximum likelihood produced an optimal tree with ln $L = -45{,}4518.728$ (Fig. 1; Supplemental Fig. 1; see Data Accessibility). The damselfishes were recovered as a monophyletic group with strong branch support (100% bootstrap). There are four major lineages

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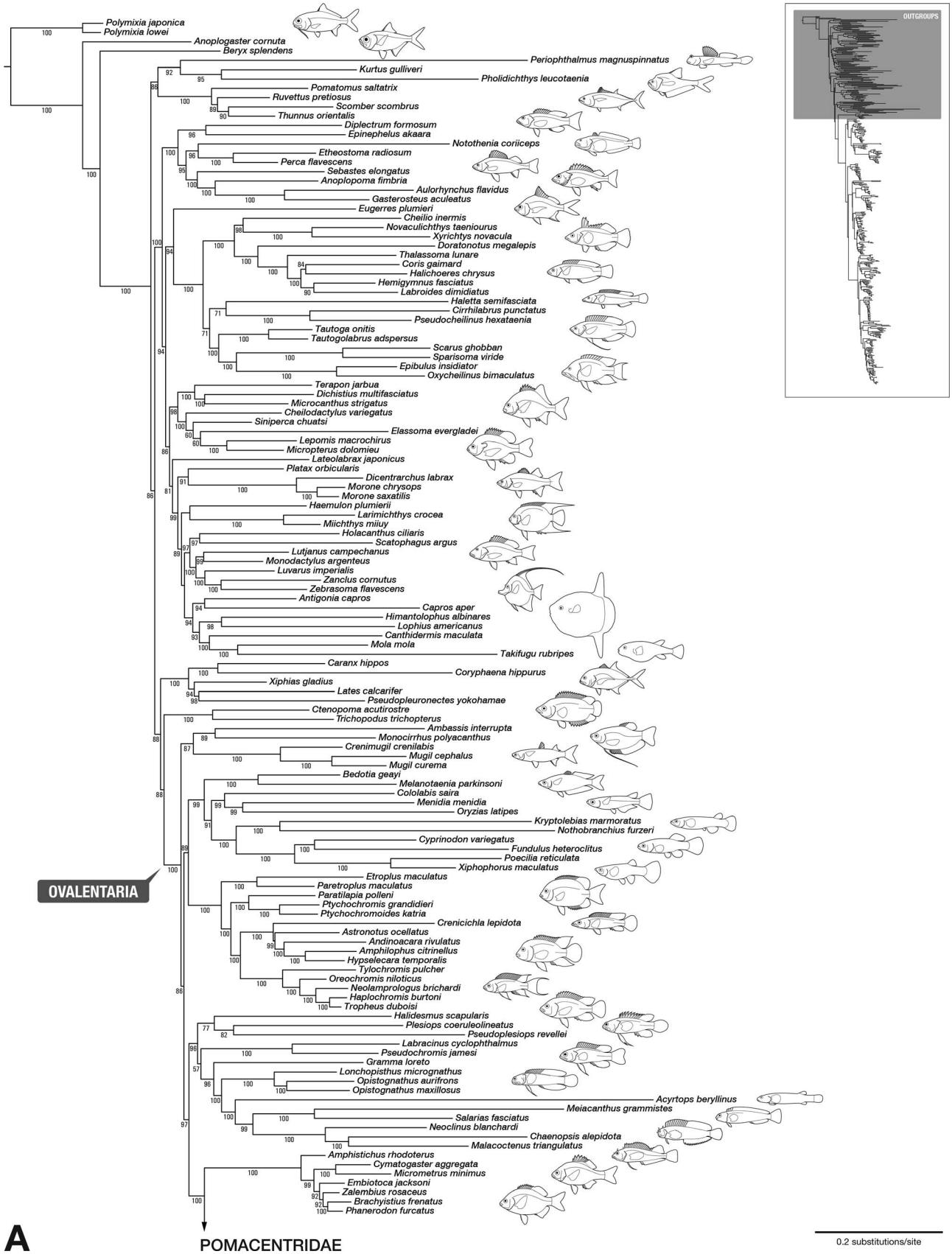

Fig. 1. The phylogenetic relationships of damselfishes (Teleostei: Pomacentridae): (A) outgroup taxa; (B) subfamilies Microspathodontinae and Glyphisodontinae; (C) subfamily Chrominae; (D) subfamily Pomacentrinae (part I); (E) subfamily Pomacentrinae (part II). The phylogeny is based on the maximum-likelihood topology with the best log likelihood score (ln $L = -45{,}4518.728$) recovered from ten independent maximum-likelihood analyses of a data matrix composed of 462 taxa and 6,865 nucleotides. Bootstrap values from 1,000 ultrafast replicates are displayed for each node

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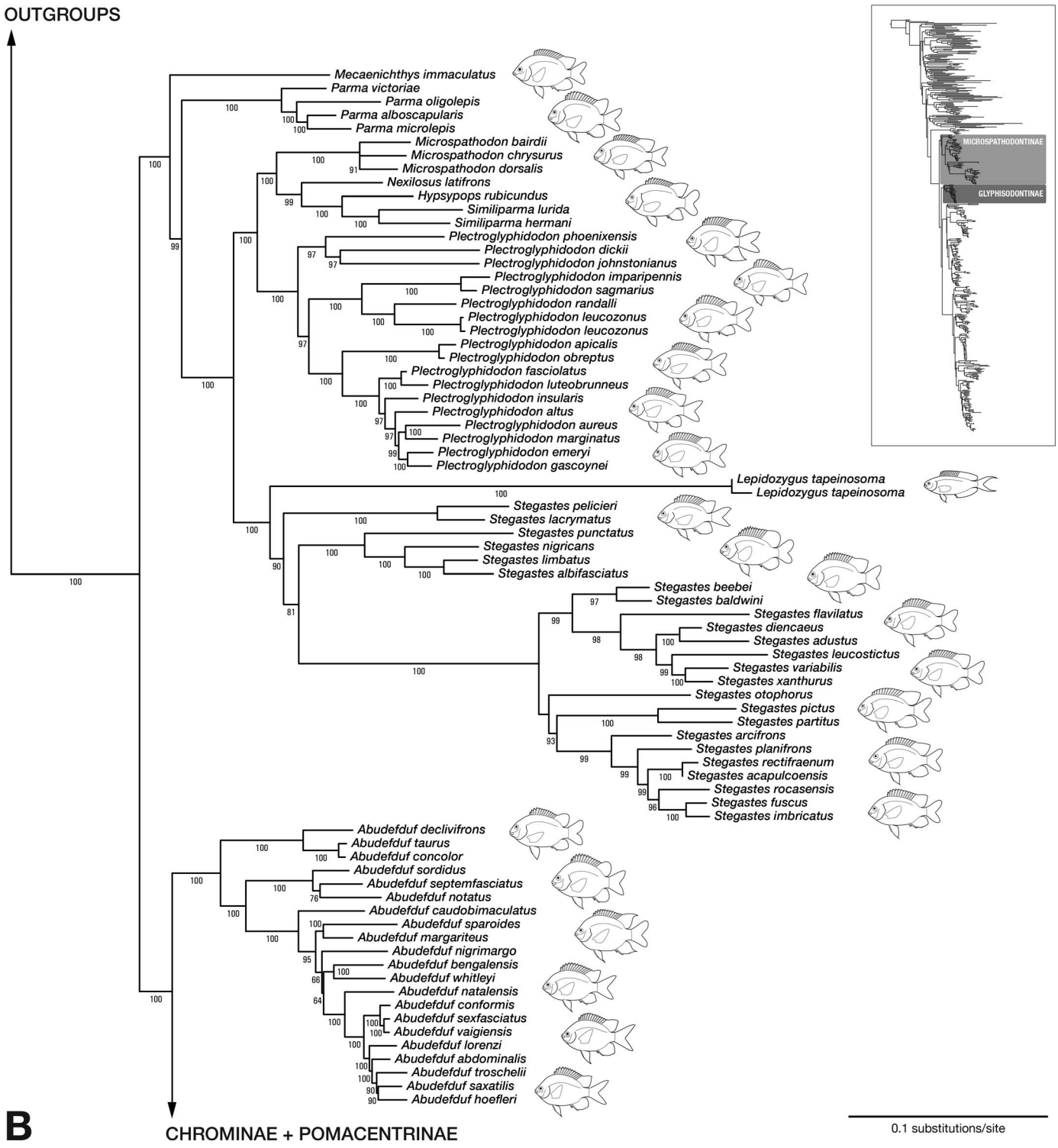

Fig. 1. (continued). (values below 50% are not reported). Illustrations (not to scale) represent the following species, from top: (A) *Polymixia japonica*, *Beryx splendens*, *Periophthalmus magnuspinnatus*, *Kurtus gulliveri*, *Thunnus orientalis*, *Diplectrum formosum*, *Notothenia coriiceps*, *Perca flavescens*, *Sebastes elongatus*, *Eugerres plumieri*, *Doratonotus megalepis*, *Halichoeres chrysus*, *Haletta semifasciata*, *Cirrhilabrus punctatus*, *Epibulus insidiator*, *Dichistius multifasciatus*, *Lepomis macrochirus*, *Morone chrysops*, *Holacanthus ciliaris*, *Lutjanus campechanus*, *Zanclus cornutus*, *Mola mola*, *Takifugu rubripes*, *Caranx hippos*, *Ctenopoma acutirostre*, *Trichopodus trichopterus*, *Mugil cephalus*, *Melanotaenia parkinsoni*, *Oryzias latipes*, *Kryptolebias marmoratus*, *Fundulus heteroclitus*, *Poecilia reticulata*, *Paretroplus maculatus*, *Crenicichla lepidota*, *Andinoacara rivulatus*, *Neolamprologus brichardi*, *Astatotilapia burtoni*, *Plesiops coeruleolineatus*, *Gramma loreto*, *Opistognathus aurifrons*, *Acyrtops beryllinus*, *Meiacanthus grammistes*, *Salarias fasciatus*, *Malacoctenus triangulatus*, *Micrometrus minimus*, *Embiotoca jacksoni*; (B) *Mecaenichthys immaculatus*, *Parma polylepis*, *Microspathodon chrysurus*, *Hypsypops rubicundus*, *Plectroglyphidodon dickii*, *P. imparipennis*, *P. leucozonus*, *P. fasciolatus*, *P. altus*, *P. gascoynei*, *Lepidozygus tapeinosoma*, *Stegastes lacrymatus*, *S. nigricans*, *S. beebei*, *S. diencaeus*, *S. xanthurus*, *S. otophorus*, *S. rectifraenum*, *S. imbricatus*, *Abudefduf declivifrons*, *A. sordidus*, *A. bengalensis*, *A. natalensis*, *A. abdominalis*, *A. saxatilis*; (C) *Azurina lepidolepis*, *A. cyanea*, *A. hirundo*, *A. multilineata*, *Dascyllus aruanus*, *D. albisella*, *D. trimaculatus*, *Pycnochromis nigrurus*, *P. vanderbilti*, *P. alleni*, *P. ovatiformis*,

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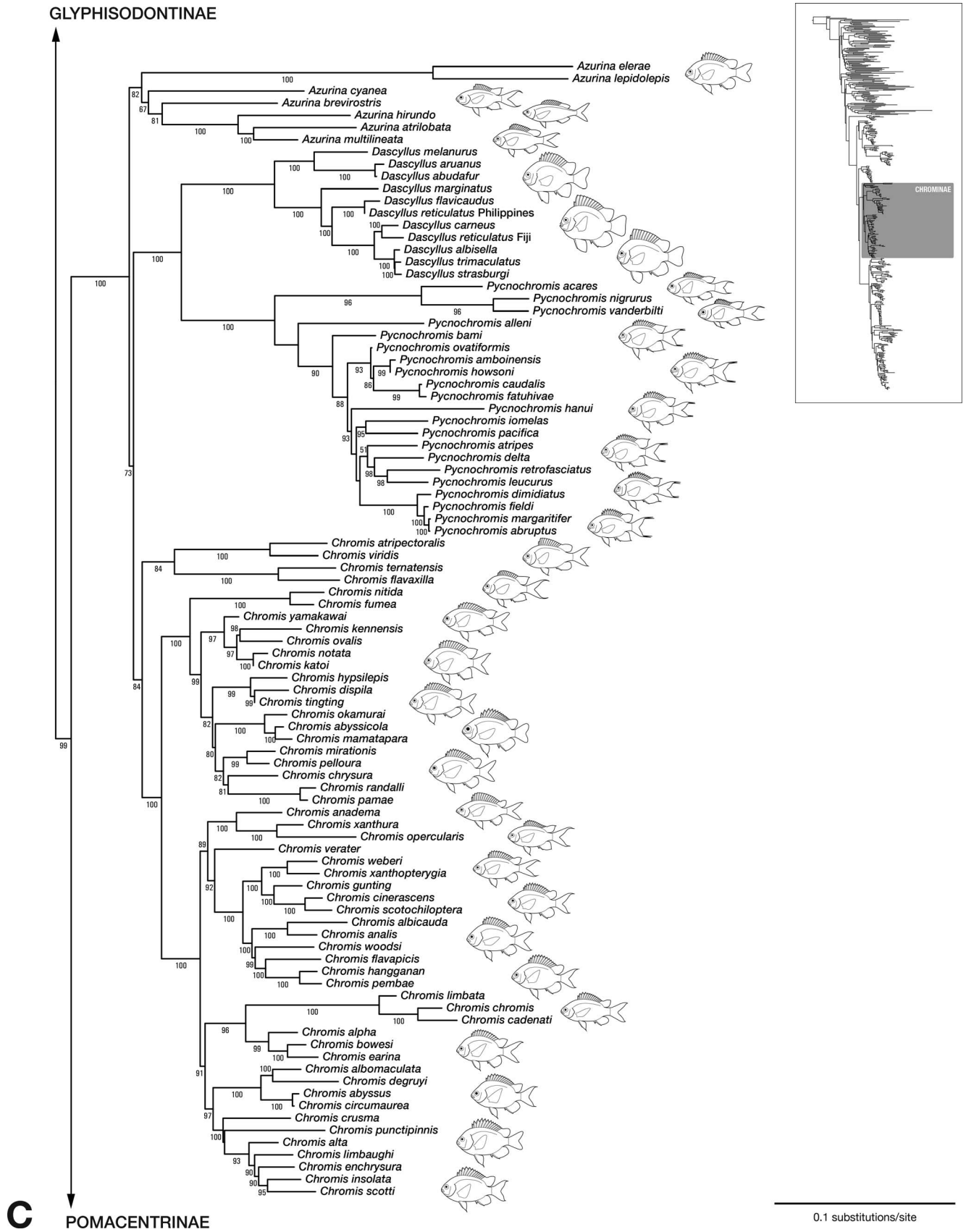

Fig. 1. (continued). *P. hanui*, *P. atripes*, *P. fieldi*, *P. margaritifer*, *Chromis viridis*, *C. ternatensis*, *C. fumea*, *C. notata*, *C. hypsilepis*, *C. okamurai*, *C. chrysura*, *C. randalli*, *C. opercularis*, *C. weberi*, *C. cinerascens*, *C. analis*, *C. pembae*, *C. chromis*, *C. alpha*, *C. abyssus*, *C. alta*, *C. insolata*; (D) "*Chrysiptera*" *rapanui*, "*C.*" *glauca*, "*C.*" *biocellata*, "*C.*" *brownriggii*, *Dischistodus chrysopoecilus*, *D. prosopotaenia*, *Pomachromis richardsoni*, *Cheiloprion labiatus*, *Chrysiptera cyanea*, *C. rex*, *C. traceyi*, *C. oxycephala*, *Hemiglyphidodon plagiometopon*, *Neoglyphidodon polyacanthus*,

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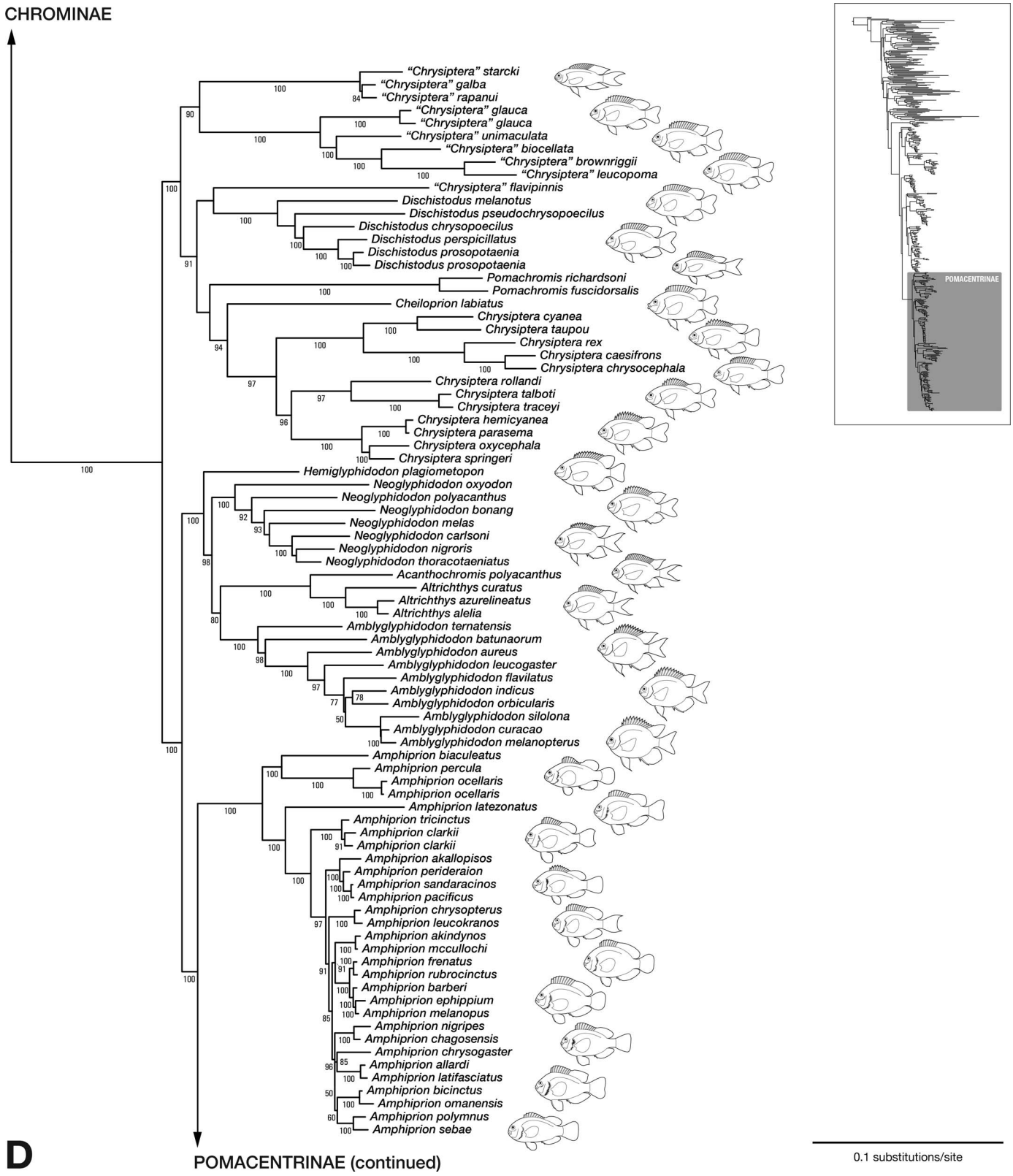

Fig. 1. (continued). *N. nigroris*, *Acanthochromis polyacanthus*, *Altrichthys azurelineatus*, *Amblyglyphidodon aureus*, *A. curacao*, *A. orbicularis*, *Amphiprion ocellaris*, *A. latezonatus*, *A. clarkii*, *A. perideraion*, *A. chrysopterus*, *A. frenatus*, *A. ephippium*, *A. chrysogaster*, *A. bicinctus*, *A. polymnus*; (E) *Amblypomacentrus tricinctus*, *A. breviceps*, *Pristotis obtusirostris*, *Teixeirichthys jordani*, *Neopomacentrus bankieri*, *N. filamentosus*, *N. xanthurus*, *N. miryae*, *N. metallicus*, *N. azysron*, *Pomacentrus pavo*, *P. caeruleus*, *P. auriventris*, *P. coelestis*, *P. aquilus*, *P. trilineatus*, *P. chrysurus*, *P. vaiuli*, *P. bankanensis*, *P. amboinensis*, *P. moluccensis*, *P. tripunctatus*, *P. taeniometopon*, *P. callainus*, *P. brachialis*, *P. nagasakiensis*, *P. stigma*, *P. nigromanus*, *P. philippinus*, *P. imitator*. See Data Accessibility for tree file.

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Fig. 1. (continued).

within the family Pomacentridae: *Pomacentrus* and its closest relatives (subfamily Pomacentrinae); *Chromis* and its closest relatives (subfamily Chrominae); *Abudefduf* (subfamily Glyphisodontinae); and *Microspathodon* and its closest relatives (subfamily Microspathodontinae). The basal clade, Microspathodontinae, includes *Hypsypops*, *Lepidozygus*, *Mecaenichthys*, *Microspathodon*, *Nexilosus*, *Parma*, *Plectroglyphidodon*, *Similiparma*, and *Stegastes*. The two largest genera, *Plectroglyphidodon* and *Stegastes*, are polyphyletic. *Abudefduf* is recovered as its own monophyletic group, making Glyphisodontinae a monogeneric subfamily. Glyphisodontinae is sister to Chrominae + Pomacentrinae. The lineage with *Chromis* (Chrominae) also includes *Dascyllus* and *Azurina*, which were both resolved inside *Chromis*, rendering it polyphyletic. The large crown clade that includes *Pomacentrus* (Pomacentrinae) also includes *Acanthochromis*, *Altrich-*

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thys, *Amblyglyphidodon*, *Amblypomacentrus*, *Amphiprion*, *Cheiloprion*, *Chrysiptera*, *Dischistodus*, *Hemiglyphidodon*, *Neoglyphidodon*, *Neopomacentrus*, *Pomachromis*, *Premnas*, *Pristotis*, and *Teixeirichthys*. *Amphiprion* is rendered non-monophyletic by the placement of *Premnas*. *Chrysiptera* is broadly polyphyletic.

The monophyly of each subfamily received 100% bootstrap support (Fig. 1; Supplemental Fig. 1; see Data Accessibility). The branches subtending the relationships among the subfamilies all display 100% bootstrap support except for Chrominae + Pomacentrinae, which had a 99% support value. Of the genera that are not monotypic, the following were monophyletic and received 100% bootstrap support: *Abudefduf*, *Altrichthys*, *Amblyglyphidodon*, *Amblypomacentrus*, *Dascyllus*, *Dischistodus*, *Microspathodon*, *Neoglyphidodon*, *Parma*, *Pomacentrus*, *Pomachromis*, *Similiparma*. *Neopomacentrus* received 98% bootstrap support. The following genera were not recovered as monophyletic: *Amphiprion*, *Chromis*, *Chrysiptera*, *Plectroglyphidodon*, and *Stegastes*. The remaining genera are either monotypic (*Acanthochromis*, *Cheiloprion*, *Hemiglyphidodon*, *Hypsypops*, *Lepidozygus*, *Mecaenichthys*, *Nexilosus*, *Premnas*, and *Teixeirichthys*) or represented by only one species (*Azurina* and *Pristotis*).

The surfperch family Embiotocidae was recovered as the sister group of Pomacentridae with 100% bootstrap support (Fig. 1; Supplemental Fig. 1; see Data Accessibility). The two families are part of a large clade consistent with Ovalentaria that also includes Atherinomorpha (Adrianichthyidae, Atherinopsidae, Bedotiidae, Cyprinodontidae, Fundulidae, Melanotaeniidae, Nothobranchiidae, Poeciliidae, Rivulidae, Scomberesocidae), Blennioidei (Blenniidae, Chaenopsidae, Labrisomidae), and the families Ambassidae, Cichlidae, Congrogadidae, Gobiesocidae, Grammatidae, Mugilidae, Opistognathidae, Plesiopidae, Polycentridae, and Pseudochromidae. Notably, the monotypic family Pholidichthyidae, often obtained as the sister group of Cichlidae (e.g., Wainwright et al., 2012; Betancur-R. et al., 2013a, 2015, 2017; Friedman et al., 2013; Near et al., 2013; Eytan et al., 2015; Rabosky et al., 2018), is not part of this group. Instead, *Pholidichthys leucotaenia* is sister to Kurtidae (Fig. 1). Bootstrap support for Ovalentaria minus Pholidichthyidae is 100%.

DISCUSSION

The family Pomacentridae is monophyletic, and its species can be divided into four subfamilies (Fig. 1; Supplemental Fig. 1; see Data Accessibility). The subfamily Microspathodontinae is the sister group to all other pomacentrids. The subfamily Glyphisodontinae is sister to a clade of Chrominae–Pomacentrinae. The composition of these clades and the relationships within each subfamily are mostly compatible with what has been inferred in previous phylogenetic studies (Tang, 2001; Quenouille et al., 2004; Tang et al., 2004; Cooper et al., 2009; Cowman and Bellwood, 2011; Hubert et al., 2011; Hofmann et al., 2012: fig. S2; Litsios et al., 2012a, 2012b; Betancur-R. et al., 2013a, 2015, 2017; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). However, our results and the earlier topologies disagree in some important aspects. Notable areas of conflict with and among prior works are in the relative positions of the Chrominae and the Glyphisodontinae, as well as in the placement of *Lepidozygus*.

Of the putative morphological synapomorphies posited for the family, our phylogeny is consistent with at least two of them (ceratomandibular ligament, two anal-fin spines) being phylogenetically informative for pomacentrids. Based on available surveys of the ceratomandibular ligament and its insertion on the lower jaw, the presence of this ligament and the position of its insertion (superior to quadrate–angular articulation) appear to be unique to members of the family (Stiassny, 1981; Frédérich et al., 2014; Olivier et al., 2016). Possession of two supernumerary spines in association with the first anal-fin pterygiophore (i.e., two anal-fin spines) appears to be distinctive for the family, which conforms to its long history as a diagnostic character and/or synapomorphy for the group (e.g., Bleeker, 1877; Jordan and Evermann, 1898; Fowler and Bean, 1928; de Beaufort, 1940; Smith, 1960; Woods and Schultz, 1960; Taylor, 1964; Munro, 1967; Allen, 1975a, 1991; Fitzpatrick, 1992; Nelson, 1994, 2006; Bellwood and Sorbini, 1996; Bannikov and Bellwood, 2014; Cooper and Santini, 2016; Nelson et al., 2016). However, Bellwood and Sorbini (1996) cautioned against assuming the derived nature of this character without a clear understanding of the sister-group relationships of Pomacentridae. The position of Embiotocidae, whose species have three (occasionally four) anal-fin spines (Tarp, 1952; Miller and Lea, 1972; Nelson, 1994), as the sister group to Pomacentridae suggests that the presence of two spines unites the Pomacentridae. However, the relationships within Ovalentaria remain uncertain (Eytan et al., 2015). A better understanding of damselfish sister-group relationships and a more in-depth survey of this character are needed.

Subfamily Chrominae

The subfamily Chrominae is recovered as the sister group of the subfamily Pomacentrinae, a phylogenetic position that corroborates some earlier studies (Tang, 2001; Jang-Liaw et al., 2002; Quenouille et al., 2004; Tang et al., 2004; Hofmann et al., 2012; Litsios et al., 2012b; Rabosky et al., 2018) but contradicts others (Cooper et al., 2009; Cowman and Bellwood, 2011; Hubert et al., 2011; Litsios et al., 2012a; Betancur-R. et al., 2013a, 2015, 2017; Frédérich et al., 2013; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Sanciangco et al., 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). The generic composition of the group has been stable since Cooper et al. (2009) restricted Chrominae to include only *Chromis*, *Dascyllus*, and *Azurina*, a taxonomic change supported by a host of other studies that have found the other putative chromine genera (*Acanthochromis*, *Altrichthys*, and *Mecaenichthys*) elsewhere in the pomacentrid tree (e.g., Tang, 2001; Jang-Liaw et al., 2002; Quenouille et al., 2004; Tang et al., 2004; Cowman and Bellwood, 2011; Hofmann et al., 2012; Litsios et al., 2012a, 2012b; Betancur-R. et al., 2013a, 2015, 2017; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Sanciangco et al., 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). The subfamily is dominated by a single genus, *Chromis*. As the most species-rich genus in the family, *Chromis* has always been a broad, expansive taxon, though it was generally considered to be a natural assemblage (e.g., Randall and Swerdloff, 1973). However, no study with sufficient taxon sampling has inferred a monophyletic *Chromis*. It is always rendered non-monophyletic by the placement of *Azurina* and *Dascyllus*

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(Tang, 2001; Jang-Liaw et al., 2002; Quenouille et al., 2004; Tang et al., 2004; Cooper et al., 2009; Cowman and Bellwood, 2011; Hubert et al., 2011; Hofmann et al., 2012; Litsios et al., 2012a, 2012b; Betancur-R. et al., 2013a, 2015, 2017; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Sanciangco et al., 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019).

Based on the extent of taxon sampling herein, it is feasible to address the polyphyly of *Chromis*. The type species of all genus-group names in the synonymy of *Chromis* are included in this analysis except for *Azurina eupalama*, the type of *Belochromis*, which may be extinct (Grove and Lavenberg, 1997; Roberts and Hawkins, 1999; Hawkins et al., 2000; Allen et al., 2010c; McCosker and Rosenblatt, 2010) though more extensive surveying is needed for confirmation (Dulvy and Polunin, 2004; Russell and Craig, 2013). Eighty-one of the 108 currently recognized species of *Chromis* were examined; Fricke et al. (2020) recognizes 109 species, including *C. flavomaculata*, which we treat as a synonym of *C. notata* (see below), following Iwatsubo and Motomura (2013). The results of this study corroborate earlier findings which consistently demonstrated that *Chromis*, as currently constituted, is broadly polyphyletic. Based on the phylogeny (Fig. 1; Supplemental Fig. 1; see Data Accessibility), the putative species of *Chromis* fall into three disjunct clades. The crown clade includes the type species, *Chromis chromis*. A second clade is sister to a monophyletic *Dascyllus*; this group includes various two-tone species (e.g., *C. fieldi*, *C. iomelas*, *C. margaritifer*) as well as the miniature species (*C. acares*, *C. nigrura*, *C. vanderbilti*). The third clade includes *Azurina*. The two most obvious solutions for the polyphyly of *Chromis* are: 1) place *Azurina* and *Dascyllus* in the synonymy of *Chromis*; or 2) assign those species currently classified as *Chromis*, but not most closely related to *Chromis chromis*, to different genera. The first choice would result in the reclassification of two species of *Azurina* and 11 species of *Dascyllus* into an already sprawling *Chromis*, which would cause at least one instance of secondary homonymy (*Chromis flavicauda* vs. *Dascyllus flavicaudus*; ICZN, 1999: Art. 57.3.1). The second choice would retain both *Azurina* and *Dascyllus*, and break up *Chromis* into multiple genera. We have chosen the latter option.

Because the crown group includes the type species *Chromis chromis*, it remains *Chromis*. The clade sister to *Dascyllus* includes *C. vanderbilti*, the type species of *Pycnochromis*. Therefore, we hereby refer all species of *Chromis* in that clade (*abrupta*, *acares*, *alleni*, *amboinensis*, *atripes*, *caudalis*, *delta*, *dimidiata*, *fatuhivae*, *fieldi*, *hanui*, *howsoni*, *iomelas*, *leucura*, *margaritifer*, *nigrura*, *ovatiformis*, *pacifica*, *retrofasciata*, and *vanderbilti*) to *Pycnochromis*. The genus is masculine so several specific epithets must change to agree in gender (e.g., *abruptus*, *dimidiatus*, *retrofasciatus*). The species name *pacifica* is treated as a noun in apposition (Allen and Erdmann, 2020: 109), so the suffix does not change to match the masculine gender of *Pycnochromis*. This usage of *Pycnochromis* expands the original limits of the genus, initially established for small, elongate species typified by *C. vanderbilti*, to absorb a grouping equivalent to Allen's (1975a: 38) *margaritifer* complex [= *Chromis amboinensis* complex *sensu* Allen and Erdmann, 2020], which was characterized by the presence of XII dorsal spines, exposed suborbital [= infraorbital] margin, and bifurcate (occasionally trifurcate) filaments at the margin of each caudal-fin lobe. Those species of *Chromis* most closely related to *Azurina hirundo* (*C. atrilobata*, *C. brevirostris*, *C. cyanea*, *C. elerae*, *C. lepidolepis*, and *C. multilineata*) are referred to *Azurina*. *Azurina* is feminine, so no name changes are necessary for gender agreement. Following this reorganization within the Chrominae, the subfamily is divided into four genera: *Azurina sensu novum*, *Chromis sensu stricto*, *Dascyllus*, and *Pycnochromis sensu novum*.

The total number of procurrent rays on each edge of the caudal peduncle is variable across the Pomacentridae, with species of *Chromis* (5–6) and *Dascyllus* (5) having fewer than other genera in the family (Randall et al., 1981). Without a comprehensive survey of this character, it is impossible to know if the number of procurrent caudal rays is phylogenetically informative at this level. However, the presence and numbers of a subset of these rays, the protruding spiniform rays (occasionally called caudal spinules; e.g., Randall et al., 1981; Shao et al., 1985; Yamakawa and Randall, 1989), have played a role in the classification of the subfamily (e.g., Allen, 1975a, 1999a; Koh et al., 1997; Kavanagh et al., 2000) and within *Chromis* (Randall and Swerdloff, 1973; Allen, 1975a; Greenfield and Woods, 1980). Since its prominent role in the classification proposed by Allen (1975a), the presence of spiniform procurrent rays has been regarded as a diagnostic character for the Chrominae. However, it is now apparent that some non-chromine taxa also possess this feature. *Acanthochromis*, *Altrichthys*, and *Mecaenichthys*, three genera previously classified in Chrominae, and *Parma*, a genus not historically associated with Chrominae, all possess this type of ray (Allen, 1975a, 1991; Hensley, 1986). Hensley (1986: 861) reported the presence of protruding procurrent caudal-fin rays in *Parma*, noting its significance as a diagnostic feature for the subfamily Chrominae (*sensu* Allen, 1975a). Cooper et al. (2009) discouraged the use of this character for taxonomic purposes because of its appearance in species outside of Chrominae *sensu stricto*. Cooper and Santini (2016) considered it unreliable as a diagnostic character. Although their presence does not characterize Chrominae as originally constituted, the number of exposed spiniform rays appears to have phylogenetic signal within the subfamily. The character state varies between 0 and 3 rays across the Chrominae; this condition has not been reviewed for the entire subfamily and its state is not available for all species so data were compiled from the following: Emery (1968); Greenfield and Hensley (1970); Randall and Swerdloff (1973); Randall and McCarthy (1988); Allen (1976, 2018); Randall and Allen (1977, 1982); Bruner and Arnam (1979); Greenfield and Woods (1980); Smith-Vaniz and Emery (1980); Allen and Randall (1981, 1985, 2004a); Randall et al. (1981); Emery and Smith-Vaniz (1982); Shao et al. (1985); Edwards (1986); Randall (1988a, 1988b, 1994, 2001); Randall and Follett (1989); Yamakawa and Randall (1989); Randall and McCosker (1992); Moura (1995); Randall and Randall (2001); Lecchini and Williams (2004); Allen and Erdmann (2005, 2008a, 2009a, 2014); McEachran and Fechhelm (2005); Senou and Kudo (2007); Pyle et al. (2008); Quéro et al. (2010); Aguilar-Medrano (2013); Iwatsubo and Motomura (2013); Randall and DiBattista (2013); Motomura et al. (2017); Yoshigou (2017); Arango et al. (2019); Tea et al. (2019); Allen and Erdmann (2020); Shepherd et al. (2020). The presence of two spiniform rays is widespread across the subfamily, whereas the presence of three spiniform rays appears mostly confined to the subgenus *Chromis* (see below) within *Chromis sensu stricto*.

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However, three spiniform rays are also observed elsewhere (e.g., *C. atripectoralis*, *C. flavaxilla*; Randall et al., 1981; Randall, 1994).

The majority of the species within the subfamily possess XII dorsal-fin spines. Except for *A. brevirostris* (XIII) and *A. eupalama* (XIII–XIV), species of *Azurina sensu lato* have XII dorsal spines (Allen, 1991; Pyle et al., 2008). All species of *Dascyllus* exhibit XII spines (Allen, 1991). All species of *Pycnochromis* display XII spines, at least modally (sometimes XI in *P. howsoni*, sometimes XIII in *P. abruptus*, *P. acares*, *P. alleni*, *P. ovatiformis*; Allen, 1991; Randall and McCosker, 1992; Randall, 2001; Randall and DiBattista, 2013; Allen and Erdmann, 2014). The species of *Chromis sensu stricto* show the most variation, ranging from XII to XV. The species of the subgenus *Hoplochromis* (see below) modally have XII (Randall et al., 1981; Allen, 1991; Randall, 1994). The remaining members of *Chromis sensu stricto* generally have XIII or more dorsal spines (Griffin, 1923; Allen, 1991, 2018; Randall and McCosker, 1992; Moura, 1995; Randall, 2001; Allen and Randall, 2004a; Lecchini and Williams, 2004; Allen and Erdmann, 2005, 2008a, 2009a; Senou and Kudo, 2007; Pyle et al., 2008; Quéro et al., 2010; Iwatsubo and Motomura, 2013, 2018; Motomura et al., 2017; Arango et al., 2019; Tea et al., 2019; Shepherd et al., 2020).

Other morphological characters may be phylogenetically informative, but a thorough review of these characters will be necessary to assay their phylogenetic utility. The presence of the ceratomandibular ligament has been interpreted as a synapomorphy of the family as a whole (Stiassny, 1981; Frédérich et al., 2014; Olivier et al., 2016) and there is considerable variation in the condition within the subfamily Chrominae, but the ligament has been either lost and/or regained independently multiple times among chromines (Frédérich et al., 2014: fig. 2). As a result, the phylogenetic significance of its loss is difficult to determine. Tooth shape is a trait with a long history in damselfish taxonomy, where putative chromines were diagnosed on the basis of conical teeth (e.g., Bleeker, 1877; Whitley, 1929; Aoyagi, 1941; Smith, 1949; Norman, 1957; Woods and Schultz, 1960; Marshall, 1964; Masuda et al., 1975). However, the condition of the teeth is highly variable within the subfamily and across the family. Several non-chromine taxa also possess similarly shaped teeth (e.g., *Acanthochromis*, *Amphiprion*, *Lepidozygus*; Allen, 1972, 1975a, 1991; Emery, 1980).

Azurina.—The genus was first described as being "closely allied to *Chromis*" (Jordan and McGregor, 1898 [in Jordan and Evermann, 1898]). It originally encompassed long, slender damselfishes with a continuous lateral line and deeply forked caudal fin (Jordan and McGregor, 1898 [in Jordan and Evermann, 1898]; Heller and Snodgrass, 1903). It has been consistently recovered within *Chromis sensu lato* (Tang et al., 2004; Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). Cowman and Bellwood (2011: figs. 2b, S6) included *Azurina* in a group they called "*Chromis* EP/WA." Cooper et al. (2009) placed *Azurina* in the synonymy of *Chromis*, a change that was supported by Aguilar-Medrano (2013) but largely ignored by others (e.g., Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Betancur-R. et al., 2013a, 2015, 2017; Frédérich et al., 2013, 2014; Cooper et al., 2014; Lobato et al., 2014; Aguilar-Medrano et al., 2015; DiBattista et al., 2016). Cooper and Santini (2016) formally reversed this decision and resumed treating *Azurina* as a distinct genus. In studies with sufficient sampling, *Azurina hirundo* is always found in a clade with some combination of *A. atrilobata*, *A. cyanea*, and/or *A. multilineata* (Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019), which is usually apart from *Chromis sensu stricto*. The sister-group relationship of *A. atrilobata* and *A. multilineata* shown herein corroborates some previous studies (Quenouille et al., 2004; Rocha et al., 2008) but those did not include *A. hirundo*. Others that did examine *A. hirundo* found it more closely related to either *A. atrilobata* (Frédérich et al., 2013; Rabosky et al., 2013, 2018; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019) or *A. multilineata* (Cowman and Bellwood, 2011; DiBattista et al., 2016). The two species of *Azurina sensu stricto* plus *A. atrilobata* are the only three species in Chrominae with no exposed spiniform procurrent rays (Greenfield and Woods, 1980; Aguilar-Medrano, 2013). Those three species also lack gill rakers on the upper branchial limb, though that character is also observed in a few other species (*C. punctipinnis* and *C. scotti* in Chrominae; *Microspathodon frontatus* and *Stegastes diencaeus* in Microspathodontinae; Allen, 1991). *Azurina sensu lato* also includes *A. elerae* and *A. lepidolepis*, two species from the Indo-Pacific. This relationship was also recorded in other phylogenies (Frédérich et al., 2013; Delrieu-Trottin et al., 2019). However, some alternate hypotheses more closely affiliate *A. lepidolepis* with *C. ternatensis* (Mirande, 2016; Gaboriau et al., 2018; Rabosky et al., 2018). Our expanded *Azurina* includes all species of "*Chromis*" from the Atlantic and eastern Pacific with XII dorsal-fin spines (viz., *A. atrilobata*, *A. cyanea*, *A. multilineata*) plus two Indo-West Pacific species (*A. elerae* and *A. lepidolepis*) that also have XII dorsal-fin spines.

The inclusion of *A. brevirostris* in this clade is unexpected, although Gaboriau et al. (2018: fig. A5) did report a similar relationship. Some key meristic counts differ from the rest of *Azurina sensu lato*: 14 (rarely 13) dorsal-fin rays versus 10–13; 15–16 anal-fin rays versus 10–13; XIII dorsal-fin spines versus XII (Allen, 1991; Pyle et al., 2008), except for *A. eupalama* (XIII, occasionally XIV; Heller and Snodgrass, 1903). Furthermore, its placement is highly unstable. There is no consensus for its phylogenetic position in past studies, with differing hypotheses placing it sister to: *C. acares* + *C. vanderbilti* (Litsios et al., 2012a); *C. cyanea* (Gaboriau et al., 2018); *C. notata* (Frédérich et al., 2013); *Chromis* (*Hoplochromis*; DiBattista et al., 2016); *Azurina sensu novum* + (*Dascyllus* + *Pycnochromis*; Delrieu-Trottin et al., 2019). Rabosky et al. (2018: Dryad file "dropped_rogues.csv") identified this species as a rogue taxon (Wilkinson, 1996; Aberer et al., 2013) and pruned it from their analyses. All studies that have examined it, including this one, are based on the same COI sequences from Pyle et al. (2008); additional data are needed to improve its resolution. The placement of *brevirostris* in *Azurina* is provisional.

Of the species not examined herein, *Chromis intercrusma* is likely a member of *Azurina sensu lato* considering it has XII dorsal-fin spines and an eastern Pacific distribution, a combination of traits it shares only with *A. atrilobata* and

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A. hirundo among chromines. If we expand the criteria to all New World chromines with XII dorsal-fin spines, that would include *A. cyanea* and *A. multilineata*, both of which have been reclassified herein as members of *Azurina sensu lato*. Moreover, its combination of a New World distribution and two exposed spiniform procurrent caudal-fin rays on each caudal lobe is shared with only *A. cyanea* (variably 2–3 rays), *A. multilineata*, and *C. meridiana* among chromines (Greenfield and Woods, 1980; McEachran and Fechhelm, 2005). Except for *C. meridiana*, which we were unable to examine (see below), the only chromine species with this combination of features were all recovered in *Azurina*. A neighbor-joining (NJ) tree (Saitou and Nei, 1987) generated by a tree-based search using the Identification System in BOLD v.4 (Ratnasingham and Hebert, 2007) appears to confirm this by placing unreleased sequences of *C. intercrusma* with *A. atrilobata*, *A. hirundo*, and *A. multilineata* (not shown). We hereby assign *intercrusma* to *Azurina sensu lato* (Table 2).

Chromis meridiana is likely a member of *Azurina*. Greenfield and Woods (1980) originally suggested that *C. meridiana* might have closer affinities to Indo-Pacific species based on the number of exposed spiniform procurrent rays on the upper and lower caudal peduncle (2 vs. 3 in other deep-bodied *Chromis* from the eastern Pacific except *C. intercrusma*). They proposed *C. randalli* as a possible close relative because it also has a high dorsal-fin spine count (XV in *C. randalli*; XIV, occasionally XIII, in *C. meridiana*). Lecchini and Williams (2004) compared it to *C. planesi* and *C. struhsakeri* based on similarities in coloration. Shepherd et al. (2020) stated that it shares a white spot at the junction of the dorsal-fin base and the caudal peduncle with *C. mamatapara*, *C. notata*, and *C. planesi*; they noted that it also shares an array of meristic characters, including XIV dorsal-fin spines, with *C. mamatapara*, *C. mirationis*, and *C. verater*. Aguilar-Medrano (2013: fig. 6) found it sister to *A. atrilobata* whereas Aguilar-Medrano et al. (2013: fig. 9) found it sister to *C. crusma*. Its eastern Pacific distribution is consistent with either *Azurina sensu lato* or the *C. insolata* clade of *Chromis sensu stricto*. The number of dorsal spines (XIII or XIV) observed in *C. meridiana* is seen in species from both of those groups. However, among chromines, only three other species have a New World distribution and two spiniform rays: *A. cyanea*, *A. intercrusma*, and *A. multilineata* (Greenfield and Woods, 1980; McEachran and Fechhelm, 2005). Both *A. cyanea* and *A. multilineata* are part of *Azurina*. We were unable to examine *A. intercrusma*, but provisionally classified that species in *Azurina* partially on the basis of the same combination of traits (see above). Therefore, we tentatively assign *meridiana* to *Azurina sensu lato* (Table 2).

Chromis sensu stricto.—The largest genus within the subfamily is composed of the species most closely related to *Chromis chromis*. It retains the majority of species originally classified in *Chromis sensu lato*. A group with a similar composition has been recovered by other studies (Quenouille et al., 2004; Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Dibattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). We resolved three clades within *Chromis sensu stricto*: *Chromis ternatensis* and its allies; *C. ovalis* and its allies; and *C. chromis* and its allies. The group formed by *C. ternatensis* and its nearest relatives has an available genus-group name, *Hoplochromis*. The clade that includes *C. ovalis* also has an available genus-group name, *Thrissochromis*. We treat these as subgenera of *Chromis* in the following discussion of relationships within *Chromis sensu stricto*. As such, *Chromis* (*Hoplochromis*) is sister to a clade of *Chromis* (*Chromis*) + *Chromis* (*Thrissochromis*).

The subgenus *Hoplochromis* consists of *C. atripectoralis*, *C. flavaxilla*, *C. ternatensis*, and *C. viridis*. Species of this group possess XII dorsal-fin spines, as seen in much of Chrominae, though *C. ternatensis* sometimes has XIII (Randall et al., 1981). These four species appear to share the presence of three spiniform procurrent caudal rays on both upper and lower margins of the caudal-fin base (Randall et al., 1981; Randall, 1994, 2005; Yoshigou, 2017), a condition which is also widely seen in the subgenus *Chromis* (see below). However, Allen and Randall (1981) reported only two for *C. ternatensis* and *C. viridis* (as *C. caerulea*). This group has been called "*Chromis* I (paraphyletic)" (Cooper and Santini, 2016: fig. 1) and "*Chromis* IP Clade 1" (Cowman and Bellwood, 2011: figs. 2b, S6). Resolving a sister-group relation between *C. atripectoralis* and *C. viridis* corroborates earlier studies (Quenouille et al., 2004; Cooper et al., 2009; Steinke et al., 2009; Cowman and Bellwood, 2011; Hubert et al., 2012, 2017; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019) and a close association described in the literature (Allen, 1975a, 1991; Randall et al., 1981, 1997; Myers, 1999; Randall, 2005; Allen and Erdmann, 2012), one that dates back to the original description of *C. atripectoralis* by Welander and Schultz (1951), who separated it from *C. viridis* (as *C. caerulea*). Randall (1994) described *C. flavaxilla* from what had been previously considered the Arabian population of *C. ternatensis*. Moyer and Ida (1976) suggested that *C. caerulea* [= *C. viridis*] and *C. ternatensis* were members of a *Chromis caerulea* group. A group containing some or all four of these species has been consistently recovered (Quenouille et al., 2004; Cooper et al., 2009; Cowman and Bellwood, 2011; Hubert et al., 2011; Hofmann et al., 2012; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). However, *Hoplochromis* often has been resolved outside of *Chromis sensu stricto* (e.g., Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019).

A nomenclatural problem previously linked *C. ternatensis* to the blue-green damselfishes when the name *Chromis caerulea*, a senior synonym of *Chromis ternatensis*, was consistently misapplied in earlier works to the species now called *Chromis viridis*; see Randall et al. (1985, 1987) for further details (ICZN, 1989). Of note, a taxon labeled as the suppressed name "*Chromis caerulea*" has appeared in some phylogenetic studies (GenBank FJ583146–FJ583148: Steinke et al., 2009; FJ583147: Litsios et al., 2012a; Frédérich et al., 2013; Delrieu-Trottin et al., 2019; FJ583148: DiBattista et al., 2016) where it is consistently found with *C. atripectoralis* and *C. viridis*. This could represent cryptic diversity, but Froukh and Kochzius (2008) reported that, although there is population structure within *C. viridis*, individuals of *C. atripectoralis* and *C. viridis* formed reciprocally monophyletic groups. In that study, *C. atripectoralis* exhibited no phylogeo-

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Table 2. Provisional classification of species previously assigned to *Chromis sensu lato* and not examined herein.

Revised classification	Previous classification	Comments/remarks
Azurina intercrusma	*Chromis intercrusma*	XII dorsal-fin spines; eastern Pacific Ocean distribution; 2 exposed spiniform procurrent caudal-fin rays (Greenfield and Woods, 1980); tree-based BOLD searches recover this species in a group with *A. atrilobata*, *A. hirundo*, and *A. multilineata*; see Discussion
Azurina meridiana	*Chromis meridiana*	Eastern Pacific Ocean distribution; 2 exposed spiniform procurrent caudal-fin rays (Greenfield and Woods, 1980); see Discussion
Chromis athena	*Chromis athena*	XIII dorsal spines; few (13–14) tubed lateral line scales; 3 exposed spiniform procurrent caudal-fin rays; similar to *C. monochroma* (Allen and Randall, 2004a; Allen and Erdmann, 2008a)
Chromis axillaris	*Chromis axillaris*	XIV dorsal spines; western Indian Ocean distribution; part of deep-dwelling complex (Allen and Erdmann, 2009a); similar to *C. pelloura* and *C. woodsi* (Randall and Allen, 1982); see Discussion
Chromis bermudae	*Chromis bermudae*	XIII dorsal spines; western Atlantic Ocean distribution; likely in the same clade as *C. insolata*; see Discussion
Chromis dasygenys	*Chromis dasygenys*	XIII dorsal spines; recovered in subgenus *Thrissochromis* (DiBattista et al., 2016); see Discussion
Chromis durvillei	*Chromis durvillei*	XIII dorsal spines; western Indian Ocean distribution; most similar to *C. earina* (Quéro et al., 2010); part of "*Chromis alpha* complex" (*sensu* Pyle et al., 2008)
Chromis flavicauda	*Chromis flavicauda*	XIII dorsal spines; western Atlantic Ocean distribution; likely in the same clade as *C. insolata*; see Discussion
Chromis jubauna	*Chromis jubauna*	XIII dorsal spines; western Atlantic Ocean distribution; likely in the same clade as *C. insolata*; see Discussion
Chromis klunzingeri	*Chromis klunzingeri*	XIII dorsal spines; eastern Indian Ocean distribution
Chromis lubbocki	*Chromis lubbocki*	XIV dorsal spines; eastern Atlantic Ocean distribution; similar to *C. cadenati*, *C. chromis*, and *C. limbata* (Wood, 1977; Edwards, 1986); tree-based BOLD searches recover this species in a group with *C. cadenati*, *C. chromis*, and *C. limbata*; see Discussion
Chromis monochroma	*Chromis monochroma*	XIII–XIV dorsal spines; few (14–15) tubed lateral line scales; three exposed spiniform procurrent caudal-fin rays; similar to *C. alpha* (Allen and Randall, 2004a; Allen and Erdmann, 2008a)
Chromis nigroanalis	*Chromis nigroanalis*	XIII dorsal spines; similar to *C. alpha* (Randall, 1988a; Allen, 1991; Myers, 1999; Randall, 2005; Pyle et al., 2008; Allen and Erdmann, 2012)
Chromis onumai	*Chromis onumai*	XIV dorsal spines; similar to *C. albomaculata* and *C. verater* (Senou and Kudo, 2007) or *C. mirationis* (Pyle et al., 2008)
Chromis planesi	*Chromis planesi*	XIV dorsal spines; similar to *C. fumea*, *C. mirationis*, *C. notata*, and *C. verater* (Lecchini and Williams, 2004; Pyle et al., 2008) and/or *C. mamatapara* (Shepherd et al., 2020)
Chromis pura	*Chromis pura*	XIII dorsal spines; similar to *C. kennensis* (Allen and Randall, 2004a; Allen and Erdmann, 2012; Iwatsubo and Motomura, 2013) and *C. notata* (Iwatsubo and Motomura, 2013); part of *Chromis notata* species complex (Iwatsubo and Motomura, 2018)
Chromis sanctaehelenae	*Chromis sanctaehelenae*	XIII–XIV dorsal spines; eastern Atlantic Ocean distribution; tree-based BOLD searches recover this species in a group with *C. cadenati*, *C. chromis*, and *C. limbata*; see Discussion
Chromis struhsakeri	*Chromis struhsakeri*	XIII–XIV dorsal spines; similar to *C. mamatapara* (Shepherd et al., 2020); *C. mirationis* (Allen and Randall, 1985; Yamakawa and Randall, 1989), *C. okamurai* (Yamakawa and Randall, 1989), and/or *C. tingting* (Tea et al., 2019)
Chromis torquata	*Chromis torquata*	XIII dorsal spines; part of *C. xanthura* complex (Allen, 2018)
Chromis trialpha	*Chromis trialpha*	XII dorsal spines; recovered in subgenus *Hoplochromis* (DiBattista et al., 2016); see Discussion
Chromis unipa	*Chromis unipa*	XIV dorsal spines; similar to *C. degruyi* (Allen and Erdmann, 2009a)
Chromis westaustralis	*Chromis westaustralis*	XIII dorsal spines; similar to *C. fumea* (Allen, 1976), *C. kennensis* (Allen et al., 2003), *C. notata* (Iwatsubo and Motomura, 2013), or *C. xanthopterygia* (Randall and McCarthy, 1988); part of *Chromis notata* species complex (Iwatsubo and Motomura, 2018)
Chromis xanthochira	*Chromis xanthochira*	XIII dorsal spines; similar to *C. weberi* (Moyer and Ida, 1976; Randall et al., 1981, 1997; Myers, 1999) and *C. xanthura* (Moyer and Ida, 1976); see Discussion
Chromis xouthos	*Chromis xouthos*	XIII dorsal spines; similar to *C. pembae* (Allen and Erdmann, 2005); tree-based BOLD searches recover this species sister to *C. pembae*

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Table 2. Continued.

Revised classification	Previous classification	Comments/remarks
Pycnochromis agilis	*Chromis agilis*	XII dorsal spines, exposed suborbital margin, caudal-fin lobes with filamentous branched tips (Randall, 1988a); similar to *P. atripes* (Randall, 1988a; Allen, 1991; Myers, 1999; Randall, 2005) and *P. pacifica* (Allen and Erdmann, 2020); see Discussion
Pycnochromis flavipectoralis	*Chromis flavipectoralis*	XII dorsal spines, exposed suborbital margin, caudal-fin lobes with filamentous branched tips (Randall, 1988a); similar to *P. amboinensis* (Allen, 1991; Allen and Erdmann, 2012) or *P. ovatiformis* (Randall, 1988a); see Discussion
Pycnochromis lineatus	*Chromis lineata*	XII dorsal spines; small adult size (approximately 40–45 mm SL), elongate body, compact head, yellowish coloration with blue markings; similar to *P. acares*, *P. nigrurus*, and *P. vanderbilti* (Allen, 1975a, 1997; Moyer and Ida, 1976; Randall et al., 1981; Myers, 1999; Allen and Erdmann, 2012); see Discussion

graphic structure, but Hubert et al. (2012: fig. S1; table S3) discovered genetically distinct populations in the Indian and Pacific basins (their "Pattern 2"). Others have also found divergent lineages within *C. atripectoralis* and/or *C. viridis* (Hubert et al., 2012, 2017; Messmer et al., 2012; Liu et al., 2019). The identity of the taxon identified as "*Chromis caerulea*" remains unclear.

The appearance of XIII (or more) dorsal-fin spines occurs in the clade composed of *Chromis* (*Chromis*) + *Chromis* (*Thrissochromis*), though *C. earina* occasionally has XII spines (Pyle et al., 2008). The subgenus *Thrissochromis* consists of *C. abyssicola*, *C. chrysura*, *C. dispila*, *C. fumea*, *C. hypsilepis*, *C. katoi*, *C. kennensis*, *C. mamatapara*, *C. mirationis*, *C. nitida*, *C. notata*, *C. okamurai*, *C. ovalis*, *C. pamae*, *C. pelloura*, *C. randalli*, *C. tingting*, and *C. yamakawai*. Most species in this group are confined to the western Pacific Ocean. Based on the condition of the ceratomandibular ligament reported in Frédérich et al. (2014: fig. 2), presence of the ligament may unite *Thrissochromis*. However, their taxon sampling within *Thrissochromis* was limited to *C. chrysura*, *C. fumea*, *C. nitida*, and *C. notata* for the species that we recovered in this subgenus. Although not formally named, earlier phylogenetic studies have found support for a grouping with congruent composition. Quenouille et al. (2004) resolved a clade comprising *C. chrysura*, *C. flavomaculata* [= *C. kennensis*], and *C. nitida*. Several studies expanded the group to include *C. fumea* and *C. notata* (Cowman and Bellwood, 2011; Litsios et al., 2012a; Rabosky et al., 2013, 2018; Gaboriau et al., 2018). The latter two studies inferred "*Chromis bami*" as part of this clade but used sequences (Gaboriau et al., 2018: appendix 2; Rabosky et al., 2018: Dryad file "accession_numbers.csv") generated by Frédérich et al. (2013: table S1) from a specimen (USNM 336492, KU T764) that has been reidentified as *C. chrysura* (A. C. Bentley, pers. comm.). All three studies tellingly found their "*C. bami*" sister to *C. chrysura*. This affects the following GenBank accession numbers: JQ707032, JQ707067, JQ707102, JQ707135, JQ707169, JQ707191, JQ707225, JQ707261. Cowman and Bellwood (2011: figs. 2b, S6) called this group "*Chromis* IP Clade 2." Song et al. (2014), with more limited taxon sampling than the other studies, resolved relationships among *C. fumea*, *C. notata*, and *C. tingting* (as *C. mirationis*; see Tea et al., 2019) that are consistent with the results of this analysis. DiBattista et al. (2016) added *C. pelloura* to the clade. Delrieu-Trottin et al. (2019) did not examine *C. pelloura* but recovered *C. pamae* and *C. randalli* inside of an equivalent clade. A close relationship between *C. kennensis* (as *C. flavomaculata*) and *C. notata* has been suggested based on morphological similarities (Randall et al., 1981; Iwatsubo and Motomura, 2013). We follow Iwatsubo and Motomura (2013) in treating *C. flavomaculata* as a synonym of *C. notata* and recognizing *C. kennensis* as the appropriate name for the species previously identified as *C. flavomaculata*. A sister-group pairing of *C. pamae* [= *Chromis* sp. "H" in Allen, 1975a; *Chromis* sp. 5 in Allen, 1991] and *C. randalli* matches statements by previous authors (Allen, 1975a, 1991; Randall and McCosker, 1992; Randall, 2005) who commented on their distinctive appearance. In their description of *C. pamae*, Randall and McCosker (1992) named *C. randalli* as its closest relative. Both species possess a fusiform or terete body, XV dorsal-fin spines, very small scales on the head, and fleshy orbital papillae similar to those seen in *Lepidozygus tapeinosoma* (Greenfield and Hensley, 1970; Emery, 1983; Randall and McCosker, 1992). They are the only two species of *Chromis* that exclusively have XV dorsal-fin spines (Randall and McCosker, 1992), which is unique for the subfamily (*C. struhsakeri* rarely has XV; Randall and Swerdloff, 1973).

Iwatsubo and Motomura (2018) delimited a *Chromis notata* species complex composed of *C. katoi*, *C. kennensis*, *C. notata*, *C. pura*, *C. westaustralis*, and *C. yamakawai*. They diagnosed the group by the following: "XIII (rarely XII or XIV) [dorsal-fin spines], 11–14 (usually 12 or 13) dorsal-fin rays; II [anal-fin spines], 10–12 (usually 11) anal-fin rays; 15 principal caudal-fin rays; 2 spiniform caudal-fin rays; 3–5 scale rows above lateral line, 9–12 scale rows below; 15–21 tubed lateral-line scales; 6–10 + 18–25 = 26–34 gill rakers; caudal-fin lobes not filamentous; a prominent black blotch covering more than two-thirds of pectoral-fin base; caudal fin yellowish or brownish (not white); and uniformly brownish or grayish head in adults." All putative members of this species group included in our phylogeny (*C. katoi*, *C. kennensis*, *C. notata*, and *C. yamakawai*) clustered together in a clade, along with *C. ovalis* (Fig. 1). Iwatsubo and Motomura (2018) did not examine *C. ovalis*, a Hawaiian endemic, but it does share characters and overlap in meristic counts with what they observed in their *Chromis notata* species group (Randall and Swerdloff, 1973; Randall and Follett, 1989). However, *C. ovalis* has three spiniform procurrent caudal-fin rays (vs. 2 in the *Chromis notata* group), and its axillary black spot only

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covers the upper half of the pectoral-fin base (vs. more than two-thirds; only covers upper half in juvenile *C. yamakawai*).

Chromis (*Chromis*) encompasses the remaining species of *Chromis sensu stricto*. Cooper and Santini (2016: fig. 1) referred to an equivalent clade as "*Chromis* I (paraphyletic)." The species of this group are distinguished from most other chromines by the presence of three exposed spiniform procurrent caudal-fin rays on the upper and lower caudal margins, though some species outside of this group also display three such rays (e.g., *Chromis atripectoralis*, *C. flavaxilla*, *C. ovalis*, *C. ternatensis*, *C. viridis*; Randall et al., 1981; Randall and Follett, 1989; Randall, 1994, 2005; Yoshigou, 2017). The subgenus *Chromis* includes two clades that fall entirely outside of the Indo-West Pacific. The first comprises all of the species with XIV dorsal-fin spines found in the central and eastern Atlantic (*C. cadenati*, *C. chromis*, and *C. limbata*). *Chromis limbata* has recently extended its range to the western Atlantic along the coast of Brazil, possibly by rafting via transported oil rigs (Anderson et al., 2017, 2020). Wood (1977) noticed similarities among *C. cadenati* (as *C. lineatus*), *C. chromis*, and *C. limbata*. Gaboriau et al. (2018) also recovered all three species together in a clade. We were unable to examine *C. lubbocki*, but it is most likely related to this clade, based on its XIV dorsal-fin spines and eastern Atlantic distribution. When describing *C. lubbocki*, Edwards (1986) stated that it closely resembled the three other species of eastern Atlantic *Chromis* with XIV dorsal-fin spines (i.e., *C. cadenati*, *C. chromis*, and *C. limbata*) and suggested that it was most similar to *C. cadenati*. He noted that previous workers had treated *C. lubbocki* as either *C. lineatus* [= *C. cadenati*] or *C. chromis* (e.g., Bowdich, 1825; Cadenat, 1951). A tree-based BOLD identification appears to confirm this by placing unreleased sequences of *C. lubbocki* with *C. cadenati*, *C. chromis*, and *C. sanctaehelenae* (not shown). *Chromis sanctaehelenae* is therefore most likely a member of *Chromis sensu stricto* and part of this clade too. In the original description, Edwards in Edwards and Glass (1987) compared it to *C. insolata* and other XIII-spined Atlantic *Chromis*. However, *C. sanctaehelenae* occasionally displays XIV dorsal-fin spines and has an eastern Atlantic distribution, characteristics that suggest it is more closely related to *C. chromis* and its allies (*C. cadenati*, *C. limbata*, and *C. lubbocki*). As mentioned above, the NJ tree generated by the BOLD identification engine favors the latter hypothesis, finding *C. cadenati* sister to *C. sanctaehelenae*.

The second group that occurs entirely outside of the Indo-West Pacific is found on both sides of the Isthmus of Panama. This Western Hemisphere group includes *C. enchrysura*, *C. insolata*, and *C. scotti* from the western Atlantic (*C. enchrysura* reaches St. Paul's Rocks; Lubbock and Edwards, 1981) and *C. alta*, *C. crusma*, *C. limbaughi*, and *C. punctipinnis* from the eastern Pacific. Some combination of these species has been recovered as a clade in other phylogenetic studies (Frédérich et al., 2013; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Rabosky et al., 2018). Of these, *Chromis insolata* is the type species of the genus-group name *Heliases*, which has been treated as a subgenus by some workers (e.g., Emery, 1968, 1973, 1980; Colin, 1974, 1976; Hensley and Smith, 1977; Greenwood and Woods, 1980; Smith-Vaniz and Emery, 1980). All of the New World *Chromis sensu stricto* with XIII dorsal-fin spines fall into this group. Beyond these two groups of *Chromis*, the only other chromine species outside of the Indo-West Pacific reside in *Azurina sensu lato* (see above).

Besides the eastern Atlantic clade mentioned above, the other species with XIV dorsal-fin spines (exclusively or modally) occur in the Indo-Pacific: *Chromis abyssus*, *C. albomaculata*, *C. axillaris*, *C. circumaurea*, *C. degruyi*, *C. mamatapara*, *C. mirationis*, *C. okamurai*, *C. onumai*, *C. ovalis*, *C. pelloura*, *C. planesi*, *C. struhsakeri*, *C. tingting*, *C. unipa*, *C. verater*, and *C. woodsi* (Allen, 1991; Lecchini and Williams, 2004; Senou and Kudo, 2007; Pyle et al., 2008; Allen and Erdmann, 2009a; Tea et al., 2019; Shepherd et al., 2020). Randall and Allen (1982) noted that many of the species with XIV dorsal-fin spines occur in deeper water, listing *C. axillaris*, *C. mirationis*, *C. pelloura*, *C. struhsakeri*, *C. verater*, and *C. woodsi* as examples of this phenomenon. They mentioned *C. ovalis* as an exception: a species with XIV dorsal-fin spines that does not extend past 45 m in depth. Pyle et al. (2008) discussed a deep-dwelling complex composed of *C. abyssicola* (XIII dorsal-fin spines), *C. abyssus*, *C. axillaris*, *C. circumaurea*, *C. degruyi*, *C. mirationis*, *C. okamurai*, *C. onumai*, *C. planesi*, *C. struhsakeri*, and *C. woodsi*. Allen and Erdmann (2009a) expanded on this by noting that species with XIV dorsal-fin spines are either confined to deep reefs (>50 m in depth) or found in subtropical regions (e.g., Hawaii, Japan). Recent explorations of mesophotic coral reefs have discovered additional deeper water *Chromis* with XIV spines (Tea et al., 2019; Shepherd et al., 2020). Despite the shared dorsal-fin spine count of XIV, Allen and Erdmann (2009a) doubted that these *Chromis* formed a monophyletic group because of diverse morphological variation observed among the species. The results from our analysis concur, finding these species scattered throughout *Chromis sensu stricto* (Fig. 1). However, we did find evidence of a monophyletic group composed of a subset of these XIV-spined species: *C. abyssus*, *C. albomaculata*, *C. circumaurea*, and *C. degruyi* (modally XIV in *C. degruyi*).

Although not named as such, Cowman and Bellwood (2011: figs. 2b, S6) circumscribed a clade that corresponds to *Chromis* (*Chromis*), which was composed of what they called *Chromis* EA (*C. chromis* and *C. limbata*), *Chromis* EP (*C. alta* and *C. punctipinnis*), and *Chromis* IP Clade 3 (*C. analis* and allies). The sister-group relationship shown between *C. albicauda* and *C. analis* (Fig. 1) corresponds to published works that have noted their similarity (Allen and Erdmann, 2009a, 2012; Song et al., 2014). The clade that includes *C. analis* has an available name, *Dorychromis*. A close relationship between *C. opercularis* and *C. xanthura* has been proposed previously (Randall et al., 1981; Myers, 1999; Allen and Erdmann, 2012) and was confirmed by Motomura et al. (2017), who delimited a "*Chromis xanthura* species group" composed of those two species plus *C. anadema*. Our results agree with their topology of these three species.

Provisional classifications.—The following species previously classified in *Chromis sensu lato* are tentatively assigned to the newly restricted *Chromis sensu stricto*: *Chromis athena*, *C. axillaris*, *C. bermudae*, *C. dasygenys*, *C. durvillei*, *C. flavicauda*, *C. jubauna*, *C. katoi*, *C. klunzingeri*, *C. lubbocki*, *C. mirationis*, *C. monochroma*, *C. nigroanalis*, *C. onumai*, *C. planesi*, *C. pura*, *C. sanctaehelenae*, *C. struhsakeri*, *C. torquata*, *C. trialpha*, *C. unipa*, *C. westaustralis*, *C. xanthochira*, *C. xouthos*, and *C. yamakawai*. Because we were unable to examine these species, the assignments are based on a variety of informa-

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tion, including comparisons to unpublished BOLD sequences, previous literature, and geographic distribution (Table 2). More detailed explanations for select species are provided below.

Chromis axillaris is likely part of *Chromis sensu stricto* based on its XIV dorsal-fin spines and similar coloration to *C. pelloura* and *C. woodsi*, with which it shares a western Indian Ocean distribution (Bruner and Arnam, 1979; Randall and Allen, 1982). Allen and Randall (1981) tentatively treated specimens of the then undescribed *C. pelloura* as *C. axillaris*, noting that the latter species was poorly known at the time. After examining material of *C. axillaris*, Randall and Allen (1982) described *C. pelloura* as a new species and identified its closest relative as *C. axillaris*. Even though *C. pelloura* and *C. woodsi* are not closely related in our phylogeny, both were recovered within *Chromis sensu stricto*.

Chromis bermudae, *C. flavicauda*, and *C. jubauna* are likely in the same clade as *C. insolata* because of their XIII dorsal-fin spines and western Atlantic distribution. That particular combination of attributes is distinctive for this group. The only other New World chromines (i.e., *Azurina sensu novum*) almost always have XII dorsal-fin spines (see above). All three species share a similar color pattern: dark colored body; yellow caudal fin; varying amount of yellow on caudal peduncle and anal and dorsal fins. Emery (1968) classified *C. flavicauda sensu lato* as one of four species in the subgenus *Heliases*, which also included *C. enchrysura*, *C. insolata*, and *C. scotti*. *Chromis bermudae* was treated as a junior synonym of *C. flavicauda* (e.g., Smith-Vaniz and Emery, 1980; Allen, 1991; Moura, 1995; Smith-Vaniz et al., 1999) until recently (Smith-Vaniz and Collette, 2013). The two species, both with bright blue bodies, are distinguished by the extent of yellow on the caudal peduncle and anal and dorsal fins, where the yellow is more prevalent in *C. bermudae* (Smith-Vaniz and Emery, 1980; Moura, 1995; Smith-Vaniz and Collette, 2013). The extent of yellow on the anal fin is a trait that also serves to differentiate *C. flavicauda* and *C. jubauna* (Moura, 1995).

Chromis dasygenys is conditionally classified in *Chromis sensu stricto* based on the presence of XIII dorsal-fin spines. All currently published GenBank sequences (HQ945824, JF493173, MG220302) appear to be misidentified. GenBank BLAST (Altschul et al., 1990; Johnson et al., 2008; Boratyn et al., 2013) and BOLD searches suggest they originate from an unknown pomacentrine (either not barcoded or described yet), most similar to *Neopomacentrus miryae* (approximately 96–97% similarity). Litsios et al. (2012a) recovered it as the sister species of *Chrysiptera kuiteri* in Pomacentrinae. DiBattista et al. (2016) recovered it as the sister group of a clade composed of *Chromis chrysura*, *C. flavomaculata* [= *C. kennensis*], *C. fumea*, *C. nitida*, *C. notata*, and *C. pelloura*. Gaboriau et al. (2018) found it sister to *Teixeirichthys*. Rabosky et al. (2018: Dryad file "dropped_rogues.csv") identified it as a rogue taxon and pruned it from their analyses.

Chromis trialpha possesses XII dorsal-fin spines, which is not diagnostic on its own. Allen and Randall (1981) remarked on its similarity to *C. elerae* which we consider a member of *Azurina sensu lato* (see above). However, DiBattista et al. (2016) recovered *C. trialpha* sister to *Chromis* (*Hoplochromis*), another group with XII dorsal-fin spines. Furthermore, they resolved *Hoplochromis* outside of *Chromis sensu stricto* as part of a basal sister group to the rest of Chrominae. Their data for *C. trialpha* are not presently available on GenBank. *Chromis trialpha* is tentatively assigned to *Chromis sensu stricto*, but that is contingent on the placement of *Hoplochromis*.

Chromis xanthochira is likely a member of *Chromis sensu stricto* based on the presence of XIII dorsal-fin spines and its similarity to *C. weberi* (Moyer and Ida, 1976; Randall et al., 1981, 1997; Myers, 1999) and *C. xanthura* (Moyer and Ida, 1976). The other two species of its eponymous species group (*sensu* Moyer and Ida, 1976), *C. weberi* and *C. xanthura*, are part of *Chromis sensu stricto*, though not most closely related. Published GenBank sequences for samples identified as *C. xanthochira* were not included because of ambiguity as to their identity. Some were obtained from specimens (JF434909–JF434914; JF457398–JF457403; JF458071–JF458076) collected in the western Indian Ocean (Madagascar and Réunion) where *C. xanthochira* is not known to occur (Allen, 1991; Fricke, 1999; Fricke et al., 2018); AY289561 appears to be from *C. fatuhivae*, based on BLAST searches; others appear to be *C. weberi* (FJ616327, FJ616435, FJ616654, MF123819), based on BLAST and BOLD searches.

Dascyllus.—The species of *Dascyllus* all share a distinctive orbiculate body shape which differentiates them from other chromines. The genus is broadly distributed across the Indo-West Pacific. The composition and limits of *Dascyllus* have been stable for many years. In their revision, Randall and Allen (1977) recognized nine species: *Dascyllus albisella*, *D. aruanus*, *D. carneus*, *D. flavicaudus*, *D. marginatus*, *D. melanurus*, *D. reticulatus*, *D. strasburgi*, and *D. trimaculatus*. In the intervening four decades, only one new species has been described, *D. auripinnis*, and one species has been resurrected, *D. abudafur* (Randall and Randall, 2001; Borsa et al., 2014). However, possible cryptic diversity has been identified in *D. trimaculatus* (Bernardi et al., 2001, 2002, 2003; Leray et al., 2010; Hubert et al., 2012, 2017). Species of *Dascyllus* generally have a conserved or low fundamental chromosome number (NF) but reduced diploid (2n) number (Arai and Inoue, 1976; Ojima and Kashiwagi, 1981; Klinkhardt et al., 1995; Molina, 2007; Arai, 2011), which is likely the result of Robertsonian translocations (Ojima, 1983; Takai and Ojima, 1995; Molina and Galetti, 2002, 2004b), a phenomenon that is uncommon in teleosts (Takai and Ojima, 1995).

Following information drawn from Randall and Allen (1977), Godwin (1995) delimited three species complexes based on "morphology, biogeography, and striking coloration differences." He observed that the smaller species of the *aruanus* (*D. aruanus* and *D. melanurus*) and *reticulatus* (*D. carneus*, *D. flavicaudus*, *D. marginatus*, and *D. reticulatus*) complexes are closely associated with branching corals and often have protogynous sex change and resource-defense polygyny, whereas the larger species of the *trimaculatus* complex (*D. albisella*, *D. strasburgi*, and *D. trimaculatus*) only associate with corals as juveniles and do not exhibit sex change nor polygyny. He hypothesized that the hermaphroditism is linked to a harem-based mating system in which males defend the coral heads where females reside. Our results seem congruent with Godwin's (1995) hypothesis that protogynous sex change evolved in the ancestor of *Dascyllus*, as seen in the small-bodied species plus *D. flavicaudus*, followed by a reversal to gonochorism in the species of the *trimaculatus* complex. However, Asoh et al. (2001) cautioned that evidence for either gonochorism or protogyny in these species was often equivocal, after they showed evidence for protogyny in *D. albisella*, a large-bodied species hypothesized

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to be gonochoristic. Further complicating matters was their discovery that, despite gonadal development transitioning through an ovarian stage in all individuals, the protogyny was non-functional and likely an example of phylogenetic inertia. Asoh and Kasuya (2002) reported a similar pattern of non-functional protogynous gonad development in *D. trimaculatus*, another large, putatively gonochoristic species. Whether size or phylogenetic inertia was the primary factor in the evolution of protogyny remains unresolved, with different studies finding ambiguous and sometimes conflicting results (Bernardi and Crane, 1999; McCafferty et al., 2002).

Bernardi and Crane (1999) produced the first explicit phylogeny of the genus, inferred from 16S and cytochrome *b* sequences. They determined that *D. aruanus* and *D. melanurus* are sister to the rest of the genus and that species assigned to the *reticulatus* complex are paraphyletic relative to a clade of *D. trimaculatus* and its nearest relatives. Subsequent studies generated similar results (e.g., McCafferty et al., 2002; Quenouille et al., 2004), with disagreement mainly in the exact placement of *D. reticulatus* (see below). All agreed that the four species of the *reticulatus* complex are paraphyletic to a crown clade comprising *D. trimaculatus* and its allies.

Our data matrix included all species but *D. auripinnis*. The tree shows strong support (100% bootstrap) for the monophyly of *Dascyllus* and for the relationships within the genus (Fig. 1; Supplemental Fig. 1; see Data Accessibility). The topology agrees with the consensus that the humbug damselfishes, consisting of *D. aruanus* and its allies, are monophyletic and sister to the remaining species of *Dascyllus* (Bernardi and Crane, 1999; McCafferty et al., 2002; Quenouille et al., 2004; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019), and that the domino damselfishes, consisting of *D. trimaculatus* and its allies, form the crown group (Bernardi and Crane, 1999; McCafferty et al., 2002; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). The separation of the humbug damsels from the rest of *Dascyllus* is also supported by cytogenetic data, where *D. aruanus* has distinctive chromosomal rearrangements and fewer chromosomes overall than other species (2n = 28–32 vs. 48 in *D. carneus*, *D. melanurus*, and *D. trimaculatus*; Arai, 2011; Getlekha et al., 2016b). There is less agreement on the relationships among the remaining species. Several studies (Bernardi and Crane, 1999; Quenouille et al., 2004; Koh and Park, 2007; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; DiBattista et al., 2016) have resolved *D. flavicaudus* and *D. marginatus* as sister species, which our results and others (Frédérich et al., 2013; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019) do not support. Despite finding that pairing themselves, Bernardi and Crane (1999: 1216) remarked that a sister relationship between these two species is unexpected because of their geographic ranges.

The status of *D. reticulatus* is complicated, in part because its species delimitation is uncertain. A sister-group relationship between *D. carneus* and *D. reticulatus* has been suggested in the literature (Randall and Allen, 1977; Randall, 2005; Allen and Erdmann, 2012) and is supported by some studies (Quenouille et al., 2004; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Mirande, 2016) but contradicted by others (Bernardi and Crane, 1999; Koh and Park, 2007: fig. 1; Rabosky et al., 2013, 2018; DiBattista et al., 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). This discrepancy may be partially explained by McCafferty et al. (2002), who discovered that individuals traditionally classified as "*Dascyllus reticulatus*" fall into two separate lineages. They resolved a northern population (their *reticulatus* A) that is paraphyletic relative to *D. flavicaudus* and a southern population (their *reticulatus* B) that is sister to *D. carneus*. Subsequent studies have not accounted for these two populations. Of the previously published phylogenies, Cooper et al. (2009: table 1) drew from the northern population (Philippines, near Busuanga Island) and Quenouille et al. (2004: table 1) from the southern population (Australia, Great Barrier Reef). Locality information for the Bernardi and Crane (1999) sample was unknown because it came from the aquarium trade, but McCafferty et al. (2002: 1387) stated that the specimen is phylogenetically equivalent to their *reticulatus* B, the southern group. Several studies (e.g., Tang, 2001; Tang et al., 2004; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019) have mixed sequences from both populations to represent a single combined "*D. reticulatus*" taxon. Our sample of *D. reticulatus* (CAS 217404; KU T4945) originates from Fiji (16°16′54.6″S, 179°09′20.4″W) and corresponds to the southern lineage (*reticulatus* B). We also mined GenBank sequences (FJ616340, FJ616448, FJ616667; Cooper et al., 2009) with known locality data to include a representative of the northern population. In finding two disparate *reticulatus* lineages, these results corroborate McCafferty et al. (2002), where the northern population (Philippines) is with *D. flavicaudus* and the southern population (Fiji) is with *D. carneus* (Fig. 1).

Based on the geographical boundaries drawn by McCafferty et al. (2002), the type material of *D. reticulatus* appears to originate from the northern population: the description only gives "China seas" as the locality, with Richardson (1846) stating that the two type specimens were brought to him from China. McCafferty et al. (2002) could not find any differences in the molecular data to distinguish between *D. flavicaudus* and the northern lineage, *D. reticulatus sensu stricto*. If they were to be placed in synonymy, *Dascyllus reticulatus* would have priority over *Dascyllus flavicaudus*. Conversely, the southern "*D. reticulatus*," which is sister to *D. carneus*, would require a name if it were to be treated as a separate species. *Dascyllus xanthosoma* is an available name for the southern lineage based on its type locality of Banda, Indonesia. McCafferty et al. (2002) could find no discernable molecular evidence to distinguish between *D. albisella* (Hawaiian endemic) and *D. trimaculatus*. They suggested that the two species should be regarded as part of a *trimaculatus* species group. The species limits within *Dascyllus* and their nomenclature merit more detailed examination, but these issues are beyond the scope of this study.

***Pycnochromis*.—**Support for the monophyly of this genus is high (100% bootstrap) and congruent with other studies. The species we are recognizing as *Pycnochromis* have been resolved as the sister group to *Dascyllus* in numerous phylogenetic analyses (Tang, 2001; Jang-Liaw et al., 2002; Quenouille et al., 2004; Tang et al., 2004; Koh and Park,

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2007; Cooper et al., 2009; Cowman and Bellwood, 2011; Hofmann et al., 2012; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). Based on the distribution of the ceratomandibular ligament (Frédérich et al., 2014), species of the *Dascyllus* + *Pycnochromis* clade appear to be united by the reappearance of the ligament, which is otherwise lost in the subfamily (see above). All species of *Dascyllus* and almost all species of *Pycnochromis* have XII dorsal spines; *P. acares*, *P. alleni*, and *P. ovatiformis* can sometimes have XIII (Randall and Swerdloff, 1973; Randall et al., 1981); *P. howsoni* occasionally has XI (Allen and Erdmann, 2014). However, this count is widespread in the subfamily (see above). A group matching the composition of *Pycnochromis sensu novum* has been recorded in other studies (Hubert et al., 2011; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). This taxon has been variously labeled "*Chromis* II" (Quenouille et al., 2004), "*Chromis* b" (Koh and Park, 2007), "*Chromis* IP Clade 4" (Cowman and Bellwood, 2011), and "*Chromis* III" (Cooper and Santini, 2016).

The genus we are recognizing as *Pycnochromis* is composed of two morphologically distinct clades: one that comprises the miniature species, *P. vanderbilti* and its allies, and another that represents an expanded *margaritifer* complex *sensu* Allen (1975a) [= *Chromis amboinensis* complex *sensu* Allen and Erdmann, 2020]. We were unable to sample *Chromis lineata*, but it is almost certainly a member of *Pycnochromis* given its similarity to *P. acares*, *P. nigrurus*, and *P. vanderbilti* (Allen, 1975a, 1997; Moyer and Ida, 1976; Randall et al., 1981; Myers, 1999; Allen and Erdmann, 2012). Hence, we refer it to *Pycnochromis* as *P. lineatus*. With that generic reassignment, *Chromis lineata* Cadenat, 1950 is no longer a secondary homonym of *Chromis lineata* Fowler and Bean, 1928, but is considered permanently invalid because it was replaced by Whitley (1951) before 1961 (ICZN, 1999: Art. 59.3) and its substitute name, *Chromis cadenati*, is in use (e.g., Wood, 1977; Edwards, 1986; Allen, 1991; Edwards et al., 2003; Lecchini and Williams, 2004; Domingues et al., 2005). The four miniature species are characterized by their small adult size (approximately 40–45 mm SL), elongate body, compact heads, and yellowish coloration with blue markings (Randall and Swerdloff, 1973; Allen, 1975a; Randall et al., 1981, 1997; Myers, 1999; Allen and Erdmann, 2012). Three of the four have blue spots on the opercle and along the scale rows, forming stripes that run the length of the body. *Pycnochromis acares* possesses blue spots on the head but lacks the lateral bands on the body (Randall and Swerdloff, 1973).

Species of the *margaritifer* complex differ markedly in their coloration and overall appearance from *Pycnochromis vanderbilti* and its immediate relatives. Allen (1975a: 38) characterized them as possessing XII dorsal spines, an exposed suborbital (i.e., infraorbital) margin, and prolonged bifurcate filaments at the tips of the caudal lobes. Moyer and Ida (1976) identified the group by their filamentous caudal-fin rays. The presence of filamentous caudal-fin margins in these species was also noted by Randall et al. (1981). As stated above, due to the widespread presence of XII dorsal spines across chromines, that meristic count has limited value for distinguishing among genera. Similarly, the condition of the suborbital margin is not unique to the group; there are other species of Chrominae that exhibit the same character state (e.g., *Azurina elerae*, *A. lepidolepis*, *Chromis abyssus*, *C. albomaculata*, *C. athena*, *C. circumaurea*, *C. degruyi*, *C. earina*, *C. flavapicis*, *C. mirationis*, *C. monochroma*, *C. okamurai*, *C. planesi*, *C. pura*, *C. unipa*, and *C. xouthos*; Randall et al., 1981; Yamakawa and Randall, 1989; Randall, 2001; Allen and Randall, 2004a; Lecchini and Williams, 2004; Allen and Erdmann, 2005, 2008a, 2009a; Pyle et al., 2008). However, species of the sister clade (*P. vanderbilti* and relatives) lack an exposed suborbital (Fowler and Bean, 1928; Fowler, 1941; Randall and Swerdloff, 1973; Moyer and Ida, 1976; Randall et al., 1981), so the condition of the suborbital in the species of the *margartifer* complex may distinguish the group from the rest of *Pycnochromis*. A more exhaustive survey of this trait is necessary. Of the three diagnostic characters detailed by Allen (1975a), the presence of extended, branching filaments on each caudal-fin lobe seems to be most reliable for identifying members of this complex. They are present in all species of the group (Smith, 1960; Randall and Swerdloff, 1973; Randall et al., 1981; Randall, 1988a, 1988b, 2001; Randall and McCosker, 1992; Randall and DiBattista, 2013; Allen and Erdmann, 2014; Froese and Pauly, 2019) and absent in other chromine species. A few have extensions of the caudal fins but not like what is seen in the *margaritifer* complex: *Chromis albomaculata* (as juveniles), *C. atripectoralis*, and *C. xanthura* have filamentous caudal-fin rays but none are described as being branched (Randall et al., 1981). *Pycnochromis* includes many of the black-and-white species (e.g., *P. fieldi*, *P. iomelas*, *P. leucurus*, and *P. margaritifer*), but some white-tailed species were recovered elsewhere (e.g., *C. chrysura* and *C. xanthura*). The placement of *C. chrysura* outside of *Pycnochromis* is expected; in comparing other species to *P. fatuhivae*, Randall (2001) noted in passing that *C. chrysura* "is in a different lineage." He specifically commented on its XIII dorsal spines and lack of filamentous caudal rays. Even though the bicolor species with abrupt dark-to-light color patterns do not form a monophyletic group within *Pycnochromis*, a subset of them (*P. abruptus*, *P. dimidiatus*, *P. fieldi*, and *P. margaritifer*) are closely related (100% bootstrap), which has been proposed before (Randall, 2001; Allen and Erdmann, 2012; Randall and DiBattista, 2013; He et al., 2019b). Our results corroborate the sister relationship hypothesized for *P. abruptus* (= *Chromis* sp. "F" in Allen, 1975a) and *P. margaritifer* (Allen, 1975a; Randall, 2001). *Pycnochromis iomelas*, which shares a similar half-and-half color pattern with these species and has been previously associated with them (e.g., Allen, 1975a; Randall et al., 1997; Randall, 2005; Randall and DiBattista, 2013), was recovered as a more distant relative within *Pycnochromis*. Our phylogeny resolves *P. amboinensis* and *P. howsoni* as sister species, as hypothesized by Allen and Erdmann (2014).

Provisional classifications.—*Chromis agilis* is probably a member of this genus because of its similarity to *P. atripes* (Randall, 1988a; Allen, 1991; Myers, 1999; Randall, 2005; *C. agilis* treated as *C. xutha*) and *P. pacifica* (Allen and Erdmann, 2020). *Chromis flavipectoralis* is likely another species of *Pycnochromis*, based on its similarity to *P. amboinensis* (Allen, 1991; Allen and Erdmann, 2012) and *P. ovatiformis* (Randall, 1988a). Both *C. agilis* and *C. flavipectoralis* possess the diagnostic features of the *margaritifer* complex: XII dorsal spines, exposed suborbital margin, and caudal-fin lobes with filamentous branched tips (Randall, 1988a). Therefore, we

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provisionally classify these two species as *Pycnochromis* (Table 2). This would bring the total number of species in this complex to 20, matching the diversity of the *Chromis amboinensis* complex mentioned by Allen and Erdmann (2020: 110), who placed *C. xutha* in the synonymy of *C. agilis* [= *P. agilis*]. We treat *Chromis lineata* as *Pycnochromis lineatus* because of its similarity to *P. acares*, *P. nigrurus*, and *P. vanderbilti* (see above).

Subfamily Glyphisodontinae

The species of *Abudefduf*, the sole genus in this subfamily, have a widespread circumtropical distribution. We included all 21 currently recognized species (Wibowo et al., 2018; Fricke et al., 2020), but there is compelling evidence of undescribed diversity within *Abudefduf vaigiensis* (Quenouille et al., 2011; Bertrand et al., 2017; Campbell et al., 2018; Wibowo et al., 2018) which we did not include. All species except *A. sparoides* have a distinctive color pattern of alternating light and dark vertical bars (Hensley, 1978), giving the group its common name, "sergeants." They are united by their deep bodies and possession of "uniserial teeth with compressed tips and bicuspid or entire margins (in adults)" and "13 dorsal spines (rarely 12 or 14)" (Hensley and Allen, 1977). The monophyly of *Abudefduf* (with the exception of *Similiparma lurida*) has not been in doubt since Allen (1975a) greatly restricted the genus to a taxon equivalent to the subgenus *Glyphidodon* [= *Glyphisodon*] *sensu* Bleeker (1877). According to Getlekha et al. (2016a), the genus exhibits "chromosomal conservatism," based on the limited variation in cytogenetic characteristics (e.g., conserved chromosome and fundamental numbers, karyotype structure) among its species. They suggested that this lack of divergence contributed to the hybridization observed between *A. abdominalis* and *A. vaigiensis* (Maruska and Peyton, 2007; Coleman et al., 2014), because cytogenetic differences (e.g., pericentric inversions) can serve as strong post-zygotic barriers to viable hybrids. Despite the degree of chromosomal similarity seen in *Abudefduf*, Getlekha et al. (2016a: fig. 5) did report a potential cytogenetic synapomorphy within the genus. In their investigation of pomacentrid egg and larval morphology, Muñoz-Cordovez et al. (2019) observed that larvae of *Abudefduf* concentrate pigmentation in the pre-anal segment of the body, whereas pigment is primarily postanal in the other subfamilies.

Our phylogeny (Fig. 1; Supplemental Fig. 1; see Data Accessibility) resolves a monophyletic *Abudefduf sensu stricto*, excluding "*Abudefduf*" *luridus* [= *Similiparma lurida*], which Cooper et al. (2014) referred to the microspathodontine genus, *Similiparma*. We follow Cooper and Santini (2016) in recognizing the subfamily Glyphisodontinae for the species of *Abudefduf*. The subfamily is sister to a clade comprising the subfamilies Chrominae and Pomacentrinae. This placement of *Abudefduf* is supported by some studies (Quenouille et al., 2004; Hofmann et al., 2012; Litsios et al., 2012b; Stieb et al., 2017: fig. 1; Rabosky et al., 2018) but disagrees with those that have located Glyphisodontinae as the sister group of Chrominae (Hubert et al., 2011; Stieb et al., 2017: fig. 2), Microspathodontinae (Delrieu-Trottin et al., 2019), or Pomacentrinae (Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a; Betancur-R. et al., 2013a, 2015, 2017; Frédérich et al., 2013; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Sanciangco et al., 2016; Gaboriau et al., 2018). Regardless of its exact position, the genus is consistently resolved apart from the other subfamilies, supporting its treatment as a distinct subfamily by Cooper and Santini (2016). Karyotype data (Molina and Galetti, 2004a; Molina, 2007) appear to corroborate this conclusion by finding substantial divergence between *Abudefduf* and members of Pomacentrinae.

The genus can be divided into three monophyletic groups that correspond to the genus-group names *Euschistodus* (type species: *A. declivifrons*), *Abudefduf* (type species: *A. sordidus*), and *Glyphisodon* (type species: *A. saxatilis*). We treat these as subgenera in the following discussion of relationships within *Abudefduf*. Thus, *Abudefduf* (*Euschistodus*) is sister to a clade of *Abudefduf* (*Abudefduf*) + *Abudefduf* (*Glyphisodon*). We found strong bootstrap support for each clade and that pattern of relationships (100% bootstrap at each node; Fig. 1). These relationships are consistent with earlier studies (Quenouille et al., 2004; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; DiBattista et al., 2016; Bertrand et al., 2017; Campbell et al., 2018; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). Aguilar-Medrano et al. (2011) identified two different trophic types in the genus: one with an inferior mouth associated with benthic prey; the other with a superior mouth associated with zooplanktivory. The ancestral condition of the genus, as seen in *Abudefduf* (*Abudefduf*) and *Abudefduf* (*Euschistodus*), appears to be characterized by the following traits (Hensley, 1978; Aguilar-Medrano and Barber, 2016; Campbell et al., 2018): dark bars usually distinctly wider than or at least equal in width to light interspaces, generalist diet (algae, benthic invertebrates, zooplankton), solitary or in small aggregations, preference for shallow surf zones (group *a* of Aguilar-Medrano and Barber, 2016). The species-rich crown group, *Abudefduf* (*Glyphisodon*), is characterized by the following: thin dark bars distinctly narrower than light interspaces (barring pattern lost in *A. sparoides*), specialist diet (zooplankton), in large aggregations, preference for reefs, occurrence in water column (group *b* of Aguilar-Medrano and Barber, 2016). Group *a* is paraphyletic relative to group *b*. Campbell et al. (2018) characterized these as benthivores (group *a*) versus planktivores (group *b*), with one species, *A. notatus*, described as "in transition from benthivory to planktivory."

The New World night sergeants (subgenus *Euschistodus*) are composed of *A. concolor*, *A. declivifrons*, and *A. taurus*. This benthivorous group corresponds to "Clade A" or the "*taurus* clade" of Campbell et al. (2018). These species form a clade that is sister to the remaining *Abudefduf*. Other studies have corroborated a monophyletic *Euschistodus* sister to the rest of the genus (e.g., Quenouille et al., 2004; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; DiBattista et al., 2016; Campbell et al., 2018; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). Lessios et al. (1995) examined their relationships using a mix of isozymes, DNA sequences, and morphological data. They recognized *A. declivifrons*, previously considered a subspecies of *A. concolor* (e.g., Allen, 1991: 234), as a distinct species sister to *A. concolor* + *A. taurus*. Hensley (1978) identified a potential synapomorphy for the trans-isthmus geminate pair of *A. concolor* and *A. taurus*: suborbitals adnate (vs. suborbitals free from cheek in *A. declivifrons*). Campbell et al. (2018) reported possible cryptic diversity within *A. taurus*, with a divide between the eastern and western Atlantic

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populations. There does not appear to be an available name for the eastern Atlantic lineage, if it is a separate species. Species of *Euschistodus* tend to have fewer anal rays (usually ten) than other species of *Abudefduf*, which usually have 11 or more, though *A. saxatilis* and *A. troschelii* occasionally have ten (Hensley, 1978; Allen, 1991; Allen and Robertson, 1994; Lessios et al., 1995; Robertson and Allen, 2015).

The three species of the subgenus *Abudefduf* (*A. notatus*, *A. septemfasciatus*, and *A. sordidus*) have been consistently recovered as a monophyletic group (Quenouille et al., 2004; Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Coleman et al., 2014; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Vella et al., 2016; Bertrand et al., 2017; Campbell et al., 2018; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). Campbell et al. (2018) identified this group as "Clade B" or the "*sordidus* clade," and they classified its species as benthivorous, except for *A. notatus* which was considered to be "in transition to planktivory." Hensley (1978) noted that *A. septemfasciatus* and *A. sordidus* are the only species of *Abudefduf* with a conspicuous black spot on the dorsal surface of the caudal peduncle, which could be potentially informative; in *A. septemfasciatus*, the spot is only present in juveniles. Frédérich et al. (2014) reported another character shared by these two species: modified ceratomandibular ligament fused to *geniohyoideus* muscle.

The subgenus *Glyphisodon* contains the majority of species of *Abudefduf*. It is equivalent to "group *b*" of Aguilar-Medrano and Barber (2016) and "Clade C" or the "*saxatilis* clade" of Campbell et al. (2018). This group within *Abudefduf* has evolved to become planktivorous, a shift accompanied by a series of changes documented in Aguilar-Medrano and Barber (2016). Based on the distribution of the ceratomandibular ligament (Frédérich et al., 2014), loss of the ligament may be a synapomorphy for *Glyphisodon*. Within *Glyphisodon*, *A. bengalensis* is the only species Frédérich et al. (2014: fig. 2) classified as a benthic feeder and the only one reported to possess the ligament. Frédérich et al. (2014) concluded that loss of the ligament was associated with zooplanktivory. Our phylogeny shows a clade that includes *A. abdominalis*, *A. conformis*, *A. hoefleri*, *A. lorenzi*, *A. saxatilis*, *A. sexfasciatus*, *A. troschelii*, and *A. vaigiensis*. Five of these species (*A. abdominalis*, *A. conformis*, *A. saxatilis*, *A. troschelii*, and *A. vaigiensis*) have been grouped together as a species complex by earlier workers (Randall and Earle, 1999; Randall, 2005). The three species distributed in the Atlantic and eastern Pacific (*A. hoefleri*, *A. saxatilis*, and *A. troschelii*) are recovered as a clade, which corroborates what has been reported before (Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Vella et al., 2016; Campbell et al., 2018; Gaboriau et al., 2018). However, *A. saxatilis* and *A. troschelii* do not form a trans-ishthmian geminate pair as previously suggested in the literature (e.g., Allen, 1976; Gorman and Kim, 1977; Vawter et al., 1980; Foster, 1987; Bermingham et al., 1997; Robertson and Collin, 2015) and shown by other phylogenies (DiBattista et al., 2016; Vella et al., 2016; Rabosky et al., 2018). Instead, the two Atlantic species (*A. saxatilis* and *A. hoefleri*) are resolved together in a clade, with *A. troschelii* as its sister taxon, a relationship which agrees with Campbell et al. (2018). They found *A. hoefleri* grouped with the eastern population of *A. saxatilis*, rendering *A. saxatilis* paraphyletic. Other phylogenies have resolved an *A. hoefleri* + *A. troschelii* sister pairing instead (Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019).

Bertrand et al. (2017) showed that *Abudefduf vaigiensis*, as currently constituted, is likely polyphyletic, encompassing up to four disjunct lineages. The non-monophyly of *A. vaigiensis* was first suggested by Bermingham et al. (1997), who recovered two separate lineages: one widespread across the Indo-Pacific and another confined to the western Pacific. Quenouille et al. (2011: fig. 2b) also showed a polyphyletic *A. vaigiensis*. Bertrand et al.'s (2017) lineage A, the most abundant of the four, is widespread in the Indo-West Pacific and nested within a paraphyletic *A. sexfasciatus*, something that was foreshadowed by other studies unable to delimit a clear interspecific boundary between *A. sexfasciatus* and *A. vaigiensis* (Hubert et al., 2012, 2017; Chang et al., 2017). Bertrand et al. (2017) identified a second, less common Indo-West Pacific group of *A. vaigiensis* as lineage B. Their lineage C is possibly restricted to the Coral Triangle. They did not name the fourth lineage, which was represented by a single GenBank specimen from Christmas Island (AY208557; Quenouille et al., 2004). Campbell et al. (2018) subsequently sequenced another individual (labeled as *A.* cf. *vaigiensis*) from Christmas Island (Kiritimati) and confirmed that it is distinct from other putative *A. vaigiensis*. Our *A. vaigiensis*, from the eastern coast of Australia (31°43′12″S, 152°47′54″E), was recovered as the sister group of *A. sexfasciatus*, a relationship which conforms to Bertrand et al.'s (2017: fig. 2a) mitochondrial tree (cytochrome *b*). We conclude that it is a representative of their widespread lineage A.

As for which lineage is the true *Abudefduf vaigiensis*, Bertrand et al. (2017: table S1) only reported lineage B from the type locality, Waigeo, Indonesia (WJC4193–WJC4194, WJC4196; 0°25′48″N, 130°49′12″E), making it the likeliest candidate. However, lineages A and C also occur in the Coral Triangle, so it is possible that either or both also occur at Waigeo but were not sampled at that location. There is evidence that different lineages can be sympatric; e.g., lineages A and B are found together at Taiping (10°22′48″N, 114°22′12″E; Bertrand et al., 2017: table S1). To further complicate matters, Wibowo et al. (2017) recognized *Abudefduf caudobimaculatus* as a separate species, removing it from the synonymy of *A. vaigiensis*. Hensley (1978: 169) remarked on the species status of *A. caudobimaculatus*, noting "[t]here is a very real possibility that two species are included" in *A. vaigiensis*, separable into what he called the "caudobimaculatus" and "vaigiensis" groups. Hensley (1978: 247) stated, "it is likely that future research will show that two species are involved." He provided a suite of characters to differentiate the two forms (Hensley, 1978: tables 32–35). Wibowo et al. (2017: 86) suggested that *A. caudobimaculatus* corresponds to Bertrand et al.'s (2017) lineage B on the basis of a personal communication from an author of the latter paper (W.-J. Chen). This designation has been followed by others (Campbell et al., 2018; Wibowo et al., 2018). However, Wibowo et al. (2018) resolved *A. caudobimaculatus* as the sister group to the rest of *Glyphisodon*, which this analysis corroborated (Fig. 1). If *A. caudobimaculatus* is lineage B, that placement would contradict Bertrand et al. (2017: fig. 2), who recovered it either as sister to *A. sparoides* or lineage C, albeit with weak branch support. If lineage B is indeed the only one to occur at Waigeo, the type locality of *A. vaigiensis*, then *A. caudobimaculatus* would need to be returned to the synonymy of *A. vaigiensis*. Resolving the status of *A. vaigiensis*

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and lineages previously identified as such will require further investigation.

Subfamily Microspathodontinae

The subfamily Microspathodontinae is the sister group of all other pomacentrids. Jordan and Evermann (1898) originally described the subfamily for only *Microspathodon*. Cooper and Santini (2016) expanded it to include a number of closely related genera, primarily housing the various genera formerly classified in the Pomacentrinae (*sensu* Allen, 1991) that are not closely related to *Pomacentrus*, plus one transplant (*Mecaenichthys*) from the Chrominae. It contains several monotypic genera (*Hypsypops*, *Mecaenichthys*, and *Nexilosus*). The subfamily includes some of the largest damselfishes, which are mainly temperate species from genera like *Hypsypops*, *Microspathodon*, *Nexilosus*, and *Parma*. Representatives from several genera (*Microspathodon*, *Hypsypops*, *Nexilosus*, and *Stegastes*) are primarily benthic grazers that feed on filamentous algae and/or invertebrates (Aguilar-Medrano et al., 2011). *Plectroglyphidodon* and *Stegastes*, the two most species-rich and widespread genera, are not monophyletic. The results of this analysis show that the subfamily is also home to the enigmatic *Lepidozygus*. There is strong bootstrap support (100%) for *Lepidozygus* being the sister taxon of *Stegastes sensu stricto* (Fig. 1; Supplemental Fig. 1; see Data Accessibility), clearly demonstrating that *Lepidozygus tapeinosoma* is a member of the Microspathodontinae. We hereby place Lepidozyginae in the synonymy of Microspathodontinae.

Hypsypops.—The Garibaldi (*Hypsypops rubicundus*), the only species in this genus, is a large damselfish (>300 mm TL) that occurs in the temperate eastern Pacific (Limbaugh, 1964; Miller and Lea, 1972; Allen, 1991), where it is found in shallow, rocky areas and feeds on benthic invertebrates (Limbaugh, 1964; Clarke, 1970; Aguilar-Medrano et al., 2011). Its position within the Microspathodontinae, as the sister group of *Similiparma*, is strongly supported (100% bootstrap) and in line with previous studies (Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). The similarity of *Hypsypops* to other representatives of Microspathodontinae has been noted in the literature (e.g., Heller and Snodgrass, 1903; Allen and Hoese, 1975; Hensley, 1986).

Lepidozygus.—This is a monotypic genus found throughout the tropical Indo-West Pacific (Allen, 1975a, 1991; Emery, 1983). The classification of the Fuselier Damsel (*Lepidozygus tapeinosoma*) warrants further attention because our results contradict earlier works that assigned *Lepidozygus* to its own monotypic subfamily (Allen, 1975a, 1991; Cooper et al., 2009; Cooper and Santini, 2016). This taxon has drawn particular interest since it was accorded subfamilial status by Allen (1975a). Cooper et al. (2009) were the first to include *Lepidozygus* in a molecular phylogeny, and they placed it as the sister group of all pomacentrids except Microspathodontinae (their Stegastinae). Cooper and Santini (2016) maintained the subfamilial rank for the Lepidozyginae but noted its uncertain status, citing the long branch connecting it to other pomacentrids. Other studies have recovered relationships for *Lepidozygus* that are at least congruent with its treatment as a separate subfamily (e.g., Cowman and Bellwood, 2011; Litsios et al., 2012a; Frédérich et al., 2013; Rabosky et al., 2013; Lobato et al., 2014; DiBattista et al., 2016; Stieb et al., 2017; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). However, they all relied on the sequences of *Lepidozygus* produced by Cooper et al. (2009). In contrast, other studies have recovered a relationship similar to the one that we found: *Lepidozygus* closely allied with *Stegastes sensu stricto* (Litsios et al., 2012b: figs. A1–3; Betancur-R. et al., 2013a: Dryad file "RAxMLThree_Plus_24_part.tre", 2015: fig. S1, 2017: "12862_2017_958_MOESM6_ESM.pdf"; Mirande, 2016: fig. S11; Sanciangco et al., 2016: fig. S1; Rabosky et al., 2018: Dryad file "actinopt_12k_raxml.tre"). What these latter studies share in common is that they either generated their own independent RAG1 sequence for *Lepidozygus* (Rabosky et al., 2018: table S2, Dryad file "accession_numbers.csv") or they did not analyze its RAG1 data (Litsios et al., 2012b: table A1; Betancur-R. et al., 2013a: table S1; Mirande, 2016: appendix S1; Sanciangco et al., 2016: table S1). For example, Litsios et al. (2012a: additional file 2) used all of Cooper et al.'s (2009) data for *Lepidozygus* and found a similar result. However, Litsios et al. (2012b: table A1) used many of the same sequences but excluded that specific RAG1 sequence. A reason for the deletion was not given, but, with that removal, the phylogenetic position of *Lepidozygus* deviated greatly between the two topologies (Litsios et al., 2012a: fig. 2; 2012b: figs. A1–3). Similarly, Rabosky et al. (2013: supplementary data 1, Dryad file "Rabosky_et_al_timetree.tre") used three sequences from Cooper et al. (2009), including RAG1, and recovered *Lepidozygus* sister to Chrominae. In contrast, Rabosky et al. (2018) replaced that RAG1 with new data. No explanation was given for the change, but they inferred a sister-group relationship between *Lepidozygus* and *Stegastes sensu stricto*. Hofmann et al. (2012: 82) used 12S and RAG1 from Cooper et al. (2009), resolving *Lepidozygus* inside *Chromis sensu stricto*, which, in hindsight, gave a clue as to the underlying problem. Despite the apparent disagreement and uncertainty in the literature concerning this taxon, we are confident that our results accurately depict the subfamilial affiliation of *Lepidozygus* because, following an examination of the available data, we suspect that its placement in Cooper et al. (2009: fig. 1) is the result of an error in a single sequence, possibly from data transposition or PCR contamination. In a GenBank BLAST search, their RAG1 sequence for *Lepidozygus tapeinosoma* (GenBank FJ616676) is identical to their RAG1 sequence for *Chromis weberi* (FJ616653). The next closest match (99.8% similarity) is another RAG1 sequence from *C. weberi* (AY208642; Quenouille et al., 2004); the other top ten BLAST results (>97.8%) were all RAG1 sequences from species of *Chromis sensu stricto*. That RAG1 sequence is a 99.6% match with the RAG1 sequence from our *Chromis weberi* but has only 91–92% similarity with the RAG1 sequences from our samples of *Lepidozygus* and that of Rabosky et al. (2018: Dryad file "alignment.phylip"). Our RAG1 and Rabosky et al.'s (2018) share 99.1% similarity. Comparing 12S and 16S sequences, the only other genes where our dataset overlaps with Cooper et al. (2009), we found high degrees of similarity between their *Lepidozygus* data and ours (12S: 97.2%; 16S: 96.8%). Conversely, their 12S and 16S for *Lepidozygus* showed limited similarity with our *C. weberi* (12S: 83.8%; 16S: 85.2%). This suggests that misidentification of their voucher specimen is unlikely. When we analyzed their non-RAG1 loci in single-gene tree searches,

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Lepidozygus was consistently recovered within the Microspathodontinae (not shown). An analysis of their data matrix minus the questionable RAG1 sequence (FJ616676) resolved *Lepidozygus* as the sister group of *Stegastes sensu stricto* (not shown), which matches the results of this study (Fig. 1). An analysis that included their sequences of *Lepidozygus*, excluding their RAG1, in our data matrix found their taxon clustered with our representatives of *Lepidozygus* (not shown), sister to *Stegastes sensu stricto* within the Microspathodontinae. All indications are that this single aberrant sequence (FJ616676) produced a misleading topology which resulted in an incorrect classification for *Lepidozygus*.

Mecaenichthys.—This is another monotypic genus and its sole representative (*M. immaculatus*) is confined to the coasts of southeastern Australia (Allen, 1991). Historically, it was classified with *Chromis* and its relatives (e.g., McCulloch, 1929; Whitley, 1929; Marshall, 1964; Allen, 1975a, 1991). Early molecular phylogenies did not support that classification but disagreed on its exact placement within the Pomacentridae (Tang, 2001; Jang-Liaw et al., 2002; Tang et al., 2004). Koh et al. (2006: fig. 1) did recover it as sister to *Chromis cyanea*, but putative members of the Chrominae did not form a monophyletic group in their tree. Cooper et al. (2009) reassigned the genus to their Stegastinae [= Microspathodontinae] based on their phylogeny, where it was sister to *Parma*. Subsequent studies have inferred *Mecaenichthys* and *Parma* as sister taxa (e.g., Cowman and Bellwood, 2011; Hofmann et al., 2012; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Delrieu-Trottin et al., 2019), though *Parma* is often not monophyletic (see below). Our results did not find the same relationship but did resolve *Mecaenichthys* within the subfamily, as the sister group of all other microspathodontines. Because both alternatives place it within this group, we agree with Cooper and Santini (2016) in classifying *Mecaenichthys* as a member of the subfamily Microspathodontinae.

Microspathodon.—This genus is composed of four species from the Atlantic and eastern Pacific, three of which are found in rocky habitats, with the fourth (*Microspathodon chrysurus*) inhabiting coral reefs. The name likely derives from their distinctive dentition (Jordan and Evermann, 1898: 1565; Scharpf and Lazara, 2020). Cooper and Santini (2016) recognized the tribe Microspathodontini for *Microspathodon* and its closest relatives: *Hypsypops*, *Nexilosus*, and *Similiparma*. They did so mostly on the basis of their large adult size, referring to them as "giant damselfishes," and geographic distribution, confined to the Atlantic and eastern Pacific. They characterized microspathodontins as benthic algal grazers that share a predominantly temperate distribution and preference for shallow, rocky habitats. Species of *Parma* display substantial overlap in the diagnostic characters for Microspathodontini (Allen and Hoese, 1975). *Parma* consists of large (some species approach or exceed 200 mm SL; Allen and Hoese, 1975; Allen, 1987a, 1991), benthic algal grazers that favor rocky substrates in shallow, temperate waters (Allen and Hoese, 1975). However, the difference in their geographic distribution, restricted to the waters off Australia and New Zealand, distinguishes them from members of Microspathodontini.

Nexilosus.—The single species of this genus is a benthic omnivore found in shallow, rocky areas of the temperate eastern Pacific (Hildebrand, 1946; Allen, 1991; Grove and Lavenberg, 1997; Angel and Ojeda, 2001; Aguilar-Medrano et al., 2011). In their description of the genus, Heller and Snodgrass (1903) remarked that most of the diagnostic characters for *Nexilosus* are shared with *Hypsypops*. Despite its classification in the tribe Microspathodontini (Cooper and Santini, 2016), the relationships of *Nexilosus latifrons* were uncertain in Cooper et al. (2009), who only had access to DNA acquired from formalin-fixed samples. The few target loci that were successfully sequenced had fragmentary data. Although it appeared in a polytomy within Microspathodontinae, Cooper et al. (2009: 12) noted that "molecular evidence for placing *Nexilosus* in the damselfish tree is weak" and its position was tentative. Cooper and Santini (2016) speculated that *Nexilosus* is a member of their tribe Microspathodontini, based on its large adult size, cranial morphology, ecology, and distribution. All subsequent works that have examined *Nexilosus* used Cooper et al.'s (2009) data. The position of this genus has been unstable in those phylogenetic studies. Cowman and Bellwood (2011: fig. S6) resolved it in the Indo-West Pacific "*Stegastes*" and not closely related to the putative genera of Microspathodontini; Lobato et al. (2014) and Gaboriau et al. (2018) reported similar findings. Litsios et al. (2012a: fig. 2) found it in a clade with *Chrysiptera starcki*, sister to the remaining pomacentrines. Litsios et al. (2012b: figs. A1, A2) recovered *Nexilosus* either as the sister group of the Pomacentrinae or sister to *Altrichthys* + *Chrysiptera galba*. DiBattista et al. (2016) recovered *Nexilosus* inside *Chromis sensu stricto*, sister to a group equivalent to *Chromis* (*Thrissochromis*). In Delrieu-Trottin et al. (2019), *Nexilosus* is sister to *Altrichthys* and together they are the sister taxon of the Pomacentrinae minus Cheiloprionini. The inconsistency in its phylogenetic position is probably due to the incomplete nature of the sequences, a basic problem with DNA extracted from formalin-preserved tissue (Shedlock et al., 1997; Schander and Halanych, 2003; Chakraborty et al., 2006). Because of their ambiguous nature, we did not include those data. Instead, we analyzed a COI sequence of *Nexilosus latifrons* retrieved from the BOLD database (Sequence ID: LIDMA1248-12; Supplemental Table 1; see Data Accessibility). Our results show that *Nexilosus* is a member of Microspathodontinae, as the sister group of a *Hypsypops*–*Similiparma* clade, which supports recent classifications (Cooper et al., 2009; Cooper and Santini, 2016).

Parma.—The scalyfins comprise ten large herbivorous species confined mainly to the temperate and subtropical waters around Australia and New Zealand (Allen, 1975a, 1987a; Allen and Hoese, 1975; Allen and Larson, 1979). Allen and Hoese (1975) noted some resemblance to the monotypic *Hypsypops* but were wary that any similarity could "be the result of convergence due to environmental similarities." Their caution was warranted because, although they are in the same subfamily, these two genera are not sister taxa, with *Hypsypops* sister to *Similiparma* and *Parma* sister to all other microspathodontines except *Mecaenichthys* (Fig. 1). In prior phylogenetic studies, sampling for the genus has been limited, including two species at most (*P. microlepis* and *P. oligolepis*). Even though it is assumed to be a natural grouping, recent studies (e.g., Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013;

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Rabosky et al., 2013, 2018; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019) have been unable to recover a monophyletic *Parma*. This may be due to irregularities in the 12S and 16S sequences of *Parma oligolepis* extracted from KU T3096 (M. W. Westneat, pers. comm.), which has been widely used (Tang, 2001; Jang-Liaw et al., 2002; Tang et al., 2004; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). That same sample was sequenced for this study, but 12S and 16S data were omitted. Our phylogeny recovers a monophyletic *Parma* with strong branch support (100% bootstrap; Fig. 1). The errant placement of *P. oligolepis* seen previously is not repeated herein.

***Plectroglyphidodon.*—**The species of this genus are predominantly herbivores found on shallow reefs of the Indo-West Pacific (Allen, 1975a, 1991). As currently constituted, the ten species of *Plectroglyphidodon* are polyphyletic (Fig. 1). Of the eight species represented in the data matrix, seven are paraphyletic relative to a clade of Indo-West Pacific "*Stegastes*" and a single species, *P. lacrymatus*, is recovered inside *Stegastes sensu stricto*, sister to *S. pelicieri*. In their description of the genus, Fowler and Ball (1924) noted the similarity of *Plectroglyphidodon* to *Parma* but with larger scales like *Abudefduf*, which served as a dumping ground at the time for what turned out to be a disparate collection of largely unrelated pomacentrid taxa (Allen and Emery, 1973; Allen, 1975a; Hensley, 1978; Allen and Randall, 1981; Allen and Woods, 1980). Fowler and Ball (1924) differentiated *Plectroglyphidodon* from *Abudefduf* on the basis of its plaited lips, analogous to how the enlarged lips of *Cheiloprion* differentiated that monotypic genus from the equally unruly *Pomacentrus* of the time. Both *Plectroglyphidodon johnstonianus* (type species) and *Cheiloprion labiatus* are corallivores (Hobson, 1974; Allen, 1975a; Masuda et al., 1975, 1984; Sano et al., 1984a, 1984b; Cole et al., 2008). The modified lips appear to be adaptations for their specialized diet (Allen, 1975a; Huertas and Bellwood, 2018). Although it has been suggested that this distinctive feature indicates some close relationship between the two genera (Woods and Schultz, 1960: 96–97), other characters do not support such an association (Allen, 1975a: 194).

There are two monophyletic groups of putative *Plectroglyphidodon* which are paraphyletic relative to the Indo-Pacific "*Stegastes*." One clade includes *P. johnstonianus*, the type of *Plectroglyphidodon*. The other includes *P. leucozonus*, the type of an available name, *Negostegastes*. Species of the latter group, which is sister to "*Stegastes*," generally have fewer dorsal- ($\leq$16) and anal-fin ($\leq$13) rays than species of the other group ($\geq$16 and $\geq$13, respectively; Allen, 1991). *Plectroglyphidodon phoenixensis* accounts for the overlap in both counts: it is in a clade with *P. johnstonianus* and the only species of its clade reported to possess 16 dorsal rays and 13 anal rays; the other species have 17 or more dorsal rays and 14 or more anal rays (Allen, 1991). Both *P. johnstonianus* and *P. phoenixensis* have discernible genetic splits between their respective Indian and Pacific populations, represented by reciprocally monophyletic lineages in each ocean basin (Hubert et al., 2012: fig. S1, table S3; Hubert et al., 2017: fig. A1, tables S3, S4). If this is recognized as cryptic diversity, the Indian Ocean population of *P. johnstonianus* may have an available name: *Plectroglyphidodon nitidus*. Species of *Plectroglyphidodon* and *Stegastes* (*P. dickii*, *P. lacrymatus*, *P. johnstonianus*, *P. imparipennis*, *P.* sp. [= *P. lacrymatus*], *S. acapulcoensis*, *S. bicolor* [= *S. partitus*], *S. dorsopunicans* [= *S. adustus*], *S. diencaeus*, *S. fasciolatus* [= *S. marginatus*], *S. flavilatus*, *S. fuscus* [= *S. adustus*], *S. leucostictus*, *S. lividus* [= *S. punctatus*], *S. planifrons*, *S. rocasensis*, and *S. variabilis*; Webb, 1988: appendix II) lack additional pitted scales posterior to the tubed lateral line scales found in other genera, which was suggested as having potential phylogenetic signal (Webb, 1988: 129). The *P. dickii–P. johnstonianus* pairing we recovered was suggested by earlier studies (Randall et al., 1997; Allen and Erdmann, 2012). We found a sister-group relationship between *P. imparipennis* and *P. sagmarius*. The latter species was originally considered a color variant of *P. imparipennis* endemic to the Marquesas Islands (Allen, 1975a, 1991; Randall and Earle, 1999), so their close relationship has been discussed before (Randall, 2005).

The recovery of "*Plectroglyphidodon*" *lacrymatus* apart from other *Plectroglyphidodon* matches prior studies (Cooper et al., 2009; Cowman and Bellwood, 2011; Hofmann et al., 2012; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). It has more gill rakers on the first arch (21–23) than species of *Plectroglyphidodon* usually do (10–17; Allen, 1975a: 191), though *P. randalli* possesses almost as many (17–20; Allen, 1991). Bleeker (1877) placed *lacrymatus* in *Stegastes* (as a subgenus of *Glyphidodon* [= *Abudefduf*]), but the taxon was used in a different sense than modern *Stegastes* (*sensu* Emery and Allen, 1980). It was the sole *Plectroglyphidodon* in a clade Cowman and Bellwood (2011: figs. 2b, S6) called "*Stegastes* IP & *Plectroglyphidodon*." Cooper and Santini (2016) included this species in a group they called "*Stegastes* I/*Plectroglyphidodon* I." They stated that it likely would have to be reassigned to *Stegastes*. Our phylogeny shows a *P. lacrymatus–S. pelicieri* relationship similar to what was seen in Hubert et al. (2011, 2012, 2017). This is not surprising because the data we used for *S. pelicieri* were generated by those same barcode sources. Support for this sister-group pairing is robust (100%). This relationship was also described in other studies that compiled the same data from GenBank (DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Rabosky et al., 2018). Allen and Emery (1985) reported that "[j]uvenile specimens of *S. pelicieri* are remarkably similar in color to" *P. lacrymatus*, differing mainly in their dorsal-spine count (XII vs. XIV). *Plectroglyphidodon lacrymatus* also maintains algal gardens like many *Stegastes* (Kuo and Shao, 1991; Meekan et al., 1995; Ceccarelli, 2007; Hoey and Bellwood, 2010). Based on the relationships recovered in our phylogeny and those reported in the literature, we hereby refer this species to *Stegastes*, as *Stegastes lacrymatus*. *Plectroglyphidodon* and *Stegastes* are both masculine, so the species name does not need to change for gender agreement. Hubert et al. (2012, 2017) suggested that there may be cryptic diversity in the species after they detected two discrete lineages (Madagascar and French Polynesia) separated by *S. pelicieri*, which is found in the western Indian Ocean. The Pacific population was actually more closely related to *S. pelicieri* in their topologies. Our sample of *S. lacrymatus* is from Tonga (21°01′39.0″S, 175°07′21.0″W; Supplemental Table 1; see Data Accessibility). If there are separate species within *S. lacrymatus*, there are two possible available species-group names, *Glyphisodon nivosus* and *Glyphidodon florulentus*. However, their type

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localities are ambiguous: origin not indicated and Indian Ocean, respectively (Hombron and Jacquinot in Jacquinot and Guichenot, 1853; Günther, 1862). Furthermore, there is no type material for *G. nivosus* (Bauchot et al., 1978: 34). The status of these populations is beyond the purview of this study.

Of the two species of *Plectroglyphidodon* that we were unable to examine, *P. flaviventris* is most likely related to *P. johnstonianus*, based on their morphological similarity (Allen and Randall, 1974). The affinities of *P. sindonis* are less clear. The species is endemic to the Hawaiian Islands, where three other species of *Plectroglyphidodon* also occur (Randall, 2007), including representatives from both clades. Based on meristic counts, it is most likely in the same clade as *P. johnstonianus*. Like others of that group, *P. sindonis* has high dorsal- and anal-fin ray counts (19–20 and 15–16, respectively), its dorsal fin-ray count overlaps with what is reported for *P. johnstonianus*, its anal fin-ray count matches that of *P. flaviventris* and overlaps with those of *P. dickii* and *P. johnstonianus*, and its gill raker count on the first branchial arch matches that of *P. phoenixensis* (Allen, 1991; Randall, 2007).

Similiparma.—Originally erected for a single species (*Glyphidodon hermani*) endemic to the Cape Verde archipelago in the eastern Atlantic Ocean, *Similiparma* remained monotypic until Cooper et al. (2014) referred the engimatic "*Abudefduf*" *luridus* to the genus as *Similiparma lurida*. The reassignment was a logical development after Cooper et al. (2009) determined that the two species were most closely related. Subsequent studies have corroborated this relationship (e.g., Cowman and Bellwood, 2011; Hofmann et al., 2012; Litsios et al., 2012a; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019), even though some have persisted in calling it *Abudefduf luridus* (e.g., Mirande, 2016; Gaboriau et al., 2018; Rabosky et al., 2018; Delrieu-Trottin et al., 2019). Our results also support Cooper et al.'s (2014) taxonomic decision, finding a monophyletic *Similiparma* (100% bootstrap). Despite its long-standing recognition as a distinct genus, Kottelat (2013) treated it as a synonym of *Chrysiptera* without explanation, possibly following Allen (1991: 243), who placed *Glyphidodon hermani* in the synonymy of *Chrysiptera unimaculata*. In the same work, Allen (1991: 252) treated *Similiparma* as a valid genus with *Glyphidodon hermani* as its type species.

In his description of the genus, Hensley (1986) commented that *Similiparma* most resembled *Hypsypops*, *Nexilosus*, and *Parma*. Our phylogeny shows that *Similiparma* forms a clade with two of those genera, *Hypsypops* and *Nexilosus*, where *Hypsypops* is the sister taxon of *Similiparma* (Fig. 1). The sister-group relationship between *Hypsypops* and *Similiparma* is consistent with previous findings (Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). Potthoff et al. (1987) hinted at a connection between *S. lurida* and other microspathodontines when they noted that "[t]he distinctive preflexion larvae of *M. chrysurus* look very similar to those of *Abudefduf luridus*." Both species share larval pigmentation not seen in other pomacentrids, notably "the oversized pigmented pectoral fin, the large dorsal and ventral mid-tail melanophores and the 1 or 2 large melanophores over the hind brain" as well as "ventral caudal finfold melanophores." They reported "D. A. Hensley believes that the similarities may indicate some unknown relationship among the two genera."

Stegastes.—The 40 circumtropical species traditionally classified in this genus (farmerfishes or gregories) are characterized as aggressive, benthic damselfishes (Allen, 1975a; Allen and Emery, 1985; Allen and Smith, 1992; Smith-Vaniz et al., 1999) that engage in territorial behavior and algal farming (Vine, 1974; Belk, 1975; Allen and Robertson, 1994; Ceccarelli et al., 2001; Hata and Kato, 2004, 2006; Frédérich et al., 2013; Hata and Ceccarelli, 2016; Pratchett et al., 2016). The genus has long posed a challenge to systematists (Bleeker, 1877; Longley and Hildebrand, 1941; Rivas, 1960; Emery and Burgess, 1974; Greenfield and Woods, 1974; Emery and Allen, 1980; Allen and Emery, 1985; Smith-Vaniz et al., 1999). *Stegastes* is not monophyletic as currently constituted (Fig. 1), which corroborates other phylogenetic studies that have shown the same (e.g., Cooper et al., 2009; Cowman and Bellwood, 2011; Hofmann et al., 2012; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). Instead, the species fall into two disjunct clades, one of which is nested within *Plectroglyphidodon* and the other includes the type species, *S. imbricatus*. The latter group, *Stegastes sensu stricto*, would have been rendered non-monophyletic by the presence of "*Plectroglyphidodon*" *lacrymatus*, if not for its reclassification as *Stegastes* (see above). The two groups can be generally distinguished by the number of dorsal-fin spines: XII in *Stegastes sensu stricto* vs. XIII or XIV in "*Stegastes*" associated with *Plectroglyphidodon*. Allen (1975a: 42), who used the number of dorsal spines in his key for *Stegastes* (as *Eupomacentrus*), suggested the genus could be divided into two subgenera based on this difference. However, although instructive, this character is not strictly diagnostic. Of the species sampled in this study, there are at least three exceptions: *S. pelicieri* (XIV, with *Stegastes sensu stricto*), *S. altus,* and *S. aureus* (XII, with "*Stegastes*," *S. altus* occasionally has XIII; Allen, 1991). The presence of XII spines in *Stegastes sensu stricto* mostly fits the original conception of *Stegastes* and *Eupomacentrus*, a widely used junior synonym, which were both characterized by XII dorsal spines (Jenyns, 1840; Bleeker, 1877; Emery and Allen, 1980). The results of this analysis imply that later additions to this genus, namely Indo-Pacific species with XIII spines (Allen, 1975a; Emery and Allen, 1980), are not part of *Stegastes sensu stricto*.

There are three junior synonyms of *Stegastes*: *Brachypomacentrus*, *Eupomacentrus*, and *Omopomacentrus*. Atlhough simultaneous, *Eupomacentrus* Bleeker, 1877 has priority over *Brachypomacentrus* Bleeker, 1877 (ICZN, 1999: Art. 24.1) because *Eupomacentrus* was proposed at a higher rank (Bleeker, 1877). The type species of all three genera appear to be members of *Stegastes sensu stricto*. We recovered *S. albifasciatus*, the type of *Brachypomacentrus*, in the same clade as *S. imbricatus*. *Stegastes lividus*, the type of *Eupomacentrus*, presents an interesting situation. Randall (2004) discovered that the widespread species universally accepted as *S. lividus* (e.g., Bleeker, 1877; Fowler and Bean, 1928; Montalban, 1928; Whitley, 1929; de Beaufort, 1940; Aoyagi, 1941; Smith, 1960; Woods and Schultz, 1960; Allen, 1975a, 1991, 1997; Masuda et al., 1975, 1984; Allen and Randall, 1981; Allen and

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Emery, 1985; Randall et al., 1997; Myers, 1999; Jang-Liaw et al., 2002; Lieske and Myers, 2002) should be called *S. punctatus* because the *S. lividus* of Forster in Bloch and Schneider (1801) is endemic to the Marquesas Islands, where it had been recognized by Randall (2001) as *Stegastes robertsoni*. The taxonomic species that Bleeker (1877) fixed as the type of *Eupomacentrus* was actually *S. punctatus*. In cases where the type species was misidentified but correctly fixed, either species involved in the misidentification may be subsequently designated as the type (ICZN, 1999: Arts. 67.9, 70.3). However, Randall (2004) did not take any taxonomic action, presumably because *Eupomacentrus* was not in use. In our phylogeny, *S. punctatus* is in the same clade as *S. imbricatus*. Even though we were unable to examine *S. lividus*, based on the number of the dorsal spines (XII) and the phylogenetic position of *S. albifasciatus*, which Randall (2001, 2005) proposed as its closest relative, it is likely that *S. lividus* is also part of *Stegastes sensu stricto*. Finally, *S. acapulcoensis*, the type species of *Omopomacentrus*, is an eastern Pacific species with XII dorsal spines found in the same clade as *S. imbricatus*. Based on the phylogenetic position of *S. acapulcoensis*, *Omopomacentrus* is a synonym of *Stegastes*, not *Pomacentrus*, as stated by Kottelat (2013). This is in agreement with numerous authors who have regarded *acapulcoensis* as a species of *Stegastes* (e.g., Allen and Woods, 1980; Allen, 1991; Allen and Robertson, 1994; Grove and Lavenberg, 1997; Thomson et al., 2000; Robertson and Allen, 2015).

Stegastes sensu stricto is resolved as a monophyletic group, with the inclusion of *S. lacrymatus*. Within it, there is 100% bootstrap support for a clade comprising the Atlantic and eastern Pacific species, which all have XII dorsal spines. The phylogeny suggests that *Stegastes sensu stricto* diversified following a colonization of Neotropical waters. In their review of eastern Pacific *Stegastes*, Allen and Woods (1980) recognized that those species were closely related to the Atlantic ones. We recovered a sister-group relationship between *S. acapulcoensis* and *S. rectifraenum*, which was posited by Thomson et al. (2000) based on similarities in juvenile color patterns. The phylogeny supports a *S. partitus*–*S. pictus* relationship (100% bootstrap) first identified by Emery and Allen (1980), on the basis of both species possessing one fewer row of cheek scales (3) than other *Stegastes* (4). In their analysis of Atlantic *Stegastes*, Souza et al. (2016) also recovered a *S. partitus*–*S. pictus* clade. Our topology shares other similarities with theirs: a clade composed of *S. adustus*, *S. beebei*, *S. diencaeus*, *S. flavilatus*, *S. variabilis*, and *S. xanthurus* (treated as a population of *S. variabilis* therein); another clade of *S. arcifrons*, *S. fuscus*, *S. planifrons*, *S. rectifraenum*, and *S. rocasensis*; a third clade of *S. albifasciatus*, *S. limbatus*, *S. nigricans*, and *S. punctatus*. They demonstrated a divergence between the Brazilian and Caribbean populations of *S. variabilis*, which corroborates the restriction of *S. variabilis* to Brazil and recognition of *S. xanthurus* as the widespread species that occurs in the Caribbean (Robertson and Van Tassell, 2012; Smith-Vaniz and Jelks, 2014; Robertson et al., 2016a).

Stegastes sensu stricto includes most of the Indo-West Pacific species that possess XII dorsal-fin spines plus *S. pelicieri*, which has XIV spines. In their revision of the Indo-Pacific *Stegastes sensu lato*, Allen and Emery (1985) noted that, unlike many other widespread genera, much of its diversity falls outside of the region. They differentiated four species (*S. albifasciatus*, *S. limbatus*, *S. lividus* [= *S. punctatus*], and *S. nigricans*) from the remainder of *Stegastes*. They linked *S. albifasciatus* and *S. nigricans* together as part of a species complex, but separated *S. limbatus* and *S. lividus* [= *S. punctatus*] each into their own lineages. In our phylogeny, all four species form a monophyletic group (100% bootstrap) that is the sister taxon of the eastern Pacific/Atlantic *Stegastes*. Hubert et al. (2017: fig. A1, tables S3, S4) reported spatial structure within *S. nigricans*, with discrete lineages representing the Indian and Pacific Oceans. Even though they described it as geographic paraphyly (their "pattern II.2"), their figure (Hubert et al., 2017: fig. A1) shows geographic monophyly (their "pattern II.1"). If those populations are recognized as cryptic diversity, there is an available name in the synonymy of *S. nigricans* that could apply to the western Indian Ocean population, *Pomacentrus scolopseus*.

The Indo-Pacific "*Stegastes*" also form a monophyletic group (100% bootstrap support; Fig. 1), but their placement renders *Plectroglyphidodon* paraphyletic. Species in this "*Stegastes*" are confined to the Indo-Pacific and typically have XIII or more dorsal spines, except for *S. altus* and *S. aureus*, which usually have XII dorsal spines (rarely XIII in *altus*; Allen and Emery, 1985). The group includes the species circumscribed as the "*fasciolatus* complex" by Allen and Emery (1985): *S. aureus*, *S. emeryi*, *S. fasciolatus*, *S. gascoynei*, and *S. insularis*. Our phylogeny found all of them together in a clade, along with *S. luteobrunneus* and *S. marginatus*, which were considered synonyms of *S. fasciolatus* by Allen and Emery (1985), as well as *S. altus*. This *fasciolatus* complex plus *S. altus* is well supported (100% bootstrap). Allen and Emery (1985) considered *S. altus* part of a different species complex that also comprised *S. apicalis* and *S. obreptus*, with the latter two species hypothesized to be most closely related. Although the topology did resolve *S. apicalis* and *S. obreptus* as sister species (100% bootstrap), our results placed *S. altus* inside the *fasciolatus* clade. The *S. apicalis* + *S. obreptus* pair is sister to the *fasciolatus* complex. All of these species form a monophyletic group (100% bootstrap) within *Plectroglyphidodon*, which is also composed entirely of Indo-Pacific taxa. In addition to rendering *Plectroglyphidodon* paraphyletic, this clade of "*Stegastes*" lacks an available name. Cowman and Bellwood (2011: figs. 2b, S6) called a group with similar composition "*Stegastes* et al. IP." Cooper and Santini (2016: fig. 1) called it "*Stegastes* II/*Plectroglyphidodon* II/*Parma* II" and suggested that several of these species (e.g., *S. altus*, *S. apicalis*, *S. fasciolatus*, *S. obreptus*) would eventually need to be classified as *Plectroglyphidodon*, but they did not formally make the taxonomic change. The diagnoses for both genera largely overlap (Allen, 1975a; Allen and Emery, 1985), with two conspicuous differences: margin of preopercle smooth in *Plectroglyphidodon* vs. serrated in adult *Stegastes*; margin of suborbital smooth in *Plectroglyphidodon* vs. variable (serrated, crenulated, or smooth) in *Stegastes*. We hereby assign the following species to *Plectroglyphidodon*: *altus*, *apicalis*, *aureus*, *emeryi*, *fasciolatus*, *gascoynei*, *insularis*, *luteobrunneus*, *marginatus*, and *obreptus*. *Plectroglyphidodon* and *Stegastes* are both masculine, so no changes for gender agreement are necessary.

Based on geographic variations in color, Allen and Emery (1985: 16, pl. I–II) recognized three distinct populations within the widespread *Stegastes fasciolatus* [= *Plectroglyphidodon fasciolatus*]: Hawaiian Islands; Indo-West Pacific Ocean (type locality: Lord Howe Island); western Indian Ocean and Cocos-Keeling Islands. Citing unpublished sequence data

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from D. R. Roberston, Randall (2005, 2007) stated that each population should be recognized as a separate species. Randall (2005) indicated that *S. fasciolatus sensu stricto* should be restricted to the population in the eastern Indian Ocean (Christmas Island and western Australia), Oceania (excluding Hawaii), and the western Pacific Ocean. Randall (2007) resurrected *Stegastes marginatus* for the Hawaiian population, removing it from the synonymy of *S. fasciolatus*. Following Randall (2005), Fricke et al. (2009) resurrected *Stegastes luteobrunneus* for the western Indian Ocean population (including Cocos-Keeling). The sequences for *Plectroglyphidodon luteobrunneus* used in this analysis (JF435094, JF457578, JF458207) come from a sample currently identified as *Pomacentrus agassizii* (BOLD record: IPCOM438-10; BOLD sample ID: REU0983). Moreover, all currently published sequences labeled as "*Pomacentrus agassizii*" (JF435094–JF435098; JF457578–JF457582; JF458207–JF458211; JQ350239–JQ350240; MF409473) appear to be *Plectroglyphidodon luteobrunneus*. Those specimens were all collected from Réunion, and their sequences are most similar to fish identified as *Stegastes fasciolatus* [= *Plectroglyphidodon fasciolatus*] (Collet et al., 2018: table 2). *Plectroglyphidodon luteobrunneus* is the only member of the *fasciolatus* clade known from the western Indian Ocean (Fricke, 1999; Heemstra et al., 2004; Letourneur et al., 2004; Fricke et al., 2009, 2018). This misidentification would explain the anomalous position of "*Pomacentrus agassizii*" seen in several studies (e.g., Hubert et al., 2011, 2012, 2017; DiBattista et al., 2016; Mirande, 2016; Rabosky et al., 2018).

Of the species that we could not examine, each can be tentatively assigned to *Stegastes sensu stricto* based on the number of dorsal-fin spines, unpublished barcode sequences, previous statements in the literature, and/or geographic distribution. All remaining Atlantic and eastern Pacific species (*S. leucorus*, *S. lubbocki*, *S. redemptus*, *S. sanctaehelenae*, and *S. uenfi*) are retained in *Stegastes sensu stricto*. We follow Souza et al. (2016) in treating *Stegastes sanctipauli* as a synonym of *S. rocasensis*. Tree-based identifications (not shown) that assayed unreleased sequences in the BOLD database support this placement of *S. leucorus*, *S. lubbocki*, *S. redemptus*, and *S. sanctaehelenae*. *Stegastes leucorus* was most similar to *S. beebei*. This would corroborate the hypothesis of Allen and Woods (1980) who suggested that the two lineages (*S. beebei* as a subspecies of *S. leucorus*) plus *S. baldwini* are most closely related. *Stegastes lubbocki* and *S. sanctaehelenae* were found to be most similar to *S. pictus* and each other. *Stegastes redemptus* was linked to *S. arcifrons* in the NJ tree generated by BOLD. The Marquesan endemic *Stegastes lividus* is retained in *Stegastes sensu stricto* based on its possession of XII dorsal spines and overall resemblance to *S. albifasciatus* and *S. nigricans* (Randall, 2001, 2005).

Subfamily Pomacentrinae

This is the largest subfamily of the Pomacentridae. The clade, which received strong branch support (100% bootstrap), holds more than half of all previously recognized genera (15 of 29) and almost half of all currently recognized species (210 of 422). The subfamily can be divided into four clades, one of which is composed wholly of the anemonefishes. When revising the damselfish classification, Cooper et al. (2009) placed the Amphiprioninae in the synonymy of the Pomacentrinae but retained the Amphiprionini as a tribe. It was the only tribe they recognized in the subfamily. We follow Cooper et al. (2009) in recognizing this group as the tribe Amphiprionini. Furthermore, we hereby recognize the tribe Cheiloprionini, which includes *Cheiloprion* and its closest relatives: *Chrysiptera sensu stricto*, *Dischistodus*, *Pomachromis*, and separate lineages of species of "*Chrysiptera*" that fall outside of *Chrysiptera sensu stricto*. We recognize the clade that includes *Hemiglyphidodon* and its nearest relatives (*Acanthochromis*, *Altrichthys*, *Amblyglyphidodon*, and *Neoglyphidodon*) as the tribe Hemiglyphidodontini. We recognize the tribe Pomacentrini as including *Amblypomacentrus*, *Neopomacentrus*, *Pomacentrus*, *Pristotis*, *Teixeirichthys*, and the remaining species of "*Chrysiptera*."

There is a potential osteological synapomorphy for Pomacentrinae reported in the literature (Emery and Allen, 1980; Randall et al., 1981): the interpenetration of pterygiophores into the spaces between the corresponding neural spines. This character has been discussed in the literature with different notation schemes (Emery and Allen, 1980; Randall et al., 1981; Randall, 1994, following Ahlstrom et al., 1976). We use the notation format of Emery and Allen (1980) herein. Emery and Allen (1980) observed two patterns in pomacentrids: (1) first dorsal pterygiophore penetrates the space between the second and third neural spines, two pterygiophores penetrate the space between the third and the fourth neural spines, with a single pterygiophore in each space thereafter (coded as "0,0,1,2,1,1..."); (2) first two dorsal pterygiophores penetrate the space between the second and third neural spines, with a single pterygiophore in each space thereafter (coded as "0,0,2,1,1,1..."). The (0,0,1,2,1,1) pattern is found in *Abudefduf*, *Chromis*, *Dascyllus*, *Lepidozygus*, *Mecaenichthys*, *Microspathodon*, *Plectroglyphidodon*, and *Stegastes* (Emery, 1980; Emery and Allen, 1980: table 1). Tang (2002) reported the character state in two additional genera, *Hypsypops* and *Parma*. Cooper et al. (2014: fig. 4a, b) illustrated *Similiparma* with that condition. Emery and Allen (1980) recorded the (0,0,2,1,1,1) pattern in species of *Acanthochromis*, *Amblyglyphidodon*, *Amphiprion*, *Cheiloprion*, *Chrysiptera*, *Dischistodus*, *Hemiglyphidodon*, *Neoglyphidodon* (as *Paraglyphidodon*), *Neopomacentrus*, *Pomacentrus*, *Premnas*, *Pristotis*, and *Teixeirichthys*. Based on the distribution of character states, the (0,0,2,1,1,1) pattern could be a synapomorphy for the subfamily Pomacentrinae. The condition of this character is unknown in *Altrichthys*, *Amblypomacentrus*, *Azurina*, *Nexilosus*, and *Pomachromis*. Based on their respective positions in the tree (Fig. 1; Supplemental Fig. 1; see Data Accessibility), *Azurina* and *Nexilosus* are predicted to have the (0,0,1,2,1,1) pattern, whereas *Altrichthys*, *Amblypomacentrus*, and *Pomachromis* are predicted to have the (0,0,2,1,1,1) pattern.

There are karyotype data reported in the literature that may support the monophyly of the subfamily. Damselfishes are characterized by large variations in chromosome numbers and fundamental numbers (Takai and Ojima, 1995). A diploid number of $2n = 48$, with a fundamental number of $NF = 48$ (all chromosomes acrocentric), is considered to be the ancestral state for the family, with most pomacentrids exhibiting those conditions (Alvarez et al., 1980; Takai and Ojima, 1987, 1991; Arai, 2011). Possession of 48 acrocentric chromosomes appears to be the ancestral state for teleosts as a whole (Ohno and Atkin, 1966; Ohno, 1974; Takai and Ojima, 1991; Mank and Avise, 2006). Increases in the conserved NF of 48 have been observed in putative

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pomacentrines (e.g., Ojima, 1983; Klinkhardt et al., 1995; Molina and Galetti, 2004b; Arai, 2011; Takai, 2011; Tanomtong et al., 2012; Takai and Kosuga, 2013; Supiwong et al., 2015). These deviations in fundamental number are hypothesized to be the result of pericentric inversions (Ojima, 1983; Takai and Ojima, 1987, 1991; Molina and Galetti, 2004b; Getlekha et al., 2018). Based on the distribution of fundamental numbers across pomacentrids (Klinkhardt et al., 1995; Arai, 2011), a high fundamental number may be synapomorphic for the subfamily Pomacentrinae. However, this character is not completely consistent because high fundamental numbers (NF $\geq$ 78) appear in *Stegastes sensu lato* (Ojima, 1983; Molina and Galetti, 2004b; Galetti et al., 2006; Arai, 2011). Conversely, low values (NF = 48) are seen in some pomacentrines (e.g., *Chrysiptera cyanea*, *Pomacentrus auriventris*, *P. coelestis*, *P. similis*; Arai and Inoue, 1976; Ojima, 1983; Takai and Ojima, 1987, 1999; Getlekha et al., 2018).

Egg morphology may also distinguish members of the Pomacentrinae from the other subfamilies. Muñoz-Cordovez et al. (2019: table S1) found that all surveyed pomacentrines share a capsule-shaped egg, whereas other subfamilies all have ellipsoid eggs, except for one species of Microspathdontinae (*Stegastes leucostictus*) that also possesses capsule-shaped eggs. Capsule eggs appear to give rise to larvae that show a wider range of development at the time of hatching compared to larvae from ellipsoid eggs (Muñoz-Cordovez et al., 2019). Pomacentrine larvae tend to be more well developed than those of other subfamilies, which Muñoz-Cordovez et al. (2019) suggested could be tied to the higher temperatures (21–28°C) in which the eggs develop.

Tribe Amphiprionini.—Of all the clades within the Pomacentrinae, this group is the most distinctive as it hosts all of the anemonefishes. Their monophyly (100% bootstrap) is not surprising given their obligate symbiotic relationship with sea anemones, a life history trait that is unique across fish diversity (Collingwood, 1868; de Crespigny, 1869; Verwey, 1930; Gudger, 1946; Mariscal, 1970; Allen, 1972; Fautin, 1991; Fautin and Allen, 1997). The symbiosis has been credited with triggering the rapid diversification (Litsios et al., 2012a; Marcionetti et al., 2019) that gave rise to 30 currently recognized species found across the Indo-West Pacific. Anemonefishes share morphological characters that further distinguish them from other damselfishes, including serration of the infraorbital and opercular series, reduced number of dorsal spines (VIII–XI vs. XII or more), and small scales (Allen, 1972; Fitzpatrick, 1992; Tang, 2002). As a result, this clade has been one of the most strongly supported within the family in past phylogenies (e.g., Quenouille et al., 2004; Cooper et al., 2009; Litsios et al., 2012a). Although evidence for their monophyly is robust, the exact number of species is uncertain. There are currently either 28 or 30 recognized in this tribe, depending on the status of *A. leucokranos* and *A. thiellei*, two putative species of possible hybrid origin (Fautin and Allen, 1997; Ollerton et al., 2007; see below).

The anemonefish relationships reported herein share some similarities with aspects of earlier works (e.g., Santini and Polacco, 2006; Litsios et al., 2012a, 2014; Litsios and Salamin, 2014; O'Donnell, 2014; Dhaneesh et al., 2015; Rolland et al., 2018; Thongtam na Ayudhaya et al., 2019; Nguyen et al., 2020). A monophyletic group (100% bootstrap) composed of the two clownfishes (*A. ocellaris* and *A. percula*) and *Premnas* is sister to all other amphiprionins. Two morphological characters have been hypothesized to unite these three species: distinct notch at dorsal-fin junction (spinous vs. soft sections) and naked occipital region (Allen, 1972; Fitzpatrick, 1992; Tang, 2002). Concerning the first trait, Salis et al. (2018) discovered a correlation between the extent of dorsal-fin indentation and the number of vertical white bars (*sensu* Barlow, 1972; Hensley and Randall, 1983). These three species display the greatest number of bars (3) among anemonefishes, a condition shared with several other species (e.g., *A. clarkii*, *A. latezonatus*, *A. tricinctus*). *Amphiprion latezonatus* is sister to a clade of the remaining anemonefishes (100% bootstrap). It is in the crown group where the relationships shown herein begin to diverge from other phylogenies, which also disagree with each other in some instances. Part of the discordance could be the result of gene choice because there is evidence of incongruence between the mitochondrial and nuclear data in these fishes (Litsios and Salamin, 2014). The instability in this part of the tree might also stem from a lack of sufficient phylogenetically informative variation due to rapid diversification. The genus appears to have undergone a recent radiation where the bulk of its diversity has arisen within the last 5–10 million years (Santini et al., 2009; Cowman and Bellwood, 2011, 2013; Litsios et al., 2012a; Frédérich et al., 2013; Lobato et al., 2014; DiBattista et al., 2016; Rabosky et al., 2018; Rolland et al., 2018). Several areas of agreement do emerge among different studies: a monophyletic *A. polymnus* and *A. sebae*; a monophyletic skunk clade consisting of *A. akallopisos*, *A. pacificus*, *A. perideraion*, and *A. sandaracinos*; an "*ephippium* complex" *sensu* Allen (1980), minus *A. mccullochi*, consisting of *A. barberi*, *A. ephippium* (type species), *A. frenatus*, *A. melanopus*, and *A. rubrocinctus*; an Indian Ocean clade consisting of *A. allardi*, *A. bicinctus*, *A. chagosensis*, *A. chrysogaster*, *A. latifasciatus*, *A. nigripes*, and *A. omanensis*. The latter group appears to be a recent invasion into the Indian Ocean followed by rapid diversification (Cowman and Bellwood, 2013: fig. S4; Litsios et al., 2014). This is where our tree diverges most dramatically from the consensus, as we recovered *A. polymnus* and *A. sebae* nested deep within the Indian Ocean clade, which has not been reported in other studies except Nguyen et al. (2020: fig. 2) who found a similar relationship for *A. polymnus* (*A. sebae* was recovered with *A. clarkii* therein).

Allen (1972) treated *Premnas* as a subgenus of *Amphiprion*, stating that the two most prominent characters used to differentiate *Premnas*, prominent infraorbital spine and high number of transverse scale rows, were of "relatively minor phylogenetic importance." Allen (1975a, 1975b) reversed this decision. However, early molecular studies (Tang, 2001; Quenouille et al., 2004; Santini and Polacco, 2006) resolved the monotypic *Premnas* within *Amphiprion*, prompting some (e.g., Quenouille et al., 2004; Nelson, 2006; Santini and Polacco, 2006) to return *Premnas* to the synonymy of *Amphiprion*. Although some phylogenies have resolved *Premnas* as the sister group to *Amphiprion* (e.g., Mirande, 2016; Thongtam na Ayudhaya et al., 2017), a multitude of other studies (Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b, 2014; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Litsios and Salamin, 2014; Lobato et al., 2014; Dhaneesh et al., 2015; Li et al., 2015; DiBattista et al., 2016; Gaboriau et al., 2018; Rolland et al., 2018; Delrieu-Trottin et al., 2019; Marcionetti et al., 2019; Thong-

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tam na Ayudhaya et al., 2019) have recovered *Premnas biaculeatus* within *Amphiprion*, as the sister group of the clownfishes (*A. ocellaris* + *A. percula*). Nonetheless, workers have continued to recognize *Premnas* as a distinct genus despite its phylogenetic position. Based on the relationships presented herein, as well as the overwhelming consensus from past studies, we treat *Premnas* as a junior synonym of *Amphiprion*. Both genera are masculine in gender, so the species name remains unchanged in the new combination as *Amphiprion biaculeatus*.

Allen (1975a, 1975b) recognized four subgenera within *Amphiprion*: *Actinicola*, *Amphiprion*, *Paramphiprion*, and *Phalerebus*. Allen (1975b, 1980, 1991) further subdivided the subgenus *Amphiprion* into an *ephippium*-complex (*A. ephippium*, *A. frenatus*, *A. mccullochi*, *A. melanopus*, *A. rubrocinctus*) and a *clarkii*-complex (remaining species of the subgenus). Our study and many others (Koh et al., 2006; Santini and Polacco, 2006; Timm et al., 2008; Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b, 2014; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Litsios and Salamin, 2014; O'Donnell, 2014; Dhaneesh et al., 2015; Li et al., 2015; DiBattista et al., 2016; Mirande, 2016; Thongtam na Ayudhaya et al., 2017, 2019; Gaboriau et al., 2018; Rolland et al., 2018; Delrieu-Trottin et al., 2019; Nguyen et al., 2020) have provided ample evidence for the monophyly of *Actinicola*, which encompasses the two clownfish species, *A. ocellaris* and *A. percula*. As a subgenus of *Amphiprion*, *Premnas* is sister to *Actinicola*. *Paramphiprion* is not monophyletic; *A. polymnus* and *A. sebae* are sister species but *A. latezonatus* is never recovered with them. Instead, *A. latezonatus* is often found as the sister group of all *Amphiprion* excluding the subgenera *Actinicola* and *Premnas* (Santini and Polacco, 2006; Cowman and Bellwood, 2011; Frédérich et al., 2013; Litsios and Salamin, 2014; Litsios et al., 2014; O'Donnell, 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Rolland et al., 2018; Delrieu-Trottin et al., 2019; Nguyen et al., 2020). *Phalerebus* is not monophyletic either, with *A. nigripes* recovered apart from the skunk anemonefishes (*A. akallopisos*, *A. pacificus*, *A. perideraion*, *A. sandaracinos*), which do form a clade (100% bootstrap). A monophyletic *Phalerebus* without *A. nigripes* is also seen in many other studies (e.g., Santini and Polacco, 2006; Timm et al., 2008; Steinke et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2014; Litsios and Salamin, 2014; O'Donnell, 2014; Dhaneesh et al., 2015; DiBattista et al., 2016; Mirande, 2016; Thongtam na Ayudhaya et al., 2017; Gaboriau et al., 2018; Rolland et al., 2018; Delrieu-Trottin et al., 2019; Nguyen et al., 2020). These four species share similarities in color pattern (dorsal white stripe), body shape (slender body where body depth $\geq$ 2.1 in SL; rounded caudal fin), and preference for host species of the genus *Heteractis* (Allen, 1972, 1991; Fautin and Allen, 1997; Timm et al., 2008; Allen et al., 2010a). The subgenus *Amphiprion*, which includes the remaining anemonefish species, is rendered polyphyletic by the phylogenetic positions of putative *Paramphiprion* and *Phalerebus*. The *ephippium* complex (*sensu* Allen, 1980), which is composed of species with a single bar or no bars (*A. barberi*, *A. ephippium*, *A. frenatus*, *A. mccullochi*, *A. melanopus*, and *A. rubrocinctus*), would be monophyletic if *A. mccullochi* is excluded. Other species with one or fewer bars are also found outside of this clade (e.g., *A. nigripes*, *A. omanensis*, and *A. perideraion*). The subgeneric names have seen sporadic use (e.g., Elliott et al., 1999; Tang, 2001; Santini and Polacco, 2006; Timm et al., 2008; Steinke et al., 2009; Dhaneesh et al., 2015; Li et al., 2015; Hu et al., 2016; Nguyen et al., 2020), and any future recognition would require revision of their limits.

Species boundaries for several anemonefishes may be in flux and require closer inspection. Strong population substructure has been reported in both *A. ocellaris* and *A. percula* (Timm and Kochzius, 2008; Timm et al., 2008, 2012). Timm et al. (2008) detected possible cryptic diversity and hybridization within what they called the "*A. ocellaris*/*A. percula* species complex." Thongtam na Ayudhaya et al. (2017) found evidence of undescribed species diversity in not only those two species, but also in their close relative, *A. biaculeatus* (as *P. biaculeatus*), as well as in *A. bicinctus* and *A. clarkii*. Litsios et al. (2014) suggested that *A. clarkii* is a complex of previously undetected species. That would not be surprising given its enormous range, extending from the Persian Gulf to the western Pacific Ocean, and highly variable coloration (Allen, 1972, 1991). Rolland et al. (2018: fig. 1b) also illustrated a divergence within *A. clarkii*. Litsios et al. (2014) resolved *A. chrysopterus* in two separate lineages: one with individuals from Fiji and Moorea sister to a large *Amphiprion* clade vs. one with individuals from the Solomon Islands sister to *A. akindynos* + *A. mccullochi*. However, Litsios and Salamin (2014) found all three populations of *A. chrysopterus* together in the same clade. That result was recovered in both their mitochondrial and nuclear phylogenies, though the position of *A. chrysopterus* differed between the two topologies (Litsios and Salamin, 2014: fig. 1). With access to the same samples, Rolland et al. (2018) only included *A. chrysopterus* from the Solomon Islands. Hubert et al. (2017: fig. S1) also found two different lineages of *A. chrysopterus*, one from Moorea and the other from New Caledonia, mirroring the Fiji + Moorea vs. Solomon Islands split observed by Litsios et al. (2014).

Hybridization may have played a large role in the evolutionary history of *Amphiprion* (Timm et al., 2008; van der Meer et al., 2012; Litsios and Salamin, 2014; Litsios et al., 2014). Steinke et al. (2009) noted that there is "little, if any, barcode divergence" among the skunk anemonefishes (*A. pacificus* not examined). They ruled out incomplete lineage sorting as the reason for low interspecific variation in COI, instead positing hybridization as a more likely explanation because of the widespread sympatry of these species. Based on microsatellite and mitochondrial data, van der Meer et al. (2012) suggested that *A. akindynos* and *A. mccullochi* have a history of hybridization. They also conceded that another possible explanation for their results was that *A. akindynos* and *A. mccullochi* are color morphs of a single species; they noted that further investigation would be necessary. Recent genetic studies (Litsios and Salamin, 2014; Gainsford et al., 2015; He et al., 2018) have confirmed the long-standing suspicion that *Amphiprion leucokranos* is a natural hybrid of *A. chrysopterus* and *A. sandaracinos* (Carlson, 1996; Fautin and Allen, 1997; Ollerton et al., 2007), where *A. chrysopterus*, as the larger of the two species, is always the maternal parent. Three of the four sequences representing *A. leucokranos* in this study, all mined from GenBank (Supplemental Table 1; see Data Accessibility), are of mitochondrial origin. Considering the nature of its hybrid parentage, resolving it as the sister of *A. chrysopterus* is not surprising and matches the results shown in Litsios and Salamin (2014: fig. 3). Because of its putative hybrid origin, *A. leucokranos* often is not

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considered a valid species (e.g., Ollerton et al., 2007; Litsios and Salamin, 2014; Litsios et al., 2014). Santini and Polacco (2006) regarded it as valid because they observed *A. leucokranos* forming breeding pairs with each other and to the exclusion of either parental species. However, Gainsford et al. (2015) demonstrated that, in one locality where *A. leucokranos* hybrids occur, there are instances of extensive hybridization and backcrossing among all three populations. Resolving the status of *A. leucokranos* requires considerably more investigation. The issues surrounding *A. leucokranos* also apply to *A. thiellei*, another possible hybrid believed to be produced by the same two parental species (Fautin and Allen, 1997; Ollerton et al., 2007). If hybrids of *A. chrysopterus* and *A. sandaracinos* are recognized as a distinct species and if the hybrid origins of *A. leucokranos* Allen, 1973a and *A. thiellei* Burgess, 1981 arise from the same circumstances, then *A. thiellei* would need to be placed in the synonymy of *A. leucokranos*.

Tribe Cheiloprionini.—This tribe is the basal member of the subfamily Pomacentrinae. It contains four genera (*Cheiloprion*, *Chrysiptera sensu stricto*, *Dischistodus*, and *Pomachromis*) and lineages of "*Chrysiptera*" not most closely related to *C. cyanea*. Most studies with sufficient taxon sampling have found a clade consistent with that composition in the same part of the tree (Cooper et al., 2009; Cowman and Bellwood, 2011; Hofmann et al., 2012; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). In addition to the coral specialist, *Cheiloprion*, the rest of the tribe shows a wide variety of diets, ranging from herbivores (including algal farmers) to omnivores (including detritivores) and planktivores (Pratchett et al., 2016). Most of the diversity in this group comes from species historically classified as *Chrysiptera*, which is broadly polyphyletic.

Cheiloprion.—The sole species of the genus (*Cheiloprion labiatus*) is an obligate corallivore, one of only two known in the family, along with *Plectroglyphidodon johnstonianus* (Allen, 1975a; Masuda et al., 1975, 1984; Sano et al., 1984a, 1984b; Cole et al., 2008). This uncommon diet is linked to its most noteworthy feature and the origin of its common name (Big-lip Damsel): thick lips that curl over the upper and lower jaws. The enlarged, modified lips may act as a protective mechanism against the stinging nematocysts of their prey (Allen, 1975a). *Cheiloprion* is distributed throughout the Indo-Australian Archipelago where, due to its dietary requirements, it occurs in close association with coral reefs (Allen, 1975a, 1991; Randall et al., 1997; Allen and Erdmann, 2012). It is the sister taxon of *Chrysiptera sensu stricto* in our phylogeny, which matches previous studies (Cowman and Bellwood, 2011; Litsios et al., 2012b; Lobato et al., 2014; DiBattista et al., 2016; Rabosky et al., 2018; Delrieu-Trottin et al., 2019).

Chrysiptera.—There are 40 currently recognized species of *Chrysiptera* found throughout the Indo-West Pacific. Allen (1975a) split the genus into two broad complexes. The one that included *C. biocellata*, *C. glauca*, *C. leucopoma*, *C. niger*, and *C. unimaculata* was united by fin-ray and gill-raker counts, extent of predorsal scalation, lack of preorbital and suborbital (i.e., infraorbital) scalation, elongate teeth, similar head shape, and continuous dorsal-fin profile. The other complex, with *C. hemicyanea*, *C. oxycephala*, *C. rollandi*, *C. talboti*, and *C. traceyi*, displayed fewer dorsal- and pectoral-fin rays, less elongate teeth, a distinctive dorsal-fin profile with deeply incised membranes between anterior dorsal spines, and a prominent notch between the spinous and soft portions of the dorsal fin. He was unsure about the affinities of *C. caeruleolineata*, *C. cyanea*, *C. flavipinnis*, *C. rex*, and *C. tricincta*. He suggested that *C. galba*, *C. notialis*, *C. rapanui*, and *C. starcki* may be related, but did not speculate as to their relationship to other *Chrysiptera*. Allen (1975a: 42) warned that this diverse genus, then called *Glyphidodontops*, probably was not monophyletic, remarking that it presented "some of the most serious problems for students of pomacentrid taxonomy." This statement remains true today. Hensley (1978: 15) referred to it as a catch-all genus, one that "is likely to be separated into other genera after detailed studies." Allen (1987b: 109) concurred, saying that it "may ultimately be split into several genera." Doubts about its monophyly were reiterated in his later works (Allen and Adrim, 1992; Allen, 1999b; Allen and Erdmann, 2008b; Allen et al., 2010b, 2015b). Quenouille et al. (2004) published the first molecular phylogeny with significant sampling within *Chrysiptera* and confirmed the disarray by recovering putative *Chrysiptera* in three different lineages. Subsequent studies (Cooper et al., 2009; Cowman and Bellwood, 2011; Hubert et al., 2011, 2012, 2017; Hofmann et al., 2012; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019) have further reinforced this, finding species of *Chrysiptera* scattered across the Pomacentrinae. Chromosomal variation hinted at this polyphyly. Takai and Ojima (1995) commented that "*Chrysiptera* may be one of the genera in which the karyotypes have altered most actively in Pomacentridae," a statement that was made under the assumption of its monophyly. Differences in early development among putative *Chrysiptera* also suggested that the genus was not monophyletic (R. E. Thresher, pers. comm.).

The results of this analysis agree with recent phylogenies: *Chrysiptera*, in its current state, is broadly polyphyletic. The putative species of *Chrysiptera* are distributed in several disjunct lineages, most of which are confined to the tribe Cheiloprionini (Fig. 1). The remaining "*Chrysiptera*" are paraphyletic relative to *Amblypomacentrus*, in the tribe Pomacentrini. Because the putative species of *Chrysiptera* are dispersed across the subfamily Pomacentrinae, we hereby restrict *Chrysiptera sensu stricto* to the clade that encompasses the following species: *C. caesifrons*, *C. chrysocephala*, *C. cyanea* (type species), *C. hemicyanea*, *C. oxycephala*, *C. parasema*, *C. rex*, *C. rollandi*, *C. springeri*, *C. talboti*, and *C. taupou*. This assemblage contains the majority of bright blue species (e.g., *C. cyanea*, *C. hemicyanea*, *C. springeri*) and is sister to *Cheiloprion*. *Chrysiptera sensu stricto* is equivalent to "*Chrysiptera* I" of Quenouille et al. (2004: fig. 2), "*Chrysiptera* 2" of Cooper et al. (2009: fig. 2), "*Chrysiptera* Clade II" of Cowman and Bellwood (2011: figs. 2b, S6), and a clade within "*Chrysiptera* II" of Frédérich et al. (2013: 98). A group comprising some combination of these species has been recognized in the literature. Allen and Lubbock (1976) characterized *C. hemicyanea*, *C. oxycephala* (as *Glyphidodontops azurepunctatus*), *C. rollandi*, *C. springeri*, *C. talboti*, and *C. traceyi* by their deeply incised spinous dorsal-fin membrane,

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similar dentition, lower meristic counts (viz., soft dorsal, anal, and pectoral rays), and deeper, more ovate body compared to congeners. Allen (1987b) also made note of the deeper body and incised spinous dorsal fin when grouping together *C. hemicyanea*, *C. oxycephala*, *C. sinclairi*, and *C. springeri*. Allen and Adrim (1992) and Allen (1999b) added *C. pricei* and *C. cymatilis*, respectively, to the species complex on the basis of those features. Allen and Erdmann (2008b) named it the "*hemicyanea* complex" when they added the newly described *C. giti*. Subsequently, Allen et al. (2010b, 2015a, 2017a, 2018a) expanded the complex to include *C. arnazae*, *C. burtjonesi*, *C. ellenae*, *C. maurineae*, *C. papuensis*, and *C. uswanasi*. Within this *hemicyanea* complex, Allen et al. (2015a) further demarcated a "*Chrysiptera oxycephala* species complex" that consisted of *C. ellenae*, *C. maurineae*, *C. oxycephala*, *C. papuensis*, and *C. sinclairi*. Allen et al. (2017a, 2018a) recently added a sixth, *C. burtjonesi*, and seventh representative, *C. uswanasi*.

The phylogenetic relationships within *Chrysiptera sensu stricto* produced by this analysis show three distinct clades, a result which largely agrees with earlier works. One clade includes a sister-group pairing of *C. cyanea* and *C. taupou* (Randall et al., 1997; Randall, 2005) plus a monophyletic *C. rex* complex (Allen et al., 2015b). Drew et al. (2010) first detected genetic variation within *C. rex* that corresponded to regional color morphs. Allen et al. (2015b) described this cryptic diversity as a "*Chrysiptera rex* species complex" composed of *C. caesifrons*, *C. chrysocephala*, and *C. rex*. Steinke et al. (2009) recorded genetic divergence within *C. cyanea*, which may also represent undescribed diversity. They reported a clear break between COI sequences of Indonesian *C. cyanea* and those from the Philippines. They proposed resurrecting *Chrysiptera punctatoperculare* for the population in the South China Sea. However, *C. punctatoperculare* was not described from the Philippines, instead coming from the Ryukyu Islands in the neighboring East China Sea (Fowler, 1946). Furthermore, there are other junior synonyms of *Chrysiptera cyanea* described from the Philippines (*Glyphidodon assimilis*, *Abudefduf turchesius*, and *Abudefduf sapphirus*) that have seniority over *C. punctatoperculare* and could have priority instead. More detailed examination will be necessary to resolve this nomenclatural issue if additional species are recognized within *C. cyanea*. A second clade within *Chrysiptera sensu stricto* includes *C. rollandi*, *C. talboti*, and *C. traceyi* (Allen, 1975c). The third clade includes the *hemicyanea* complex (Allen and Erdmann, 2008b; Allen et al., 2010b), which contains *C. oxycephala*. The composition of these three clades is consistent with other pomacentrid phylogenies (Quenouille et al., 2004; Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012b; Lobato et al., 2014; Mirande, 2016; Delrieu-Trottin et al., 2019), though the interrelationships between them do vary from one study to the next. Based on control region data (Allen et al., 2010b, 2015a, 2017a, 2018a), the following species also should be considered part of *Chrysiptera sensu stricto*: *C. arnazae*, *C. burtjonesi*, *C. ellenae*, *C. giti*, *C. maurineae*, *C. papuensis*, *C. sinclairi*, and *C. uswanasi*. Following remarks in the literature (Allen and Adrim, 1992; Allen, 1999b; Allen et al., 2003, 2010b; Allen and Erdmann, 2008b, 2012), we provisionally designate *C. cymatilis* and *C. pricei* as members of *Chrysiptera sensu stricto*. If these assignments are correct, this newly reorganized genus would include more than half (22) of the species formerly classified in *Chrysiptera*.

The remaining "*Chrysiptera*" in the Cheiloprionini present taxonomic challenges that cannot be resolved herein. We recovered a clade composed of *C. galba*, *C. rapanui*, and *C. starcki* (100% bootstrap) as the sister to another group of "*Chrysiptera*." Prior studies have linked *C. galba* and *C. rapanui* with a third species, *C. notialis* (Allen and Randall, 1974; Allen, 1975a, 1975c). All four species occur along southern Oceania, with all but *C. starcki* restricted to the Southern Hemisphere (Allen, 1973b, 1975a, 1975c; Allen and Randall, 1974); "*Chrysiptera*" *starcki* appears to have an antiequatorial distribution (Allen, 1975a; Ida and Moyer, 1975; Randall, 1981). For the purposes of our discussion, we refer to this clade as the Oceanic "*Chrysiptera*" for their geographic distribution. They are united by the condition of their teeth: "All except *G. rapanui* have uniserial teeth, which is atypical for *Glyphidodontops*" (Allen, 1975a: 42). The position and relationships of these species vary greatly among molecular phylogenies. Quenouille et al. (2004) were the first to sequence a member of this group, *C. galba*, and recovered it in their "*Chrysiptera* II," as the sister species to *C. glauca* + *C. leucopoma*, a relationship equivalent to the one reported herein. However, Cooper et al. (2009: 14) understandably questioned the identity of the sample because Quenouille et al. (2004: table 1) specified that it was collected from Indonesia, well outside of the known range of *C. galba* in southeastern Oceania (Allen and Randall, 1974; Allen, 1975a, 1991). Further complicating matters, the stated Indonesian provenance of that specimen (stri-x-2814) is in doubt because its GenBank entries (AY208431, AY208568) list the source as "aquarium traders." In BLAST searches, the cyt *b* sequence (AY208568) is a >99% match with published records of *C. galba* collected from the Gambier Islands (KM455353–KM455364) and Rapa Nui (MK100728), which are within its native range (Delrieu-Trottin et al., 2014, 2019). These data strongly suggest that, despite its unclear origin, the specimen probably is *C. galba*. Cowman and Bellwood (2011: figs. 2b, S6), using those sequences from Quenouille et al. (2004), resolved *C. galba* as the sister group of *Pomachromis* in their "*Chrysiptera* I et al." Litsios et al. (2012b: figs. A1–A3) found *C. galba* as the sister group of either *Altrichthys* or a large pomacentrine clade that included genera like *Amphiprion*, *Amblyglyphidodon*, *Neopomacentrus*, and *Pomacentrus*. Rabosky et al. (2013) inferred *C. galba* as the sister group to a clade of *Cheiloprion*, *Chrysiptera sensu stricto*, and *Pomachromis*. Several studies (Litsios et al., 2012a; Frédérich et al., 2013; DiBattista et al., 2016; Gaboriau et al., 2018) have examined both *C. galba* and *C. starcki* but failed to recover them together. Litsios et al. (2012a) showed *C. galba* as sister to *Pomachromis* but grouped *C. starcki* with *Nexilosus* in a clade sister to the rest of Pomacentrinae. Frédérich et al. (2013) found *C. starcki* (part of their "*Chrysiptera* I") sister to *Pomachromis* and *C. galba* (part of their "*Chrysiptera* II") sister to *Cheiloprion*. DiBattista et al. (2016) resolved *C. galba* as the sister species of a clade equivalent to our Cheiloprionini. However, they found *C. starcki* as the sister group of the herbivorous "*Chrysiptera*" (see below). Gaboriau et al. (2018) reported the same relationship for *C. starcki* but recovered *C. galba* sister to *Cheiloprion*. The discordant results may be due, in part, to sequences from specimens incorrectly identified as *C. galba*. In addition to the sequences of *C. galba* from Quenouille et al. (2004), both Litsios et al. (2012a: additional file 2) and Frédérich et al. (2013: table S1) used a COI sequence (FJ583183) attributed to a sample of "*C. galba*"

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collected from the Philippines, which is extralimital for *C. galba*, one of several deposited in GenBank (FJ583183–FJ583187). DiBattista et al. (2016: appendix S1) used another COI sequence (FJ583184) from the Philippines to represent *C. galba*. Gaboriau et al. (2018) looked at another barcode sequence from the Philippines (FJ583187). Rabosky et al. (2018: Dryad files "accession_numbers.csv", "dropped_rogues.csv") also examined FJ583183 but identified *C. galba* as a rogue taxon before pruning it from their analyses. They resolved *C. starcki* as the sister group to the rest of the Pomacentrinae. Delrieu-Trottin et al. (2019) generated novel DNA sequences for *C. galba* and *C. rapanui*. They recovered both species with *C. starcki*. In finding a group composed of *C. galba*, *C. rapanui*, and *C. starcki*, our result is consistent with Delrieu-Trottin et al. (2019) and traditional classifications (Allen and Randall, 1974; Allen, 1975a, 1975c). Steinke et al. (2009) detected COI sequence divergence showing a geographic divide between individuals of *C. starcki* from the Philippines and those from Tonga. Their finding suggests that the disjunct northern and southern populations may be different species.

The Oceanic "*Chrysiptera*" are sister to a monophyletic group containing *C. biocellata*, *C. brownriggii*, *C. glauca*, *C. leucopoma*, and *C. unimaculata*. That composition closely follows one of Allen's (1975a) complexes. The species of this group are primarily herbivorous (Allen, 1975a; Kuo and Shao, 1991) and include all of the *Chrysiptera* (*C. biocellata*, *C. brownriggii*, *C. glauca*, *C. leucopoma*, and *C. unimaculata*) known to engage in algal farming (Ceccarelli, 2007; Pratchett et al., 2016). For the purposes of discussion, we will refer to this clade as the herbivorous "*Chrysiptera*." They usually occur in shallow waters exposed to surge and wave action, often over rubble and rocky substrates (Allen, 1975a, 1991; Masuda et al., 1984; Myers, 1999; Allen et al., 2003). The grouping recovered in our phylogeny (100% bootstrap) is equivalent to "*Chrysiptera* II" of Quenouille et al. (2004: fig. 2), "*Chrysiptera* 1" of Cooper et al. (2009: fig. 2), a clade within "*Chrysiptera* I et al." of Cowman and Bellwood (2011: figs. 2b, S6), and a clade within "*Chrysiptera* I" of Frédérich et al. (2013: 98). The composition matches those of previous phylogenies, and the relationships among the species are mostly congruent with them as well. Masuda et al. (1984) remarked on the resemblance of *C. biocellata*, *C. leucopoma*, and *C. unimaculata*. All three were found together in a clade, along with *C. brownriggii*. The *C. brownriggii*–*C. leucopoma* sister-group relationship is expected considering *C. leucopoma* was, until recently, regarded as a junior synonym of *C. brownriggii* (e.g., Randall et al., 1997; Allen and Bailey, 2002; Quenouille et al., 2004; Randall, 2005; Cooper et al., 2009; Motomura et al., 2010). Allen et al. (2015b) resurrected *C. leucopoma*, removing it from the synonymy of *C. brownriggii*, with *C. brownriggii* restricted to the Indian Ocean and *C. leucopoma* as its sister species in the Pacific. They did so on the basis of genetic distances between the two populations first reported by Hubert et al. (2012: fig. S1, table S3).

The other lineage of "*Chrysiptera*" in the Cheiloprionini contains a single species, *C. flavipinnis*. Its phylogenetic position is highly unstable. Our phylogeny recovers it as sister to *Dischistodus*. However, the placement of this species is variable, with it often appearing elsewhere within Cheiloprionini, e.g., as the sister taxon of *Pomachromis*. DiBattista et al. (2016), the only other phylogeny to examine *C. flavipinnis*, found it sister to *C. leucopoma*. In the original description, Allen and Robertson (1974) hypothesized that it is closely related to *C. cyanea* but noted the lack of deeply incised membranes between the dorsal-fin spines which is characteristic of *C. cyanea* and other *Chrysiptera sensu stricto*. They also observed that this species occurs at greater depths (9.5–37 m) than *C. cyanea* (<5 m). The sequence used in this analysis was obtained from the BOLD data portal (LIFSA265-08; UG1067; Australia: 14°38′09.6″S, 145°27′18.0″E) and appears to be correctly identified based on the photo of the voucher specimen available online.

The last of the putative "*Chrysiptera*" include *C. annulata*, *C. kuiteri*, and *C. tricincta*, which are the black-and-white species (footballers). These fishes are equivalent to "*Chrysiptera* III" of Quenouille et al. (2004: fig. 2) and Frédérich et al. (2013: 98), and "*Chrysiptera* 3" of Cooper et al. (2009: fig. 2). They are not closely related to *Chrysiptera sensu stricto* or the other "*Chrysiptera*" in the Cheiloprionini. Instead, the three species are paraphyletic relative to a monophyletic *Amblypomacentrus* in the tribe Pomacentrini. This *Amblypomacentrus*–"*Chrysiptera*" clade is sister to the rest of the Pomacentrini. A connection between these "*Chrysiptera*" and *Amblypomacentrus* has been discussed by other workers (Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). Cowman and Bellwood (2011: figs. 2b, S6) labeled a similar group as "*Chrysiptera* Clade III et al." Frédérich et al. (2013) called it "*Chrysiptera* III + *Amblypomacentrus clarus*." Similarities in coloration between these species have been noted in the literature (Randall et al., 1997: 252; Cooper et al., 2009). The presence of black bars (or saddles) in all five species may be phylogenetically informative as Merilaita and Kelley (2018) demonstrated that barred color patterns are generally concentrated in a few groups of closely related damselfishes (e.g., *Abudefduf*, *Amphiprion*); this group would be another example. Among these fishes, all have uniserial teeth (Allen, 1975a; Allen and Rajasuriya, 1995; Allen and Adrim, 2000) except for *C. annulata*, which has biserial teeth (Smith, 1960; Allen and Randall, 1974, 1981); *Chrysiptera tricincta* occasionally has irregularly biserial teeth anteriorly (Allen and Randall, 1974). They all share a habitat preference for sand or silt substrates (Allen, 1975a, 1991; Allen and Rajasuriya, 1995; Randall et al., 1997; Allen and Adrim, 2000; Allen et al., 2003; Randall, 2005; Cooper et al., 2009; Lepoint et al., 2016). Parts of the diagnosis for *Amblypomacentrus* given in Allen (1975a) apply to the three "*Chrysiptera*" (e.g., notch between preorbital and suborbital absent; dorsal spines XIII; preorbital and suborbital naked; snout mostly naked; Peters, 1855; Smith, 1960; Allen and Randall, 1974, 1981; Allen, 1991; Allen and Rajasuriya, 1995). Aside from the variation in tooth rows already mentioned, other deviations from the diagnosis include the extent of preopercular and suborbital serration (preopercle entire in *C. tricincta*, anterior portion of suborbital often entire in *C. kuiteri* and *C. tricincta*; vs. finely serrated in *Amblypomacentrus sensu stricto*) and tooth shape (conical in "*Chrysiptera*" vs. incisiform anteriorly in *Amblypomacentrus sensu stricto*; Smith, 1960; Allen and Randall, 1974, 1981; Allen and Rajasuriya, 1995). Based on the relationships shown herein (Fig. 1), these three species of "*Chrysiptera*" are hereby referred to *Amblypomacentrus*. *Amblypomacentrus* is masculine whereas *Chrysiptera* is feminine so, to match

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gender, *A. annulatus* and *A. tricinctus* are modified accordingly.

Unfortunately, there appear to be no available names for either the herbivorous or Oceanic clades of "*Chrysiptera*." *Glyphidodontops* and *Iredaleichthys*, as unneeded replacement names of *Chrysiptera* with the same type species (*Glyphisodon azureus*), are both objective synonyms of *Chrysiptera* (ICZN, 1999: Art. 61.3.3). The type species of *Paraglyphidodon* is *C. oxycephala* which is recovered within *Chrysiptera sensu stricto* (Fig. 1). Further study with more comprehensive taxon sampling is needed to resolve the limits of the different lineages. Eventually, as it is highly unlikely that *Chrysiptera sensu lato* is monophyletic, new genus-group names will need to be established for the other "*Chrysiptera*."

From comments in the literature, some tentative assignments can be made for the species of "*Chrysiptera*" we were unable to examine. *Chrysiptera albata* and *C. caeruleolineata* appear to be closely related, based on the following shared characteristics: XIV dorsal spines (vs. XIII in others); smallest "*Chrysiptera*" (<38 mm SL); deepest occurence of any "*Chrysiptera*" (>25 m); and preference for sand and rubble habitat over steep outer reefs (Allen and Bailey, 2002; Randall, 2005; Allen and Erdmann, 2012). In the original description, Allen (1973b) likened the color pattern of *C. caeruleolineata* to that of *C. leucopoma*. The two species share a neon blue dorsal stripe, for which *C. caeruleolineata* is named, that is also present in some *C. biocellata*, *C. brownriggii*, and *C. unimaculata*, all species that are closely related to *C. leucopoma*. Therefore, it is possible that *C. albata* and *C. caeruleolineata* are closely related to *C. leucopoma* and its relatives (herbivorous "*Chrysiptera*"). However, they would be the only members of the clade that are not reported to be algal farmers (Pratchett et al., 2016). Both species also occur at greater depths, below 25 m and extending past 50 m, than the other herbivorous "*Chrysiptera*" (Allen, 1973b, 1975a; Allen and Bailey, 2002). Allen (1975a) thought *C. caeruleolineata* may warrant separate subgeneric status because of its higher dorsal spine count, predorsal scalation, and uniserial teeth (all shared by *C. albata*; Allen and Bailey, 2002). Further investigation is required. We did not include sequences on GenBank labeled as *C. caeruleolineata* (FJ459574–FJ459575) for analysis because they originate from the western coast of India in the Arabian Sea, which is outside of its known range (Allen, 1973b, 1975a, 1991). *Chrysiptera niger* is also likely part of the herbivorous clade because of similarities to *C. biocellata*, *C. glauca*, *C. leucopoma*, and *C. unimaculata* in appearance, diet, habitat, and meristic counts (Allen, 1975a, 1975c). Although *C. niger* is not known to practice algal gardening (Pratchett et al., 2016), its diet does consist primarily of algae (Allen, 1975a, 1975c). *Chrysiptera sheila* is thought to be most closely related to *C. unimaculata*, which would make it another herbivorous "*Chrysiptera*" (Randall, 1994, 1995). DiBattista et al. (2016) appeared to confirm this by finding it sister to *C. unimaculata*, but their data are not currently available on GenBank. *Chrysiptera bleekeri* most resembles *C. flavipinnis* (Allen, 1991, 1997; Allen et al., 2003; Allen and Erdmann, 2012). Based on previous literature describing its overall similarity to *C. galba* (Allen and Randall, 1974) and *C. rapanui* (Allen and Randall, 1974; Allen, 1975c), *C. notialis* is almost certainly an Oceanic "*Chrysiptera*," a group that includes those species plus *C. starcki*.

Dischistodus.—Seven large (some species approach or exceed 150 mm SL; Allen, 1975a, 1991), herbivorous species that exhibit algal gardening behavior (Potts, 1977; Meekan et al., 1995; Sin et al., 1995; Frédérich et al., 2013: table S1; Hata and Ceccarelli, 2016) constitute this monophyletic group. They usually occur in shallow lagoons (<10 m) and on inshore reefs of the Indo-Australian Archipelago, often over sand or silt substrates (Allen, 1975a, 1991). Their overall similarities have led to a consistent and widely accepted generic composition since Allen (1975a) removed these species from *Pomacentrus* and recognized *Dischistodus* as a separate genus. Our results confirm this by finding strong support (100% bootstrap) for the monophyly of the five species that were sampled. The species of *Dischistodus* are arranged in a comb-like topology with *D. melanotus* sister to the remaining species in a sequential stepwise array: *D. pseudochrysopoecilus*, *D. chrysopoecilus*, *D. perspicillatus*, and *D. prosopotaenia*. These relationships are congruent with those reported in some earlier studies (Rabosky et al., 2013, 2018; Mirande, 2016). However, our phylogeny differs from others in the placement of *D. melanotus*, where it was nested further within *Dischistodus* therein (Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; DiBattista et al., 2016; Delrieu-Trottin et al., 2019).

Pomachromis.—The reef-damsels of the genus *Pomachromis* are a morphologically distinct group of four species distributed across the Indo-West Pacific. They are slender and elongate (body depth 2.7–3.0 in SL), and usually occur over outer reef slopes in midwater aggregations feeding on zooplankton (Allen and Emery, 1973; Allen and Randall, 1974; Allen, 1975a; Allen and Larson, 1975). Given their overall similarity, the genus has been stable since its inception (Allen and Randall, 1974). Allen and Larson (1975), in describing the most recent addition to the genus, stated that all four are closely related. Our phylogeny agrees (Fig. 1), displaying strong bootstrap support (100%) for the monophyly of *Pomachromis*.

Tribe Hemiglyphidodontini.—This group consists of several well-established genera, a couple of monotypic genera, and a clade containing the only damselfishes that lack a pelagic larval stage. Even though it was not named as such, the existence of a clade with some combination of these component genera (*Acanthochromis*, *Altrichthys*, *Amblyglyphidodon*, *Hemiglyphidodon*, and *Neoglyphidodon*) is consistently supported across other phylogenetic studies (e.g., Quenouille et al., 2004; Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019).

Acanthochromis.—As discussed above, *Acanthochromis* was formerly classified with *Chromis* and its relatives (e.g., McCulloch, 1929; Whitley, 1929; Marshall, 1964; Allen, 1975a, 1991), prior to its reclassification in the subfamily Pomacentrinae (Cooper et al., 2009). *Acanthochromis polyacanthus*, the sole member of the genus, was initially the only pomacentrid known to lack a dispersive planktonic phase, a rare occurence in marine species, and the only damselfish reported to engage in parental care of juvenile offspring (Robertson, 1973; Allen, 1975a; Thresher, 1984; Nakazono,

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1993; Kavanagh, 1998, 2000). With its limited capacity for dispersal, it is no surprise that different populations display variation in their coloration, genetics, life history, morphology, and ontogeny (Planes and Doherty, 1997a, 1997b; Kavanagh, 2000; Planes et al., 2001). The extensive divergence in color patterns, where individual localities often have unique color morphs, is likely the result of a strong preference for mates with similar color patterns (Allen, 1975a, 1991; Doherty et al., 1994; Planes and Doherty, 1997a, 1997b; Kavanagh, 2000). Its sister-group relationship to *Altrichthys* is well supported (100% bootstrap; Fig. 1).

Altrichthys.—The absence of pelagic larvae and concomitant parental care were subsequently observed in three additional species. After discovering that *Amblyglyphidodon azurelineatus* (*sensu* Allen, 1991) shared these traits with *Acanthochromis*, Allen (1999a) erected *Altrichthys* to house *A. azurelineatus* and another species, the newly described *A. curatus*. A third species, *A. alelia*, was recently described (Bernardi et al., 2017b). With their limited ability to disperse, all three are confined to the Palawan Province in the Philippines. Allen (1999a) classified the genus as a member of the subfamily Chrominae, noting that Allen (1991) had overlooked the presence of spiniform procurrent caudal rays when assigning *azurelineatus* to *Amblyglyphidodon*. However, as mentioned above, Cooper et al. (2009) advised against employing this character for classification because it is unreliable for diagnosing members of Chrominae *sensu stricto*. They reassigned *Altrichthys* to Pomacentrinae based on their topology, where *Altrichthys* landed in a polytomy with *Pomacentrus lepidogenys* and *P. stigma*. However, much like the situation with *Nexilosus* (see above), this unexpected result may have been due to issues with data quality. Unable to obtain fresh samples of *Altrichthys*, they resorted to sequencing formalin-fixed specimens of *A. curatus*. Bernardi (2011) acknowledged the limitations of extracting viable DNA from such material. He demonstrated that Cooper et al.'s (2009) sequences do not represent *A. curatus* and were likely the result of contamination or misidentification involving *P. stigma*. Perhaps unaware of this discovery, some workers have continued to rely on Cooper et al.'s (2009) data and still misplace *Altrichthys* inside *Pomacentrus* (e.g., Litsios et al., 2012b; Frédérich et al., 2013; DiBattista et al., 2016). DiBattista et al. (2016) found *Altrichthys* to be polyphyletic where *Altrichthys azurelineatus* was sister to *Acanthochromis* but *Altrichthys curatus* was embedded within *Pomacentrus*. There is robust support (100% bootstrap) for a monophyletic *Altrichthys* paired with *Acanthochromis* as its sister group (Fig. 1). This lends further support to the hypothesis that brood care and loss of the pelagic larval stage evolved only once in Pomacentridae (Bernardi, 2011). The relationships discovered within *Altrichthys* herein match previously published trees (Bernardi, 2011; Bernardi et al., 2017b).

Amblyglyphidodon.—The 11 Indo-Pacific species classified in *Amblyglyphidodon* are all deep-bodied and orbiculate (body depth 1.5–1.8 in SL; Allen, 1975a, 1991, 1995; Allen and Randall, 2002; Allen et al., 2012a, 2012b). Since Allen's (1975a) revision of the family recognized *Amblyglyphidodon* as a separate genus, these species have been widely accepted as forming a natural group. Monophyly of *Amblyglyphidodon* receives strong support (100% bootstrap; Fig. 1) which corresponds to all phylogenetic studies with sufficient taxon sampling (Quenouille et al., 2004; Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). Of the currently recognized species, this analysis lacks only *A. flavopurpureus*. Allen et al. (2012b: 1128) found *A. batunaorum* and *A. ternatensis* to be closely related. The two species were previously regarded as color variants (Allen, 1995). However, they are not sister species in this phylogeny. Instead we found them to be sequential sister taxa to the rest of *Amblyglyphidodon*. *Amblyglyphidodon batunai* was emended to *A. batunaorum* by Fricke et al. (2020), because the name was explicitly stated to be in honor of multiple people, one man and one woman (Allen, 1995; ICZN, 1999: Arts. 31.1.2, 32.5.1). Allen and Randall (2002) identified a "*leucogaster* complex" composed of *A. indicus*, *A. leucogaster*, *A. melanopterus*, and *A. orbicularis*. Our phylogeny found those species, minus *A. leucogaster*, together in a clade, along with *A. curacao* and *A. silolona* (Fig. 1). Although its monophyly is well supported, "the phylogeny of *Amblyglyphidodon* is complex and warrants further attention" (Allen et al., 2012a: 1134).

Hemiglyphidodon.—This monotypic genus is characterized by a high gill-raker count that is unique in the family (>65 on first branchial arch vs. <40, in rest of family; Allen, 1975a, 1991; Masuda et al., 1984). *Hemiglyphidodon plagiometopon* occurs in the Indo-Australian Archipelago. It is another damselfish species that tends and harvests algal gardens (Lassuy, 1980; Sammarco, 1983; Sammarco et al., 1986; Hoey and Bellwood, 2010; Hata and Ceccarelli, 2016) though there is evidence that it derives a large part of its diet from detritus which accumulates on the algae in its territory and not the algae itself (Wilson and Bellwood, 1997). It seems that a strategy involving territorial defense and maintenance of an algal lawn, whether as a direct food source or as a collection system for food items, has evolved multiple times within Pomacentridae (e.g., herbivorous "*Chrysiptera*," *Dischistodus*, *Stegastes*). Even though there is little doubt about the nearest relatives of *Hemiglyphidodon*, its phylogenetic position within the tribe is unstable. We recover it as the sister group to the rest of Hemiglyphidodontini which agrees with some earlier works (e.g., Cowman and Bellwood, 2011; Rabosky et al., 2013; Lobato et al., 2014), but diasagrees with others which have shown it to be sister to *Acanthochromis* (Cooper et al., 2009; Mirande, 2016), *Ambylglyphidodon* (Litsios et al., 2012a, 2012b; Frédérich et al., 2013; DiBattista et al., 2016; Gaboriau et al., 2018; Rabosky et al., 2018), or both (Quenouille et al., 2004).

Neoglyphidodon.—Since these species were placed in their own genus (as *Paraglyphidodon*; Allen, 1975a) and then relocated to the newly erected *Neoglyphidodon* (Allen, 1991), the composition of the group has been widely accepted and its monophyly has been corroborated consistently by subsequent phylogenetic studies (Quenouille et al., 2004; Cooper et al., 2009; Cowman and Bellwood, 2011; Hofmann et al., 2012; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). There are currently nine species classified in *Neoglyphidodon*, most of which inhabit the East Indies (Allen and Erdmann, 2012). We examined seven of the nine, missing only *N. crossi*

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and *N. mitratus*, and found robust support (100% bootstrap) for the monophyly of the genus. Our phylogeny shows a ladder-like topology of sequential sister taxa (*N. oxyodon*, *N. polyacanthus*, *N. bonang*, *N. melas*, *N. carlsoni*, *N. nigroris*, and *N. thoracotaeniatus*) that is congruent with all of the studies cited above except Gaboriau et al. (2018) and Rabosky et al. (2018), where the positions of *N. carlsoni* and *N. nigroris* are switched. Of the two species not sampled, Allen (1991: 221) stated that *N. crossi* most closely resembled *N. bonang* and Allen and Erdmann (2012: 1137) stated that *N. mitratus* and *N. thoracotaeniatus* are a geminate species pair. If that is accurate, then the two most basal species, *N. oxyodon* and *N. polyacanthus*, would be the only ones that lack scales on the suborbital (Allen, 1991: 246) and the remaining seven species would share a scaled suborbital.

Tribe Pomacentrini.—The tribe contains *Amblypomacentrus sensu novum*, *Neopomacentrus*, *Pomacentrus*, *Pristotis*, and *Teixeirichthys*. In terms of diversity, the group is dominated by *Pomacentrus*. Though not so named, some workers have inferred phylogenies containing a clade consistent with what we report herein (Litsios et al., 2012b; Frédérich et al., 2013; Rabosky et al., 2013; DiBattista et al., 2016). However, other studies did not find these taxa together, instead resolving a separate clade composed of some combination of *Neopomacentrus*, *Pristotis*, and *Teixeirichthys* (Cooper et al., 2009; Cowman and Bellwood, 2011; Hofmann et al., 2012; Litsios et al., 2012a; Lobato et al., 2014; Gaboriau et al., 2018; Rabosky et al., 2018; Delrieu-Trottin et al., 2019), which was often sister to Amphiprionini. Where those recent phylogenies have agreed is in consistently finding *Amblypomacentrus*, frequently associated with stray "*Chrysiptera*" (equivalent to our *Amblypomacentrus sensu lato*), in a clade with *Pomacentrus* (Cooper et al., 2009; Cowman and Bellwood, 2011; Hofmann et al., 2012; Litsios et al., 2012a; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019).

Amblypomacentrus.—As noted above, this genus is revised herein to include three species formerly classified as *Chrysiptera* (*A. annulatus*, *A. kuiteri*, and *A. tricinctus*) because these black-and-white striped species are more closely related to species of *Amblypomacentrus sensu stricto* in our phylogeny (Fig. 1). This result corroborates Cooper et al. (2009), who found "*Chrysiptera*" *kuiteri* more closely related to *A. clarus*. They noted that all three species of "*Chrysiptera*" shared similarities in size, coloration, and habitat preference with members of *Amblypomacentrus*. Phylogenetic studies since Cooper et al. (2009) have recovered similar relationships between those three "*Chrysiptera*" and *Amblypomacentrus* (e.g., Cowman and Bellwood, 2011; Litsios et al., 2012a; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). Allen (1975a: 42) mentioned that *Amblypomacentrus* closely resembles some species of *Chrysiptera* (as *Glyphidodontops*), but he did not specify which ones. Randall et al. (1997: 252) commented that the coloration of *A. breviceps* is similar to *Chrysiptera tricincta* [= *A. tricinctus*]. Based on the distribution of barred color patterns in Pomacentridae, Merilaita and Kelley (2018: fig. 4) showed that distinct vertical bars are clustered in groups of closely related damselfish species (e.g., *Abudefduf*, *Amphiprion*). Other traits shared by the species of *Amblypomacentrus sensu novum* include uniserial teeth (Allen, 1975a; Allen and Rajasuriya, 1995; Allen and Adrim, 2000; biserial in *C. annulata*; Allen and Randall, 1974, 1981) and preference for sand or silt habitats (Allen, 1975a, 1991; Allen and Rajasuriya, 1995; Randall et al., 1997; Allen and Adrim, 2000; Allen et al., 2003; Randall, 2005; Cooper et al., 2009; Lepoint et al., 2016).

Neopomacentrus.—There are currently 16 described species of *Neopomacentrus*, but Allen et al. (2017d) suspected that several species remain undescribed which they estimated would raise the species count to at least 18, including one identified therein as *N.* aff. *bankieri*. These fishes are often called demoiselles, a common name shared with species in other genera, mainly *Chrysiptera* spp. (Allen, 1991). All species of *Neopomacentrus* share an elongate, gracile body shape (body depth 2.2–2.8 in SL) with a forked or lunate caudal fin, filamentous caudal-fin lobes, soft dorsal and anal fins with filamentous extensions posteriorly, and incisiform teeth with notched or flattened tips (Allen, 1975a, 1991; Jenkins and Allen, 2002; Randall and Allen, 2005; Allen et al., 2017d). Their appearance is superficially similar to zooplanktivorous species in other genera, which tend to be small and fusiform with a highly protrusible mouth and forked caudal fin for continuous swimming in the water column (Davis and Birdsong, 1973; Emery, 1983). Species of *Neopomacentrus* often assemble in midwater feeding aggregations (Allen, 1975a). Two species, *N. aquadulcis* and *N. taeniurus*, are among the few pomacentrids known to enter or reside in freshwater and brackish habitats (Allen, 1975a, 1989; Jenkins and Allen, 2002). The genus is native to the Indo-West Pacific, but one species, *N. cyanomos*, has recently become established in the Atlantic (Gulf of Mexico) by hitchhiking on offshore petroleum platforms transported across ocean basins (González-Gándara and de la Cruz-Francisco, 2014; Robertson et al., 2016a, 2016b, 2018). A similar dispersal mechanism has been suggested as a possibility for the westward colonization of Brazilian waters by *Chromis limbata* (Anderson et al., 2017, 2020).

Because the condition of the preopercular margin (smooth vs. serrated) was the main character serving to distinguish between membership in the then-sprawling *Abudefduf* versus the equally sprawling *Pomacentrus* of the time, variation in that character among different species of *Neopomacentrus* led to their uncertain classification prior to the establishment of the genus (Allen, 1975a; Dor and Allen, 1977; Allen et al., 2017d). Since its description by Allen (1975a), the composition of the genus has remained stable even though species identifications have been challenging in some cases (Allen and Randall, 1981; Robertson et al., 2018), including for the presumed type species, *N. anabatoides* (Randall et al., 2005). Allen and Randall (1981) divided the genus into two groups based on the conditon of the suborbital (i.e., infraorbital) margin: exposed vs. hidden by scales. They recognized the species with an exposed suborbital margin as the " '*bankieri*' complex" (*anabatoides*, *bankieri*, *fallax* [= *taeniurus*], *filamentosus*, *fuliginosus*, *taeniurus*, *violascens*, and *xanthurus*). Subsequently, Allen et al. (2017d) considered *N. aktites* a part of this complex because of its exposed suborbital margin. *Neopomacentrus aquadulcis* was not designated as a member of the *bankieri* complex, but it was described as having a naked suborbital (Jenkins and Allen, 2002: 381). Within the

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bankieri complex, four species (*N. aktites*, *N. anabatoides*, *N. filamentosus*, and *N. taeniurus*) were further differentiated by dark outer margins (or markings) on both lobes of the caudal fin (Allen and Randall, 1981; Allen et al., 2017d). Our dataset included all currently described species except *N. anabatoides*.

Monophyly of *Neopomacentrus* was strongly supported (98% bootstrap), a result which concurs with most past studies (Quenouille et al., 2004; Hofmann et al., 2012; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019). We found support (100% bootstrap) for the previously hypothesized sister relationship of *N. aktites–N. filamentosus* (Allen et al., 2017d). However, the *bankieri* complex was not monophyletic. Instead, those species formed two separate clades: one with *N. aktites*, *N. aquadulcis*, *N. bankieri*, *N. filamentosus*, *N. taeniurus*, and *N. violascens*; the other with *N. fuliginosus* and *N. xanthurus*. The latter clade was more closely related to the remaining *Neopomancentrus*, though the branches in this part of the tree are weakly supported (<50% bootstrap). We examined three of the four putative species comprising the dark-tailed group (*N. aktites*, *N. filamentosus*, and *N. taeniurus*), and they were resolved together (99% bootstrap), which supports the existence of a subgroup within the *bankieri* complex distinguished by dark edges or tips on the caudal fin. However, DiBattista et al. (2016) resolved *N. anabatoides*, the fourth species, as the sister taxon of *N. bankieri*. Sequences for that species appear to be unavailable.

Pomacentrus.—The members of *Pomacentrus* are widely distributed across the tropical Indo-West Pacific, with the majority concentrated in the western and central Pacific (Allen and Randall, 2004b, 2005; Allen and Erdmann, 2009b; Allen et al., 2011, 2017b, 2018b). After the restructuring herein of *Chromis sensu lato* (108 species), which significantly reduced the size of *Chromis sensu stricto* (76 species), *Pomacentrus* is now the largest genus in the family (81 species; Fricke et al., 2020). Its high species diversity has been attributed to an increased rate of diversification (Cowman and Bellwood, 2011; Lobato et al., 2014). Of the 81 species currently recognized in the genus, 54 were examined for this study plus an additional undescribed species (*Pomacentrus* cf. *microspilus*). Monophyly of the genus *Pomacentrus* received strong branch support (100% bootstrap), which agrees with most prior studies (Jang-Liaw et al., 2002; Quenouille et al., 2004; Tang et al., 2004; Bernardi, 2011; Hubert et al., 2011; Hofmann et al., 2012; Litsios et al., 2012a; Rabosky et al., 2013, 2018; Lobato et al., 2014; Mirande, 2016; Gaboriau et al., 2018; Stieb et al., 2017; Delrieu-Trottin et al., 2019). Where there was disagreement, it mainly came from analyses that relied on Cooper et al. (2009) for data representing *Altrichthys curatus* (e.g., Cowman and Bellwood, 2011; Litsios et al., 2012b; Frédérich et al., 2013; DiBattista et al., 2016). As discussed above, there is convincing evidence that Cooper et al. (2009) did not infer a monophyletic *Pomacentrus* because their sequences for *Altrichthys* were erroneous (Bernardi, 2011). Aside from that anomalous result and the misidentified "*Pomacentrus agassizii*" (see above), there is robust support for the monophyly of *Pomacentrus*.

There are relatively few genus-group names currently in the synonymy of *Pomacentrus*. The type species of *Parapomacentrus* (*Pomacentrus polynema*) is currently considered a synonym of *Pomacentrus pavo*, the type species of *Pomacentrus*. *Pseudopomacentrus* was originally erected as a subgenus (type species: *P. littoralis*). Allen (1975a: 43) also established *Lepidopomacentrus* as a subgenus (type species: *P. lepidogenys*) and provided a key for the subgenera of *Pomacentrus* that he recognized (*Lepidopomacentrus*, *Pomacentrus*, and *Pseudopomacentrus*). An important character used to differentiate *Lepidopomacentrus* was the presence of scales on the preorbital and suborbital. However, other species with similar conditions (e.g., *P. littoralis*, *P. philippinus*) were referred to *Pseudopomacentrus* (Allen, 1975a). Subsequently, more species of *Pomacentrus* have been reported with such scales (e.g., *P. aquilus*, *P. arabicus*, *P. cuneatus*, *P. komodoensis*; Allen and Randall, 1981; Allen, 1991, 1999b). *Pomacentrus callainus* was originally considered a color variant of *P. lepidogenys* (Randall, 2002), and they are sister species in our phylogeny (Fig. 1), so it is not surprising they share scaled infraorbitals. Others with this feature are members of the *Pomacentrus philippinus* complex, for which it is diagnostic: *P. albiaxillaris*, *P. flavoaxillaris*, *P. magniseptus* (variable, usually absent), and *P. nigriradiatus* (Allen et al., 2017b). Therefore it would be expected that they also share that trait with the namesake of the complex. *Pomacentrus yoshii*, which Allen and Randall (2004b) regarded as closely related to *P. philippinus* but was not included in the *P. philippinus* complex (Allen et al., 2017b, 2017c), also possesses scales on the infraorbitals. Aside from a brief mention in Allen (2001), the subgeneric framework has gone unused in his subsequent works on *Pomacentrus* (e.g., Allen and Randall, 1981, 2004b, 2005; Allen, 1991, 1992, 1993, 1995, 1999b, 2002, 2004; Allen and Wright, 2003; Allen and Erdmann, 2009b; Allen et al., 2011, 2017b, 2017c, 2018b; Allen and Drew, 2012). The relationships seen in this study demonstrate that it would be difficult to make use of the existing subgenera without substantial revisions. Based on the location of *P. lepidogenys* relative to *P. littoralis* (type species of *Pseudopomacentrus*), recognition of *Lepidopomacentrus* and *Pseudopomacentrus* as subgenera *sensu* Allen (1975a) would leave several *Pomacentrus* clades not included in either. Placing *Lepidopomacentrus* in the synonymy of *Pseudopomacentrus*, thereby dividing *Pomacentrus* into two broad subgenera (*Pomacentrus* for *P. pavo* and its allies; *Pseudopomacentrus* for the bulk of *Pomacentrus*), would resolve that problem but *P. xanthosternus*, as the sister group of all other *Pomacentrus*, would still require a subgeneric name and there are no available genus-group names based on that species (Fricke et al., 2020).

There are three distinct lineages within *Pomacentrus*. As stated above, *P. xanthosternus* is the sister species of all other *Pomacentrus* examined. *Pomacentrus xanthosternus* has not been the subject of much study but, in its original description, Allen (1991: 233) remarked that the species is "[c]learly separable from other *Pomacentrus* by the combination of colour pattern, a relatively low (16) lateral-line count and 23–24 gill rakers." The remaining species are divided into two groups. The first includes the type species, *P. pavo*, and its allies. These fishes, except for *P. caeruleopunctatus* (Allen, 2002), are generally more elongate than other *Pomacentrus* (body depth usually $\geq$ 2.3 in SL; Allen, 1991; Liu et al., 2013). Allen (1975a: 202) noted that brightly colored, elongate species (e.g., *P. coelestis*, *P. pavo*) are midwater zooplankton specialists, in contrast to other *Pomacentrus* spp., which are generalist omnivores. Species of this group exhibit a similar body form as other midwater damselfishes that forage in the water column (e.g., *Neopomacentrus*, *Pomachromis*), where

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they capture individual prey items via plankton picking (Allen and Emery, 1973; Davis and Birdsong, 1973; Emery, 1983). Hubert et al. (2012: table S3) detected possible cryptic diversity in *P. pavo*, which they characterized as geographic monophyly with deep divergence (their "Pattern 2") between individuals of *P. pavo* from French Polynesia compared to those from Madagascar. Hubert et al. (2017: fig. 3, tables S3, S4) showed similar results, finding reciprocal monophyly between lineages from the Indian and Pacific Oceans (their "Pattern II.1"). Allen (1991) reported coloration differences between the two populations, where "[w]estern Indian Ocean specimens frequently have pronounced black margins on the dorsal and anal fins." Allen and Randall (2004b) noted that it has the widest range of any *Pomacentrus*, extending from the western Indian Ocean (east Africa) to the central Pacific (Tuamotu Islands), in a genus whose species are otherwise more geographically restricted and seemingly widespread species are often complexes of cryptic species (Allen et al., 2017b). As the type species of *Pomacentrus*, any changes to its species limits could have nomenclatural implications. In such a scenario, the Indo-Australian lineage (type locality: East Indies; Bloch, 1787) would retain the name *P. pavo*. No apparent available names exist for the western Indian Ocean population, if it does indeed represent hidden diversity. Of the names in the synonymy of *P. pavo* (Allen, 1991; Fricke et al., 2020), all appear to originate from regions outside of the western Indian Ocean.

The clade with *P. pavo* can be further subdivided into two lineages: *P. pavo* plus its sister species, *P. leptus*, in one and the neon damsels in the other. The latter group has been called different names by various authors: "blue damsel" complex (Allen, 1991: 232), *P. coelestis* complex (Liu et al., 2013), *Pomacentrus coelestis* species complex (Sorenson et al., 2014), *Pomacentrus coelestis* complex (Getlekha et al., 2018). This set of species currently comprises *P. alleni*, *P. auriventris*, *P. caeruleopunctatus*, *P. caeruleus*, *P. coelestis*, *P. micronesicus*, and *P. similis*. They are slender planktivores with brilliant blue coloration, sometimes accompanied by varying amounts of bright yellow markings. Their similarities have been discussed before (e.g., Allen, 1991, 2002; Myers, 1999; Liu et al., 2012, 2013; Sorenson et al., 2014). Getlekha et al. (2018) found that members of this clade displayed the conserved karyotype (2n = 48; NF = 48) compared to other *Pomacentrus*, which usually have much higher fundamental numbers ($\geq$76; Ojima, 1983; Klinkhardt et al., 1995; Molina and Galetti, 2004b; Arai, 2011). They proposed a potential synapomorphy for this group: "organization of ribosomal genes in a syntenic, but non-colocalized array" on the long arm of chromosome 5. Although their sampling was limited to only two species (*P. auriventris* and *P. similis*), both clades seen in Sorenson et al. (2014) were represented, one from each ocean basin. Our data matrix included all species except *P. caeruleopunctatus*, for the reasons discussed below. The phylogenetic relationships we recovered within this complex are compatible with those previously reported (Liu et al., 2013: fig. 4; Sorenson et al., 2014: fig. 2). The species fall into two geographically discrete clades: one inhabiting the Indian Ocean (*P. alleni*, *P. caeruleus*, and *P. similis*) and the other inhabiting the Pacific Ocean (*P. auriventris*, *P. coelestis*, and *P. micronesicus*). In the Indian Ocean clade, *P. similis* is sister to *P. alleni* + *P. caeruleus*; in the Pacific clade, *P. micronesicus* is sister to *P. auriventris* + *P. coelestis*. With denser intraspecific sampling, Sorenson et al. (2014) found possible cryptic diversity in *P. micronesicus* (corroborating Liu et al., 2012), *P. auriventris* nested within *P. coelestis*, and *P. caeruleopunctatus* nested within *P. caeruleus*. The last result caused Sorenson et al. (2014) to raise questions about whether *P. caeruleopunctatus* is distinct from *P. caeruleus*. However, that outcome was likely due to an identification error because the voucher specimen of the only *P. caeruleopunctatus* in their phylogeny (Sorenson et al., 2014: fig. 2; "cap_mad77347") appears to have been misidentified at the time of their study. Upon further examination, the fishes in SAIAB 77347 (KU T6913), originally labeled as *P. caeruleopunctatus*, have all been reidentified as *P. caeruleus* because they display only one horizontally elongate mark on the scales of the posterior body (O. Gon, pers. comm.). That character differentiates *P. caeruleus* from *P. caeruleopunctatus*, which usually has 2–3 such marks on each scale (Allen, 2002). This affects the following GenBank records: JQ707052, JQ707087, JQ707119, JQ707154, JQ707181, JQ707209, JQ707245, JQ707280 (Frédérich et al., 2013: table S1), KM198744, KM198842 (Sorenson et al., 2014: 2505). The only novel record presently available on BOLD (UKFBJ948-08) also originated from SAIAB 77347. The lone sequence attributed to this species that is not derived from SAIAB 77347 was also published in Sorenson et al. (2014). They sequenced cyt *b* (KM198771) from a different specimen (SAIAB 80854) that did not appear in their phylogeny. That fish has also been reidentified as *P. caeruleus* for the same diagnostic reasons given above (O. Gon, pers. comm.). As a result, there are no confirmed sequences of *P. caeruleopunctatus* currently available. Its relationships and status remain unresolved.

The remainder of *Pomacentrus* falls into a single large clade. Its basal group is composed of western Indian Ocean species that primarily have XIV dorsal-fin spines. Species of *Pomacentrus* typically display XIII spines (Allen, 1991; Allen and Wright, 2003). There are 21 species that possess a modal count of XIV dorsal spines: *P. aquilus*, *P. arabicus*, *P. armillatus*, *P. atriaxillaris*, *P. australis*, *P. baenschi*, *P. bangladeshius*, *P. bellipictus*, *P. fakfakensis*, *P. indicus*, *P. milleri*, *P. opisthostigma*, *P. pikei*, *P. polyspinus*, *P. proteus*, *P. reidi*, *P. rodriguesensis*, *P. stigma*, *P. sulfureus*, *P. trichrourus*, and *P. vatosoa* (Allen, 1991, 1993, 2002; Allen and Wright, 2003; Allen and Erdmann, 2009b; Allen et al., 2018b; Frable and Tea, 2019; Habib et al., 2020). Allen and Wright (2003) observed that species with XIV dorsal spines are concentrated in the Indian Ocean, particularly in the western Indian Ocean, where almost half of them are found (*P. aquilus*, *P. arabicus*, *P. atriaxillaris*, *P. baenschi*, *P. indicus*, *P. pikei*, *P. rodriguesensis*, *P. sulfureus*, *P. trichrourus*, and *P. vatosoa*; Allen, 1991, 1993, 2002; Allen and Wright, 2003; Frable and Tea, 2019). They speculated that "many of these species, particularly from the western Indian Ocean, appear to be closely related on the basis of general morphology." The five XIV-spined species from the western Indian Ocean included in our phylogeny (*P. aquilus*, *P. baenschi*, *P. sulfureus*, *P. trichrourus*, and *P. vatosoa*) did form a monophyletic group that also included two XIII-spined species, *P. albicaudatus*, which is endemic to the Red Sea, and *P. trilineatus*, which also occurs in the western Indian Ocean. Despite having fewer dorsal spines, *P. trilineatus* has been associated with *P. baenschi* (Allen, 1991: 226), which we found as its sister species. Frable and Tea (2019) resolved a similar clade consisting of *P. baenschi*, *P. trichrourus*, *P. trilineatus*, and *P. vatosoa*; they did not examine *P. albicaudatus* or *P. aquilus* and recovered *P. sulfureus* apart from the

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others. Improved taxon sampling will be necessary to ascertain if all *Pomacentrus* with XIV spines from the region are closely related. GenBank sequences reported as *Pomacentrus arabicus* from Madagascar by Hubert et al. (2011) were not included; they appear extralimital because that species is endemic to the Gulf of Oman (Allen, 1991; Randall, 1995; Fricke et al., 2018). Those sequences of "*P. arabicus*" were identified as *P. trilineatus* by the BOLD Identification Engine and GenBank BLAST. This applies to the following GenBank records: JF435099, JF457583, JF458212. True *P. arabicus* is probably closely related to *P. aquilus* on the basis of their shared dark coloration, western Indian Ocean distribution, and possession of XIV dorsal spines (Allen, 1991: 223).

The genus contains several species of territorial herbivores that cultivate algal mats (i.e., gardeners). Information on dietary habits is incomplete but they include at least *P. adelus*, *P. aquilus*, *P. bankanensis*, *P. burroughi*, *P. chrysurus*, *P. grammorhynchus*, *P. tripunctatus*, *P. vaiuli*, and *P. wardi* (Ceccarelli, 2007; Hoey and Bellwood, 2010; Frédérich et al., 2013: fig. 3; Hata and Ceccarelli, 2016; Pratchett et al., 2016). Allen (1975a, 1997) observed that herbivorous species (e.g., *P. burroughi*, *P. wardi*) tend to be drab, whereas planktivorous species (e.g., *P. alexanderae*, *P. popei*) tend to be colorful. One clade in particular contains a cluster of several algal farmers: *P. bankanensis*, *P. burroughi*, *P. grammorhynchus*, *P. vaiuli*, and *P. wardi*. However, other such species with similar diets are dispersed across the genus.

Recently, Allen et al. (2017b, 2017c) circumscribed a "*Pomacentrus philippinus* complex." In addition to its namesake species, the species group also includes *P. albiaxillaris*, *P. flavioculus*, *P. flavoaxillaris*, *P. imitator*, *P. magniseptus*, and *P. nigriradiatus*. They share several characteristic features: pale caudal fins (clear, orange, whitish, or yellow) with matching coloration for the posterior sections of the anal and soft dorsal fins; absence of dorsal-fin ocellus in juveniles; short filamentous extensions of the caudal-fin lobes; presence of infraorbital scales (usually absent in *P. flavioculus* and *P. imitator*); network pattern formed by dark scale margins; and prominent black spot at pectoral-fin base (Allen et al., 2017b, 2017c). Allen et al. (2017c) found that *P. imitator* and *P. magniseptus* share mtDNA sequences, but commented that they are easily separated because of their allopatric distributions and diagnostic differences in coloration. However, our results did not show a monophyletic *philippinus* complex, with *P. flavioculus* apart from the rest of the species complex, which is monophyletic. The COI sequences of *Pomacentrus philippinus* (KY463238, KY463239, KY463240) from Allen et al. (2017b) are more similar to *Chromis* than *Pomacentrus*, showing greater than 99% identity with published *C. alpha* (JF434867) and *C. degruyi* (EU358588) data in BLAST and BOLD searches. However, the 16S sequences (MF828512, MF828513, MF828514) from Allen et al. (2017c) are most similar to other species from the *Pomacentrus philippinus* complex. The cause of this discrepancy is unclear. Although voucher information is not available, the corresponding loci appear to have been collected from the same samples, based on GenBank record information. The specimens were collected at Palawan, Philippines (Allen et al., 2017b: fig. 17; 2017c: fig. 5). We only analyzed 16S (MF828512) for the representative of *P. philippinus* in our phylogeny (Fig. 1; Supplemental Table 1; see Data Accessibility).

Outside of the various family-wide phylogenies, there have been few studies focused on relationships within *Pomacentrus* (Liu et al., 2013; Sorenson et al., 2014; Allen et al., 2017b, 2017c; Frable and Tea, 2019; Habib et al., 2020). Many of the relationships inferred in our phylogeny corroborated earlier hypotheses. We resolved a sister-group relationship between *P. alexanderae* and *P. nigromanus* that was suggested by Allen (1991). We recovered a clade with 100% bootstrap support that included *P. amboinensis*, *P. maafu*, and *P. moluccensis* (Randall et al., 1997; Allen and Drew, 2012). Cooper et al. (2009) recovered *P. albicaudatus* sister to an equivalent group (*P. amboinensis* + *P. moluccensis*), but their specimen (FMNH 126547) was collected in the Philippines, which is well outside its native range as a Red Sea endemic (Allen and Randall, 1981; Allen, 1991; DiBattista et al., 2016; Golani and Fricke, 2018; Atta et al., 2019). This affects the following GenBank records: FJ616364, FJ616472, FJ616578, FJ616690, FJ616803, FJ616911. Our analysis resolved a specimen identified as *P. albicaudatus* from the Red Sea (MN560894; Atta et al., 2019) as sister to *P. sulfureus* and part of a western Indian Ocean clade whose members predominantly have XIV dorsal spines (see above). We recovered a clade that includes *P. armillatus*, *P. bankanensis*, and *P. vaiuli*, which have been linked in previous works (Allen, 1993; Randall et al., 1997; Myers, 1999; Randall, 2005). The *P. aurifrons*–*P. smithi* sister pairing (100% bootstrap) has also been posited in the literature before (Allen, 2004; Randall, 2005; Allen and Erdmann, 2012).

***Pristotis* and *Teixeirichthys*.**—Both genera contain elongate zooplanktivores (Allen, 1975a; Allen and Randall, 1981). *Pristotis* includes two recognized species (*P. cyanostigma* and *P. obtusirostris*) and *Teixeirichthys* is monotypic (*T. jordani*). They prefer sandy bottoms and seagrass meadows (Allen, 1975a; Allen and Randall, 1981; Allen, 1991; Randall et al., 1997; Khalaf et al., 2006), much like the species of *Amblypomacentrus sensu lato*. Earlier authors have noted that these two genera, or species now classified in these genera, are closely related (e.g., Rutter, 1897; Smith, 1960; Tyler, 1966; Allen, 1975a: 38; Kawashima and Moyer, 1982). In the description of *Pomacentrus jordani* [= *T. jordani*], Rutter (1897) stated that it was most closely related to *Pomacentrus jerdoni* [= *Pristotis obtusirostris*]. Smith (1960: 321) treated *T. mossambicus* [= *T. jordani*] as a junior synonym of *T. obtusirostris* [= *Pristotis obtusirostris*]. Tyler (1966) treated *obtusirostris* as a species of *Teixeirichthys*. Species of both genera are unique among pomacentrids in possessing a single supraneural (formerly predorsal; Mabee, 1988), versus two or more in the rest of the family (Emery, 1980: 235; Emery and Allen, 1980). Kawashima and Moyer (1982) stated that *Pristotis* and *Teixeirichthys* "are very similar in external and internal characters," differing mainly in squamation. They observed that the species of both genera share a midwater habitat preference atypical of most other pomacentrids, in that they are captured in trawls (Montalban, 1928; Yamakawa, 1966). Both genera lack the ceratomandibular ligament, whereas all other pomacentrines with available data were reported to possess the ligament (Frédérich et al., 2014). DiBattista et al. (2016) was the first study to examine all three species and found *Teixeirichthys* sister to a monophyletic *Pristotis*. Recent phylogenetic analyses have consistently recorded *Pristotis* and *Teixeirichthys* as sister taxa (Cooper et al., 2009; Cowman and Bellwood, 2011; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Delrieu-Trottin et al.,

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2019). Our phylogeny agrees and shows strong support (100% bootstrap) for the two genera forming a clade, which is the sister taxon of *Neopomacentrus*.

Sister-Group Relationship

Our results corroborate other studies that have shown the Pomacentridae as members of Ovalentaria (e.g., Wainwright et al., 2012; Near et al., 2013; Betancur-R. et al., 2013a, 2015, 2017; Friedman et al., 2013; Rabosky et al., 2013, 2018; Collins et al., 2015; Cortesi et al., 2015; Mirande, 2016; Sanciangco et al., 2016; Alfaro et al., 2018; Hughes et al., 2018). Our phylogeny resolved the family within Ovalentaria (Fig. 1; Supplemental Fig. 1; see Data Accessibility), which was represented by the following taxa: Atherinomorpha (Adrianichthyidae, Atherinopsidae, Bedotiidae, Cyprinodontidae, Fundulidae, Melanotaeniidae, Nothobranchiidae, Poeciliidae, Rivulidae, and Scomberesocidae), Ambassidae, Blenniidae, Chaenopsidae, Cichlidae, Congrogadidae, Embiotocidae, Gobiesocidae, Grammatidae, Labrisomidae, Mugilidae, Opistognathidae, Pholidichthyidae, Plesiopidae, Polycentridae, and Pseudochromidae. Among those taxa, we recovered the surfperches (Embiotocidae) as the sister group of the damselfishes (100% bootstrap; Fig. 1), which concurs with previous workers (e.g., Streelman and Karl, 1997; Sparks and Smith, 2004; Westneat and Alfaro, 2005; McMahan et al., 2013). The exclusion of Pholidichthyidae from our Ovalentaria was surprising, because that placement disagrees with recent phylogenies (e.g., Wainwright et al., 2012; Betancur-R. et al., 2013a, 2015, 2017; Rabosky et al., 2018). However, studies that have included mitochondrial ribosomal loci (12S and/or 16S) for *Pholidichthys*, as we did herein, have sometimes produced unexpected relationships for this enigmatic taxon (e.g., Smith and Wheeler, 2006; Betancur-R. et al., 2013b). This study does not solve the chaos surrounding the intrarelationships within Ovalentaria. Ours is one hypothesis for a section of the percomorph phylogeny with no shortage of alternatives (Eytan et al., 2015). Much more work concerning the identity of the damselfish sister group is needed.

Unresolved Issues

Aside from the identity of the sister group, there are several outstanding issues in the systematics of Pomacentridae. Perhaps the biggest concern involves "*Chrysiptera*," specifically the many species that are not closely related to *Chrysiptera sensu stricto*. Allen and colleagues (Allen and Erdmann, 2008b; Allen et al., 2010b) mentioned collecting preliminary data that point to the polyphyly of "*Chrysiptera*." Our results, in conjunction with earlier studies (e.g., Quenouille et al., 2004; Cooper et al., 2009; Cowman and Bellwood, 2011; Hubert et al., 2011, 2012, 2017; Hofmann et al., 2012; Litsios et al., 2012a, 2012b; Frédérich et al., 2013; Rabosky et al., 2013, 2018; Lobato et al., 2014; DiBattista et al., 2016; Mirande, 2016; Gaboriau et al., 2018; Delrieu-Trottin et al., 2019), provide compelling evidence that there are groups of "*Chrysiptera*" that are not closely related to *Chrysiptera sensu stricto* and therefore require names: "*Chrysiptera*" *flavipinnis* plus the herbivorous and Oceanic clades. Their dispersed phylogenetic positions within the tribe Cheiloprionini and the lack of available genus-group names defy easy taxonomic resolution. Determining the limits of the different constituent clades and establishing genus-group names in a revised classification will require extensive further study.

Elsewhere in Pomacentridae, although the composition and monophyly of the four subfamilies are well established, the interrelationships among the subfamilies are still unsettled, specifically the relative positions of Chrominae and Glyphisodontinae, which have vacillated in different studies. The relationships and generic limits within Chrominae have several areas of uncertainty: the provisional generic assignments of the numerous species not examined herein; the relationship of *Chromis* (*Hoplochromis*) relative to other members of the subfamily, as some studies have inferred that it is not most closely related to *Chromis sensu stricto*; the placement of *A. brevirostris*, which has been highly variable from study to study. Within Microspathodontinae, further investigation is needed for *Plectroglyphidodon sensu lato*, which we have expanded to include a subset of former species of "*Stegastes*" from the Indo-West Pacific (generally, those with XIII or more dorsal spines, with a few exceptions). Within Pomacentrinae, the composition of the tribe Pomacentrini shown herein conflicts with some previous hypotheses, which have found a subset of pomacentrin genera to be more closely related to the tribe Amphiprionini.

At the species level, certain species need further investigation because there is uncertainty about their status. In some cases, there may be unrecognized cryptic diversity (e.g., *Abudefduf taurus*, *A. vaigiensis*, *Chrysiptera cyanea*, *Dascyllus reticulatus*, *Lepidozygus tapeinosoma*, *Plectroglyphidodon johnstonianus*, *Pomacentrus pavo*, *Stegastes lacrymatus*, *S. nigricans*); in others, there is doubt as to their validity (e.g., *Amphiprion leucokranos*, *D. albisella*, *D. flavicaudus*). An unambiguous determination of the identity of true *A. vaigiensis* will be necessary before recognition of separate "*vaigiensis*" lineages can proceed. The species status of *Amphiprion leucokranos* and *A. thiellei* will require a better understanding of their life histories to determine if they are self-sustaining lineages or the products of rare hybridization events, and to confirm if they are the result of hybridization between the same parent species (*A. chrysopterus* x *A. sandaracinos*).

Conclusions

Based on the phylogenetic relationships recovered herein (Fig. 1; Supplemental Fig. 1; see Data Accessibility), the family Pomacentridae is divided into four subfamilies: Chrominae, Glyphisodontinae, Microspathodontinae, and Pomacentrinae (Table 3). The subfamily Lepidozyginae is placed in the synonymy of Microspathodontinae. The subfamily Microspathodontinae is sister to all other pomacentrids and includes nine genera: *Hypsypops*, *Lepidozygus*, *Mecaenichthys*, *Microspathodon*, *Nexilosus*, *Parma*, *Plectroglyphidodon sensu novum*, *Similiparma*, and *Stegastes sensu stricto*. The subfamily Glyphisodontinae is sister to Chrominae + Pomacentrinae and includes a single genus: *Abudefduf*. The subfamily Chrominae includes four genera: *Azurina sensu novum*, *Chromis sensu stricto*, *Dascyllus*, and *Pycnochromis sensu novum*. *Pycnochromis* is resurrected and removed from the synonymy of *Chromis*. The subfamily Pomacentrinae is subdivided into four tribes: Amphiprionini, Cheiloprionini, Hemiglyphidodontini, and Pomacentrini. The tribe Amphiprionini includes a single genus: *Amphiprion*. *Premnas* is placed in the synonymy of *Amphiprion*. The tribe Cheilo-

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Table 3. Revised classification of the family Pomacentridae.

Family Pomacentridae Bonaparte, 1831
- Subfamily Microspathodontinae Jordan and Evermann, 1898
  - *Hypsypops*
  - *Lepidozygus*
  - *Mecaenichthys*
  - *Microspathodon*
  - *Nexilosus*
  - *Parma*
  - *Plectroglyphidodon*
  - *Similiparma*
  - *Stegastes*
- Subfamily Glyphisodontinae Rafinesque, 1815
  - *Abudefduf*
- Subfamily Chrominae Bonaparte, 1831
  - *Azurina*
  - *Chromis*
  - *Dascyllus*
  - *Pycnochromis*
- Subfamily Pomacentrinae Bonaparte, 1831
  - Tribe Amphiprionini Gill, 1859
    - *Amphiprion*
  - Tribe Cheiloprionini Whitley, 1929
    - *Cheiloprion*
    - *Chrysiptera sensu stricto*
    - *"Chrysiptera"*
    - *Dischistodus*
    - *Pomachromis*
  - Tribe Hemiglyphidodontini Whitley, 1929
    - *Acanthochromis*
    - *Altrichthys*
    - *Amblyglyphidodon*
    - *Hemiglyphidodon*
    - *Neoglyphidodon*
  - Tribe Pomacentrini Bonaparte, 1831
    - *Amblypomacentrus*
    - *Neopomacentrus*
    - *Pomacentrus*
    - *Pristotis*
    - *Teixeirichthys*

prionini includes four genera: *Cheiloprion*, *Chrysiptera sensu stricto*, *Dischistodus*, and *Pomachromis*. It also contains "*Chrysiptera*" unaffiliated with *Chrysiptera sensu stricto* and lacking available genus-group names: "*Chrysiptera*" *flavipinnis*, the herbivorous "*Chrysiptera*" (*C. brownriggii* and its allies), and the Oceanic "*Chrysiptera*" (*C. rapanui* and its allies). The tribe Hemiglyphidodontini includes five genera: *Acanthochromis*, *Altrichthys*, *Amblyglyphidodon*, *Hemiglyphidodon*, and *Neoglyphidodon*. The tribe Pomacentrini includes five genera: *Amblypomacentrus sensu novum*, *Neopomacentrus*, *Pomacentrus*, *Pristotis*, and *Teixeirichthys*. We recognize 29 genera in the family with the understanding that there are currently unnamed "*Chrysiptera*" lineages that will likely require new genus-group names.

NOTE ADDED IN PROOF

After this paper went to press, a relevant preprint was posted on bioRxiv on 8 February 2021 (McCord et al., 2021: bioRxiv 2021.02.07.430149). That study includes a phylogeny of Pomacentridae, with additional focus on the evolution of body size and feeding ecology in the family. Because of the timing, their results could not be addressed in this paper. The tree shown therein is based on molecular data (mitochondrial: 12S, 16S, ATPase 8/6, COI, cyt *b*, D-loop, ND3; nuclear: BMP4, DLX2, RAG1, RAG2, Tmo-4C4) and has some overlap with the one presented in this study. There are areas where our results are congruent with theirs and others where they are not. The most notable difference was that they recovered Glyphisodontinae as the sister group of Pomacentrinae. The relationships they recovered within Pomacentrinae also differ in some key ways: *Amblypomacentrus sensu novum* is sister to *Pomacentrus*; *Neopomacentrus* + (*Pristotis* + *Teixeirichthys*) is sister to *Amphiprion*. Another difference is that they resolved a clade similar to our *Chromis* (*Hoplochromis*) as the sister group to the rest of Chrominae, rendering *Chromis sensu stricto* non-monophyletic. Other areas of disagreement are mostly minor differences in the placement of individual species and/or small clades. The similarities are more numerous and range from higher-level relationships down to the species level. The most notable similarity, where their phylogeny agrees with ours, is the position of *Lepidozygus*, which they also found as the sister group of *Stegastes sensu stricto*, within Microspathodontinae; this placement differs significantly from their previous publications (e.g., Cooper et al., 2009; Cooper and Santini, 2016). Because of its status as a preprint draft, we are hesitant to make detailed comparisons to their results and conclusions because those are subject to change prior to publication.

DATA ACCESSIBILITY

Supplemental material is available at https://www.ichthyologyandherpetology.org/i2020105. Unless otherwise indicated in the 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 in accordance with the Creative Commons Attribution CC BY License.

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