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## **A global revision of the Seahorses *Hippocampus* Rafinesque 1810 (Actinopterygii: Syngnathiformes): Taxonomy and biogeography with recommendations for further research**

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## Abstract

Nomenclatural clarity is vital for the collection, dissemination, and retrieval of natural history information, which itself is necessary for effective conservation and management of species. Seahorses (genus *Hippocampus*) are small marine fishes that in many cases are heavily exploited and suffering severe population declines worldwide, leading to conservation concern and action. Here we provide a brief history of seahorse taxonomy, and attempt to clarify seahorse nomenclature by reducing redundancy and exposing areas of disagreement in need of further study. We provide an annotated list of the 41 species we currently recognize as valid, and describe their geographical distributions to offer a solid foundation for future research and conservation efforts. We base our conclusions on available morphological, genetic and distributional data, re-examination of the relevant literature, previous examination of almost all original type specimens, familiarity with many thousands of other live and dead specimens, and photographs of seahorses. This work should lead to greater taxonomic clarity by highlighting known research gaps and by ensuring that each species designation is justified by robust and defensible taxonomic protocols. Such clarity should facilitate greater efficacy in management and conservation.

**Key words:** Nomenclature, species distribution, species range, marine fish, Syngnathidae, CITES, Catalogue of Fishes, IUCN Red List of Threatened Species, conservation, FishBase

## Introduction

Seahorses, all members of the genus *Hippocampus* Rafinesque 1810, are a unique group of fishes of conservation concern that can be challenging to distinguish at a species level. All seahorses have an unusual life history and live in some of the most vulnerable inshore marine habitats, most are captured through direct and indirect fisheries, and many are of conservation concern—listed as threatened on global and/or national red lists (as reviewed in Vincent *et al.* 2011). Although these are among the more distinctive genera of teleostean fishes, at the species level there has been considerable confusion in their taxonomy. Many species are superficially similar, yet body proportions vary due to sex and age (Lourie *et al.* 1999; Foster & Vincent 2004; Leysen *et al.* 2011; Roos *et al.* 2011; Anderson 2012). Males typically have longer tails and shorter trunks compared to females, and compared to adults of the same species, juveniles have larger heads relative to their bodies, are slimmer in form, have more pronounced body spines, and have relatively higher coronets (Lourie *et al.* 1999; Roos *et al.* 2011). Individuals also demonstrate considerable phenotypic plasticity through changes in colour, the ability to grow and lose dermal appendages (fronds), and to develop spines to different degrees (Curtis 2006; Kuitert 2009). Together these traits lead to challenges in seahorse species identification, causing problems in information gathering, storage and retrieval, and hampering communication about basic biological research, legislation, management and conservation (Mace 2004; Zachos 2013).

Seahorses are members of the family Syngnathidae, which also includes pipefishes, pipehorses, seadragons and pygmy pipehorses (Mobley *et al.* 2011; Wilson & Orr 2011). The family is united by their tube-like snouts, bony scutes in place of scales, reduced number of fins, and male brooding of the eggs (and developing embryos in some cases) (Wilson *et al.* 2003; Foster & Vincent 2004). Seahorses are the only genus of syngnathid to brood their eggs within a fully enclosed pouch. The female deposits eggs into the male's brood pouch, where he fertilises them, protects them, nourishes them, and regulates their environment. Foster & Vincent (2004) provide a comprehensive review of seahorse biology and ecology.

Conservation of seahorse populations is important for ecological, biological, economic, and medicinal reasons, as well as for their intrinsic value (Vincent *et al.* 2011). Their unique life history provides us with a significant opportunity to expand our understanding of reproductive ecology in animals (Masonjones & Lewis 2000; Jones & Avise 2001; Wilson *et al.* 2003; Stölting & Wilson 2007); they are important predators on planktonic and benthic crustaceans such as copepods, amphipods, and mysids (Kendrick & Hyndes 2005; Felício *et al.* 2006; Garcia *et al.* 2012); subsistence fishers in some nations make a substantial portion of their annual income catching seahorses (Yasué *et al.* 2015; Pajaro & Vincent 2016); and many forms of traditional medicine employ seahorses to treat a range of conditions and ailments (Kumaravel *et al.* 2012; Chen *et al.* 2015). Moreover, seahorses are charismatic symbols of their seagrass, mangrove, coral reef, estuarine and seaweed habitats (Simberloff 1998; Shokri *et al.* 2009; Scales 2010). A suite of conservation tools is being

applied in support of seahorse populations worldwide. For one example, all seahorse species are listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)—the consequence being that the 182 member countries must restrict international trade in seahorses to sustainable levels and legally sourced animals (Vincent *et al.* 2014). As another example, iSeahorse is a citizen science website and smartphone app that allows anyone (e.g. divers, snorkelers, fishers, beachcombers), anywhere in the world to contribute to seahorse science and conservation by sharing their wild seahorse sightings and population monitoring data (iSeahorse 2016). See Vincent *et al.* (2011) for a thorough review of seahorse conservation and management.

As with all taxa, efforts to advance the conservation of seahorses are highly dependent on being able to identify individual species. This is particularly true in the CITES context, where agents for Scientific, Management and Enforcement Authorities are required to identify species rapidly and reliably, and in the iSeahorse context where divers and other citizen scientists are required to do the same. The challenge is particularly difficult for CITES Authorities who must identify significant volumes of multiple species of dried seahorses which can all look much the same, and are commonly exported as mixed species shipments (Foster & Vincent 2016). Assessments for the IUCN Red List or national equivalents are done at the species level, and assume accurate species identification in the publications from which relevant information is drawn. In general, population surveys and on-going monitoring are urgently required to accurately ascertain and effectively improve the conservation status of all seahorse species. But uncertainty in seahorse nomenclature means that collection, storage and subsequent retrieval of the data required for such conservation assessments is difficult.

In spite of the challenges in seahorse nomenclature, seahorses do have body plans that allow for species identification. Some seahorse species (such as *Hippocampus abdominalis* Lesson 1827 and *H. bargibanti* Whitley 1970) have characteristics that make them immediately identifiable. Others can be identified with a moderately trained eye. Seahorse fin-ray and tail-ring counts are believed to be constant through life, and may be the most reliable characters by which to identify juvenile as well as adult specimens (Lourie *et al.* 1999). Distinctive patterns of enlarged spines, the existence and form of certain facial and body spines, and coronet shape are also useful features for adult specimens. Other characteristics, such as snout length, extent of spines, stripes, spots or patterns are also valuable although these may be more variable among individuals (Lourie *et al.* 1999).

Molecular work has helped clarify phylogenetic relationships within the genus (Casey *et al.* 2004; Teske *et al.* 2004, 2005, 2007a; Lourie *et al.* 2005; Boehm *et al.* 2013; González *et al.* 2014; Silveira *et al.* 2014). Most studies to date have focused on mitochondrial DNA, such as the cytochrome oxidase I (COI) gene (but see Teske *et al.* 2004; Teske & Beheregaray 2009). Molecular work is a valuable tool for designating natural species boundaries in groups that exhibit subtle morphological differences (Knowlton 2000; Bickford *et al.* 2007), but genetic techniques have yet to become practical for on-the-ground research and conservation efforts. There have, however, been advances in the analysis of marine fish DNA for the purposes of field investigations into ornamental fish and seafood markets (Steinke *et al.* 2009; Clark 2015; Mariani *et al.* 2015), and substantial progress has been made to sequence the complete mitochondrial genome of all seahorse species (e.g. Chang *et al.* 2013; Zhang *et al.* 2015; Wang *et al.* 2016), indicating that the use of some molecular techniques by non-specialized practitioners may not be far off. In the meantime, most seahorses will be identified by their morphology.

In addition to the roles that morphology and genetics play in defining species boundaries, an understanding of biogeography is required for a full synopsis of the taxonomy of any genus. As is the case with other marine fish taxa, the divergence from common syngnathiform ancestors, and the subsequent speciation that characterizes *Hippocampus* as a genus, has resulted from millions of years of stochastic and selective evolutionary processes (Wilson & Orr 2011). This long process has been underlain by gradual shifts in plate tectonics and ocean currents, resulting in vicariant events in which populations have been continuously separated and rejoined to provide the conditions necessary for divergence and speciation to take place (Avisé 1992; Casey *et al.* 2004; Teske *et al.* 2007a; Boehm *et al.* 2013). It has also been noted that male pregnancy in seahorses and size-assortative mating has contributed to diversity in the genus by possibly predisposing taxa to sympatric speciation (Jones *et al.* 2003). We recognize that biological organisms lie along a continuum of evolutionary divergence, and that an objective species concept has long proved elusive and divisive in the field—even for relatively well-known taxa (Dobzhansky 1935; Simpson 1951; Mayr 1975; Wheeler & Meier

2000; Agapow *et al.* 2004; De Queiroz 2007; Waples 2008). With this in mind, a firm grasp of the biogeographic history that has led to the placement of seahorse populations into their current ecological niches is paramount to both nomenclature and species conservation (Awise 1992; Lourie & Vincent 2004b).

The goal of this revision is to use the best available morphological, genetic and geographic information to provide an authoritative and yet pragmatic account of all currently valid seahorse species. We aim to both shed light on and decrease taxonomic uncertainties within the genus so as to provide clarity for research, management and conservation. While we acknowledge that it is vital for each species to represent a monophyletic lineage, it is also critical that each species have diagnostic features (preferably morphological) that clearly separate it from other species. We have compiled all observable forms of character divergence, including morphology, genetics, and biogeography, in order to best describe and delineate species (e.g. Grady & Quattro 1999; Sites & Marshall 2004; Will & Rubinoff 2004; Padiál *et al.* 2010; Chen *et al.* 2011).

**A history of seahorse taxonomy.** Seahorses have been known since antiquity (Eastman 1915) and were described and illustrated long before Linnaeus gave them their first binomial name, *Syngnathus hippocampus*, in the 10<sup>th</sup> edition of his *Systema Naturae* (Linnaeus 1758). Linnaeus only recognized a single species of seahorse (as a type of pipefish), despite the fact he had two specimens in his own collection (SL *pers. obs.*; Wheeler 1985) which, it turns out, are actually members of two different species (Lourie *et al.* 1999). Rafinesque separated seahorses from pipefishes under the genus name *Hippocampus* Rafinesque 1810, although he didn't provide descriptions of the species he mentions (*H. hippocampus* (Linnaeus 1758), *H. heptagonus* Rafinesque 1810 and *H. tetragonus* Mitchill 1814). At around the same time, other authors started to recognise multiple species within the genus (e.g. Perry 1810; Leach 1814; Cuvier 1817).

By the late 1850s nearly 40 species had been described in the genus (Table 1), but already there were multiple names for the same species. For example the two European species, *H. guttulatus* Cuvier 1829 and *H. hippocampus*, had at least seven different binomial names. Johann Jakob Kaup examined over 2000 specimens of Lophobranchiate fishes (not just seahorses) from seven different European museums, and described a total of 18 species of seahorses (Kaup 1856). A few years later, Albert Günther catalogued the specimens in the British Museum and again came up with 18 species (Günther 1870), although these were not the same as those described by Kaup. Günther synonymized some of Kaup's species, and several new species had been described in the intervening years. Other regional accounts, e.g. Japan (Jordan & Snyder 1901) and Hawaii (Jordan & Evermann 1905), and many more new species were published, adding to the confusion.

Nearly forty years later Isaac Ginsburg wrote in his review of the American and European seahorses that 'there is an utter state of chaos in the literature in regard as to the use of names for some very common species of seahorses in various parts of the world' (Ginsburg 1937). He proceeded to present a detailed study of the literature and made some sense of earlier authors' nomenclature. He also provided his own counts and measurements for 279 specimens, including five new species: *H. europaeus* Ginsburg 1937 (now *H. hippocampus*), *H. hildebrandi* Ginsburg 1933 (now *H. ingens* Girard 1858), *H. obtusus* Ginsburg 1933 (now *H. reidi* Ginsburg 1933), *H. reidi*, and *H. regulus* Ginsburg 1933 (now *H. zosterae* Jordan & Gilbert 1882); a new subgenus (*Jamsus* Ginsburg 1933); and concluded that subspecies of the European *H. guttulatus* and North American *H. hudsonius* DeKay 1842 (now *H. erectus* Perry 1810) should be recognized, although his basis for these assertions are minor modal differences in counts and measurements that subsequent authors have not taken up (Ginsburg 1933, 1937; Vari 1982).

Richard Vari made another valiant effort at ordering the chaos for the Western Atlantic seahorse specimens, reducing the number of recognized species to three: *H. erectus*, *H. reidi* and *H. zosterae* (Vari 1982). Following on from Vari's work, the senior author of this revision (SL) undertook what turned into a genus-level revision in order to publish *Seahorses: an Identification Guide to the World's Species* (Lourie *et al.* 1999), basing her conclusions on examination of the pertinent literature, over 976 specimens from 22 different museums, and 67 of 71 original type specimens known to be in existence. Other regional revisions of the genus include eastern Pacific (Fritzsche 1980), Australia (Kuitert 2001), and New Caledonia (Fricke 2004), although many of the species contained therein are not supported by unambiguous defining features and so have not been included as valid species in this revision.

Recent interest in underwater photography has led to the discovery of many new pygmy seahorse species, only some of which we consider valid here (Lourie & Randall 2003; Lourie & Kuitert 2008; Gomon & Kuitert 2009). Photographs have also increased our understanding of the variation within species and across the genus

(e.g. Kuitert 2000, 2009; iSeahorse 2016; www.guylian.com/en/project-seahorse/gallery-photo-competition). As mentioned above, colour, dermal flaps and fronds, and even degree of spininess are not always reliable taxonomic characters by which to identify seahorse species. Many species show sexual dimorphism in colour (for example female *H. kuda* Bleeker 1852 are often yellow, and males are often black) while others have turned out to be colour variations of the same species (e.g. *H. pontohi* Lourie & Kuitert 2008—white—and what was described separately as *H. severnsi* Lourie & Kuitert 2008—dark brown; H. Hamilton, *in litt.* to SL and RP, 13 Feb 2015).

Genetic data also increasingly inform our understanding of seahorse species identities and phylogenetic and phylogeographic relationships, although much uncertainty remains (Casey *et al.* 2004; Teske *et al.* 2004; Saarman *et al.* 2010; BOLD 2016). For example, specimens originally identified as *H. erectus* from the Western Atlantic turned out to be paraphyletic with respect to *H. hippocampus* (Casey *et al.* 2004). Subsequently, Argentinian and some Brazilian specimens have been identified as a separate species, *H. patagonicus* Piacentino & Luzzatto 2004 (Piacentino & Luzzatto 2004; González *et al.* 2014; Silveira *et al.* 2014). The synonymization of *H. severnsi* under *H. pontohi* is also corroborated based on genetic data (H. Hamilton *in litt.* to SL and RP, 13 Feb 2015).

**TABLE 1.** Number of valid seahorse species (genus *Hippocampus*) recognized across time by various authors.

Author, Date	Number	Comments
Linnaeus 1758	1	Recognized seahorses as a type of pipefish
Kaup 1853	19	3 differences from Kaup 1856
Kaup 1856	18	Based on specimens from 7 different museums
Günther 1870	18	Based at BMNH (London); 10 differences from Kaup 1856
Duméril 1870	34	Based at MNHN (Paris)
Whitley & Allen 1958	61	Popular book; not based on examination of specimens
Lourie <i>et al.</i> 1999	32	Based on examination of types and > 976 specimens from 22 different museums
Lourie <i>et al.</i> 2004	33	Largely a reprint of Lourie <i>et al.</i> 1999, with addition of <i>H. denise</i> , and other additional specimens
Kuitert 2000	53	Photographic guide
Kuitert 2003	59	Revised edition of Kuitert (2000) photographic guide
Kuitert 2009	83	Revised edition of Kuitert (2000, 2003) photographic guides including Vasil'Eva's (2007) conclusion regarding <i>H. hippocampus</i> (see comment below)
Catalog of Fishes (Eschmeyer 2016)	71 + 2 uncertain	Online checklist; literature-based; many changes based on Kuitert 2009; recommends suppression of Vasil'Eva (2007) which switches the use of name <i>H. hippocampus</i> considered to be disruptive to seahorse nomenclature (although taken up by Kuitert (2009))
FishBase (Froese & Pauly 2016)	54	Online checklist and repository for biological information; basis for checklist originally Lourie <i>et al.</i> 1999; new species descriptions published since then added
BOLD 2016	29	BINs (Barcode Index Numbers) or operational taxonomic units based on clustering of 94 barcodes (648 base pairs (bp), cytochrome oxidase subunit 1 (CO1) gene sequences) from 28 species from the Project Seahorse / Redpath Museum collection
Current study	41	Based on type specimens, type descriptions, > 1500 specimens measured, an additional >500 looked at in less detail, hundreds of photographs, genetic data

Past confusions and disagreements about seahorse nomenclature continue today, with no consistency in valid species lists among standard taxonomic references for fish nomenclature. Over 140 species names exist in the literature (Eschmeyer & Fricke 2016), 22 of them having been described since the year 2000 alone (Horne 2001; Kuitert 2001, 2003; Lourie & Randall 2003; Fricke 2004; Piacentino & Luzzatto 2004; Lourie & Kuitert 2008;

Gomon & Kuitert 2009; Randall & Lourie 2009; Foster & Gomon 2010), and various conflicting synonymies have been proposed. Recent comprehensive treatments of the genus list between 32 and 83 species (Table 1), and the two standard references, Catalogue of Fishes (Eschmeyer & Fricke 2016) and FishBase (Froese & Pauly 2016), recognize 73 and 54 valid seahorse names, respectively (with the 54 FishBase-recognized species being entirely contained within the 73 species recognized by the Catalog of Fishes). The CITES checklist of species recognizes 51 seahorse species (UNEP-WCMC (Comps.) 2015), the IUCN Red List has assessments for 40 species (IUCN 2015), and iSeahorse lists 48 species (iSeahorse 2016). There is a clear need to work toward an agreed list for seahorse species.

The confusion surrounding seahorse taxonomy is not easily resolved. To some extent the differences result from different philosophies as to where to draw the line between species, and to some extent they are due to the realities of seahorse variability and lack of careful identification by researchers. The names *H. hirtix* Kaup 1856 and *H. kuda* have been particularly problematic, casually used for virtually any spiny seahorse (*H. hirtix*) and any smooth seahorse (*H. kuda*) from the Indo-Pacific. In the case of *H. hirtix*, the true species to which this name should be applied has clearly distinguishing features (although genetic evidence suggests that it may encompass more than one cryptic species). However there are many other spiny seahorses to which the name has frequently been misapplied. The members of the *H. kuda* complex show localised morphological (authors' *pers. obs.*) and genetic variation (Teske *et al.* 2005), but limited defining characters.

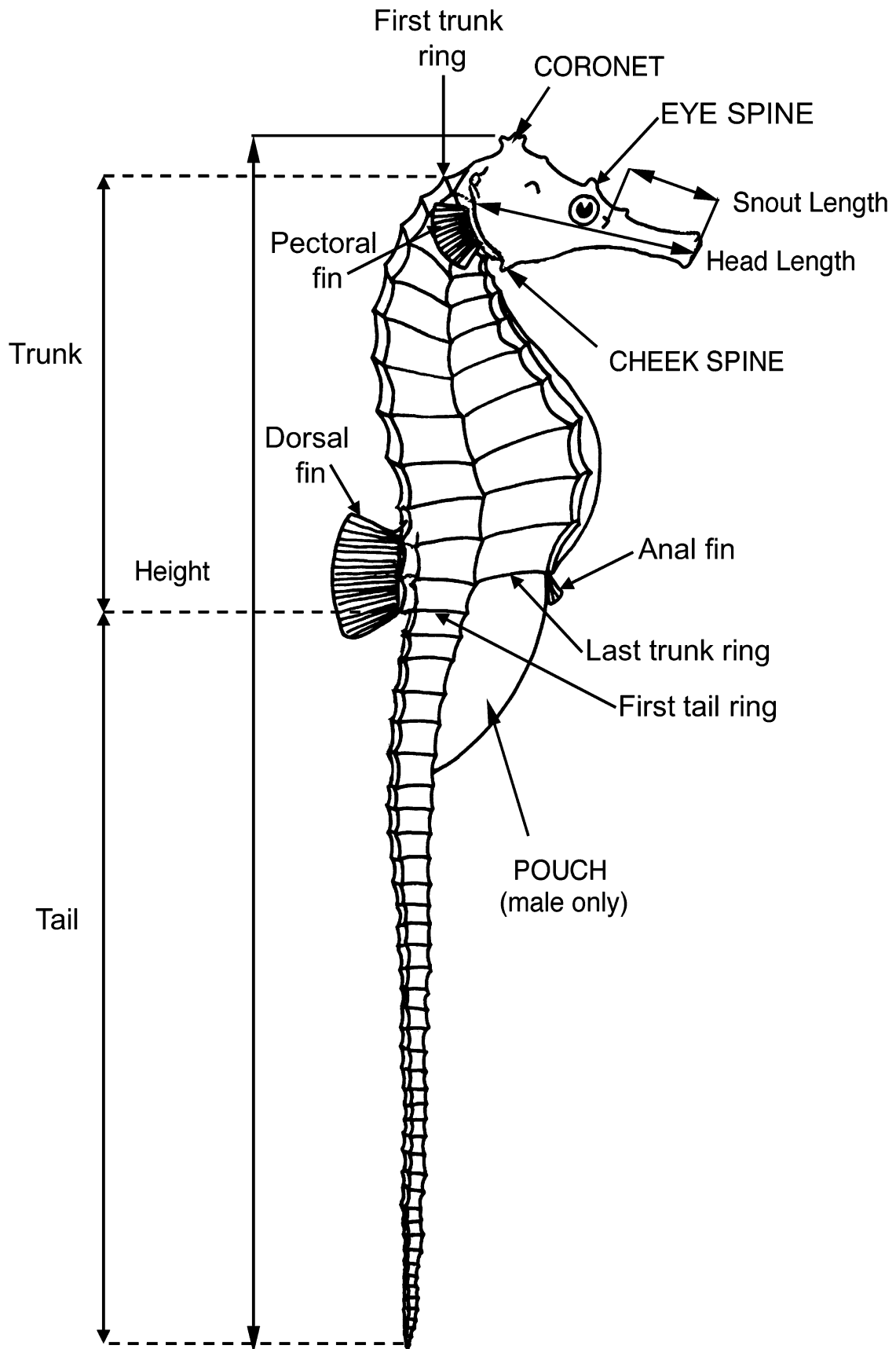
While we acknowledge that future research may change our understanding of seahorse taxonomy, especially as more genetic work is done, it seems timely to draw all available information together into a single publication in order to help reduce the confusion that currently exists. This revision should be seen as the next step in the process of refining our understanding of the biological diversity of seahorses in the ocean, and clarifying the nomenclature of the genus *Hippocampus*. We recognize the limitations of the use of species lists due to revisions and shifting perceptions of the species concept (Isaac *et al.* 2004); however, this revision should help conservationists by providing valuable knowledge for the prioritization of global seahorse taxonomic research efforts as well as conservation and management action. We intend for it to be a working document that will be updated as research further illuminates the nature and extent of seahorse diversity.

## Methods

This revision presents the results from a synthesis of all available information with respect to seahorse morphology, genetics, and geographic distribution, in order to address the validity of *Hippocampus* species currently recognized as such in the Catalogue of Fishes (CF) (Eschmeyer & Fricke 2016), which is considered by many to be the standard taxonomic reference for valid species of fish (Eschmeyer *et al.* 2010). We hope that the CF will accept our detailed analysis and be aligned as soon as possible. This paper is the continuation of work begun in 1997 for the preparation of Lourie *et al.* (1999, 2004). We critically examine other taxonomic works on seahorses produced since that time (e.g. Lourie & Randall 2003; Gomon & Kuitert 2009; Randall & Lourie 2009), compare our studies of many of the same specimens as those used by authors of works not involving us (e.g. Kuitert 2001; Fricke 2004), and review recent genetic phylogenies (Casey *et al.* 2004; Teske *et al.* 2004; Hamilton *et al.* 2010; Wilson & Orr 2011).

We considered a species to be taxonomically valid where available information on morphology and/or genetics supports it as a distinct species, employing the phylogenetic species concept (*sensu* Turner 1999). The extent of geographic separation among species that are morphologically and genetically similar was used to make decisions about putative species, although was not considered in isolation. Where available information was ambiguous we erred on the side of retaining the species name while highlighting the species as in need of further taxonomic study. The 'notes' section under each species details the rationale for all our decisions with respect to putative species. The morphological, genetic and geographical data used in this revision have been obtained through all known avenues, including previously published literature, online databases, authors' personal observations and analyses in the field and with museum specimens, and expert consultations. The details are as follows:





**FIGURE 1.** The parts of a seahorse. Adapted from Lourie *et al.* (2004).

**Morphology.** The morphological data and methodology primarily came from the first author's (SL's) examination of museum specimens in support of Lourie *et al.* (1999) and specimens she has examined since that time. Some of the over 2000 specimens examined by SL were the same specimens that Rudie Kuitert (RK) used in his 2001 revision of Australian species (Kuitert 2001) and direct comparisons have been made where possible. See Lourie (2004) for an explanation of the measurement protocol used; the complete list of specimens examined is available from authors on request.

We consider a species to be clearly distinct in terms of morphology when it has at least one diagnostic character, or a specific combination of features, that reliably separates it from other valid species. Diagnostic characters we considered include meristic data (number of tail rings—TaR, pectoral-fin rays—PF, dorsal-fin rays—DF) and spine morphology (including coronet, cheek and eye spines, and body spines) (Figure 1). The full measurement protocol for seahorses included many additional morphological measurements, but these are not tabulated here (see Lourie *et al.* 2004). We present the diagnostic meristic data we used to make decisions on the validity of various putative species in Appendices A through P.

**Genetics.** New genetic data were obtained from the Project Seahorse collection (housed at the Redpath Museum, Montreal, Canada) in 2006 by SL in collaboration with the International Barcode of Life ([www.ibol.org](http://www.ibol.org)) at the University of Guelph (Ontario, Canada), according to standard protocols (barcodes are a specific 648 bp sequence of the cytochrome oxidase—CO1—gene). The data are publicly available through the Barcode of Life Data Systems (Ratnasingham & Hebert 2007; BOLD 2016). A total of 67 (of 94) specimens, representing 28 species, yielded successful barcodes. Additional genetic information comes from Casey *et al.* (2004), Teske *et al.* (2004), G. Moore (*pers. comm., in prep.*), Saarman *et al.* (2010), H. Hamilton (*in litt.* to SL and RP, 13 Feb 2015) and CSIRO (Pogonoski *in litt.* to SL, 25 Oct 2015 to SL, data available on BOLD).

When assessing the genetic information we approximated distinctions between seahorse species to >2% divergence in mtDNA sequence data (cytochrome *b*—*cytb*, cytochrome oxidase subunit 1—CO1, control region—CR, etc.; Ratnasingham & Hebert 2013). This rule of thumb, which is larger than the average within-species divergence for fishes (0.35% for CO1 in 294 marine fish species), but significantly less than within-genus divergence (8.11% in 103 genera with multiple species) (Ward *et al.* 2009), reflects the fact that seahorses tend to exhibit significant geographical structure due to limited dispersal capabilities (Lourie 2004). This rule is a good starting point, but we encourage further molecular and ecological investigation into seahorse species distinctions. Note that genetic divergence is given as 'uncorrected *p*-distance' unless otherwise specified.

**Geography.** Geographical data was based primarily on the same specimens that were used for Lourie *et al.* (1999), including additional specimens identified at the time by SL but not measured in detail, and specimens examined since then by SL (the list of specimens is available from authors on request), as well as verifiable (with photographs) observations and specimen records available on iNaturalist ([www.inaturalist.org](http://www.inaturalist.org)), iSeahorse (iSeahorse 2016) and/or on GBIF (Global Biodiversity Information Facility; [www.gbif.org](http://www.gbif.org)) and ALA (Atlas of Living Australia; [www.ala.org.au](http://www.ala.org.au)).

We have also standardised English common names for the seahorse species that we consider valid. For Australian species we used the standardised names chosen by a panel of experts (Yearsley *et al.* 2006), with two exceptions. First, we augmented the names of the pygmy seahorses to remove ambiguity. For example, Yearsley *et al.* (2006) designated the standard common name of *H. bargibanti* as Pygmy Seahorse—but as there are several pygmy seahorses we added 'Bargibant's' in front. Second, we designated different names for species whose name in Yearsley *et al.* (2006) reflected a more restricted geographic distribution than is the case. For example, Yearsley *et al.* (2006) designated the standard common name of *H. angustus* Günther 1870 as the Western Spiny Seahorse, but as this species' range includes northern Australia we have used Narrow Bellied Seahorse. For species not in the Australian list, we went with the most frequently used common name across references such as the Encyclopedia of Life (Encyclopedia of Life 2016), FishBase (Froese & Pauly 2016) and Wikipedia (Wikipedia 2016). Standard common names are in bold and capitalized in the list of common names for each species.

Finally, we have designated neotype specimens, in collaboration with museum curators, for those species that lacked type specimens so as to (hopefully) help ensure future taxonomic stability.

**TABLE 2.** A list of all species names within the genus *Hippocampus* that are currently valid in the Catalog of Fishes (Eschmeyer & Fricke 2016), along with taxonomic status in FishBase (Froese & Pauly 2016) and that Assigned in the current revision. See text and the notes under each species account (or that of the senior synonym) for details and rationale behind our taxonomic decisions.

Purported <i>Hippocampus</i> species	Status in CF	Status in FB	Status in current revision
<i>abdominalis</i>	Valid	Valid	Valid
<i>alatus</i>	Valid	Valid	Synonym of <i>H. spinosissimus</i>
<i>algericus</i> <sup>k</sup>	Valid	Valid	Valid
<i>angustus</i>	Valid	Valid	Valid
<i>arnei</i>	Valid	Synonym of <i>H. barbouri</i>	Synonym of <i>H. barbouri</i> and <i>H. spinosissimus</i>
<i>barbouri</i>	Valid	Valid	Valid
<i>bargibanti</i>	Valid	Valid	Valid
<i>bicuspis</i>	Valid	Synonym of <i>H. guttulatus</i>	Species Inquirendum
<i>biocellatus</i>	Valid	Valid	Synonym of <i>H. planifrons</i>
<i>bleekeri</i>	Valid	Synonym of <i>H. abdominalis</i>	Synonym of <i>H. abdominalis</i>
<i>borboniensis</i>	Valid	Valid	Synonym of <i>H. kuda</i>
<i>breviceps</i>	Valid	Valid	Valid
<i>camelopardalis</i>	Valid	Valid	Valid
<i>capensis</i> <sup>k</sup>	Valid	Valid	Valid
<i>chinensis</i>	Valid	Synonym of <i>H. kuda</i>	Synonym of <i>H. kuda</i>
<i>colemanni</i>	Valid	Valid	Valid
<i>comes</i>	Valid	Valid	Valid
<i>coronatus</i>	Valid	Valid	Valid
<i>curvicauspis</i>	Valid	Valid	Synonym of <i>H. histrix</i>
<i>dahli</i> <sup>*</sup>	Valid	Synonym of <i>H. trimaculatus</i>	Valid
<i>debelius</i>	Valid	Valid	Valid
<i>denise</i>	Valid	Valid	Valid
<i>erectus</i>	Valid	Valid	Valid
<i>europaeus</i>	Valid	Synonym of <i>H. hippocampus</i>	Synonym of <i>H. hippocampus</i>
<i>fisheri</i>	Valid	Valid	Valid
<i>fuscus</i>	Valid	Valid	Synonym of <i>H. kuda</i>
<i>grandiceps</i>	Valid	Valid	Synonym of <i>H. angustus</i>
<i>guttulatus</i>	Valid	Valid	Valid
<i>hendriki</i>	Valid	Valid	Synonym of <i>H. angustus</i>
<i>hilonis</i>	Valid	Synonym of <i>H. kuda</i>	Synonym of <i>H. kuda</i>
<i>hippocampus</i>	Valid	Valid	Valid
<i>histrix</i>	Valid	Valid	Valid
<i>ingens</i>	Valid	Valid	Valid
<i>japonicus</i>	Valid	Synonym of <i>H. mohnikei</i>	Synonym of <i>H. mohnikei</i>
<i>jayakari</i>	Valid	Valid	Valid
<i>jugumus</i>	Valid	Valid	Valid
<i>kampylotrachelos</i>	Valid	Synonym of <i>H. trimaculatus</i>	Synonym of <i>H. trimaculatus</i>
<i>kelloggi</i>	Valid	Valid	Valid

.....continued on the next page

TABLE 2. (Continued)

Purported <i>Hippocampus</i> species	Status in CF	Status in FB	Status in current revision
<i>kuda</i>	Valid	Valid	Valid
<i>lichtensteinii</i>	Valid	Valid	Species Inquirendum
<i>manadensis</i>	Valid	Synonym of <i>H. trimaculatus</i>	Synonym of <i>H. trimaculatus</i>
<i>minotaur</i>	Valid	Valid	Valid
<i>mohnikei</i>	Valid	Valid	Valid
<i>moluccensis</i>	Valid	Synonym of <i>H. kuda</i>	Synonym of <i>H. kuda</i>
<i>montebelloensis</i>	Valid	Valid	Synonym of <i>H. zebra</i>
<i>multispinus</i>	Valid	Valid	Synonym of <i>H. angustus</i>
<i>natalensis</i>	Valid	Synonym of <i>H. fuscus</i>	Synonym of <i>H. kuda</i>
<i>paradoxus</i>	Valid	Valid	Valid
<i>patagonicus</i>	Valid	Valid	Valid
<i>planifrons</i>	Valid	Synonym of <i>H. trimaculatus</i>	Valid
<i>polytaenia</i>	Valid	Synonym of <i>H. kuda</i>	Synonym of <i>H. kuda</i>
<i>pontohi</i> <sup>*</sup>	Valid	Valid	Valid
<i>procerus</i>	Valid	Valid	Synonym of <i>H. whitei</i>
<i>pusillus</i>	Valid	Valid	Valid
<i>queenslandicus</i>	Valid	Valid	Synonym of <i>H. spinosissimus</i>
<i>reidi</i> <sup>*</sup>	Valid	Valid	Valid
<i>satomiae</i>	Valid	Valid	Valid
<i>semispinosus</i>	Valid	Valid	Synonym of <i>H. spinosissimus</i>
<i>severnsi</i>	Valid	Synonym of <i>H. pontohi</i>	Synonym of <i>H. pontohi</i>
<i>sindonis</i>	Valid	Valid	Valid
<i>spinosissimus</i>	Valid	Valid	Valid
<i>subelongatus</i> <sup>*</sup>	Valid	Valid	Valid
<i>suezensis</i>	Valid	Valid	Synonym of <i>H. kelloggi</i>
<i>taeniopterus</i>	Valid	Synonym of <i>H. kuda</i>	Synonym of <i>H. kuda</i>
<i>titicacaensis</i>	Valid (questionable)	N/A	Nomen nudum
<i>trimaculatus</i>	Valid	Valid	Valid
<i>tristis</i>	Valid	Synonym of <i>H. kuda</i>	Synonym of <i>H. kuda</i> (but see <i>H. kelloggi</i> account)
<i>tuberculatus</i>	Valid	Synonym of <i>H. breviceps</i>	Synonym of <i>H. breviceps</i>
<i>tyro</i>	Valid	Valid	Valid
<i>waleananus</i>	Valid	Valid	Synonym of <i>H. satomiae</i>
<i>whitei</i>	Valid	Valid	Valid
<i>zebra</i>	Valid	Valid	Valid
<i>zosteræ</i>	Valid	Valid	Valid

<sup>k</sup>Species that are members of the *H. kuda* complex (see text and species accounts).

<sup>\*</sup>Species that are retained here with uncertainty.

## Results summary

We consider 41 species of seahorse to be taxonomically valid (Tables 2 and 3). Thirty-eight of these are clearly distinct in their morphology, genetics and/or geography, and are supported by detailed and well-referenced research as annotated under the species accounts below. Indeed each of these 38 valid species is distinguishable from other valid seahorse species within its range by morphology alone. The evidence to support the remaining three species was ambiguous (*H. dahli* Ogilby 1908, *H. pontohi*, and *H. subelongatus* Castelnau 1873), and so we have retained the species until more information can be made available. We include synonyms and highlight unresolved taxonomic controversies in the descriptions of these 41 species. References for the original species descriptions of all valid species are included in the bibliography. We have designated neotypes for four species (*H. erectus*, *H. guttulatus*, *H. hippocampus* and *H. whitei* Bleeker 1855) that lacked type material, because doing so will help with nomenclatural stability in this historically confused genus. Key morphological (meristic and other) characteristics of valid species are summarized in Table 3 for ease of reference.

Overall we synonymized 29 of the species currently listed as valid in CF. These include some recently described species (e.g. *H. alatus* Kuitert 2001, *H. grandiceps* Kuitert 2001, *H. semispinosus* Kuitert 2001 and *H. severnsi*), and some recently resurrected species (e.g. *H. kampylotrachelos* Bleeker 1854 and *H. tristis* Castelnau 1872) for which insufficient evidence exists to support their distinctiveness from previously described species. For all synonymized species we have highlighted morphological and genetic discrepancies, inaccuracies in type designations, and situations where morphology overlaps significantly among species.

We have tentatively placed three species names as ‘*species inquirenda*’ that need further work (*H. bicuspis* Kaup 1856, *H. lichtensteinii* Kaup 1856, and *H. ramulosus* Leach 1814) and confirmed one species name as ‘*nomen nudum*’ (*H. titicacaensis* Posnansky 1911)—species names that appear in literature or museums without an accompanying species description. These are not included in our final count of 41 valid species. Finally, we resurrected one name (*H. planifrons*) in place of a valid but incorrectly named species (*H. biocellatus*).

## Valid *Hippocampus* species

Standard institutional codes are used for all specimens cited (see Sabaj-Pérez 2014). We include synonyms and highlight unresolved taxonomic controversies in the annotations for each species. References for the original descriptions of all valid species are included in the bibliography. Primary synonyms (i.e. those for which the type specimens represent the same species) only are given, since any attempt to rationalize subsequent misidentifications by different authors will surely lead to more confusion.

### *Hippocampus abdominalis* Lesson 1827

**English common names.** Bigbelly Seahorse, big-belly seahorse, big-bellied seahorse, eastern potbelly seahorse, pot-bellied seahorse, pot-belly seahorse.

**Syntypes.** MNHN 0000-6090, 0000-9207 (dried).

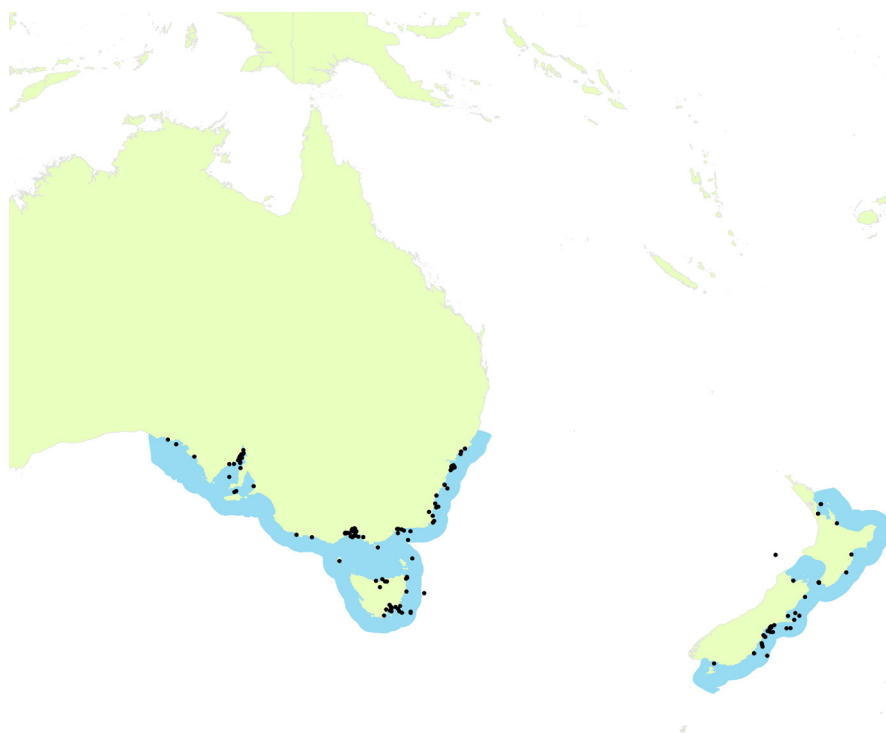
**Type locality.** New Zealand.

**Synonyms.** *H. bleekeri* Fowler 1907, *H. agnesae* Fowler 1907, *H. graciliformis* McCulloch 1911. Subgenus synonym: *Macleayina* Fowler 1907.

**Distribution.** Australia (southeast), New Zealand.

**Notes.** *H. abdominalis* was first described from New Zealand and there is a question as to whether specimens from Australia represent the same species. Studies that have addressed this question do not support the existence of multiple species based on morphological, meristic, and genetic data (357 bp, *cyt b*) and show more variation within populations than among populations (Appendix A; Armstrong 2001). There is some genetic divergence between Australian and New Zealand populations (814bp *cytb*, 624bp CO1, 404bp CR, plus four microsatellite loci), however, the level of divergence (1.4–1.7%, Nickel & Cursons 2012) is below our 2% threshold adopted for this revision. Divergence within New Zealand is 0.7–2.2% without any clear geographical structure (Nickel 2009; Nickel & Cursons 2012). The name *H. abdominalis* takes precedence with *H. agnesae* and *H. bleekeri* being

treated as synonyms. *Hippocampus graciliformis* is a juvenile specimen of *H. abdominalis* and therefore is also synonymized.



**FIGURE 2.** Range map for *Hippocampus abdominalis* based on museum specimens, authors' personal observations, and online data from GBIF, FishBase, and iSeahorse. The shaded coastline is a representative visualization of the species' coastal range that extends offshore to 200 m depth (the real range would not be readily visible at this scale as it only extends to the seahorse species' maximum depth—20–40 m or less for most species). Black dots represent author-vetted GBIF data points. Efforts were made to extend the range some distance from the outermost known points, as observed locations are not likely to represent the absolute furthest extent of the range).

### *H. algiricus* Kaup 1856

**English common name.** West African Seahorse.

**Holotype.** MNHN 0000-6084.

**Type locality.** Algeria.

**Synonyms.** *H. punctulatus* Kaup 1856, *H. deanei* Duméril 1861, *H. kaupii* Duméril 1870.

**Distribution.** Angola, Benin, Cabinda, Cameroon, Cape Verde, Congo, Cote d'Ivoire, Democratic Republic of the Congo, Equatorial Guinea, Gabon, The Gambia, Ghana, Guinea, Guinea-Bissau, Liberia, Mauritania, Nigeria, Sao Tome and Principe, Senegal, Sierra Leone, Spain (Canary Islands), Togo, Western Sahara.

**Notes.** The type specimen was sent from Algiers, Algeria by Guichenot who reported this species occurred, albeit 'very rarely', in Béjaïa (formerly Bougie) (Guichenot 1850). No other specimens have been found from Algeria since this time, and we restrict the current distribution of *H. algiricus* to West Africa. *H. algiricus* is very closely related to the *H. kuda*-complex (Teske *et al.* 2005) and is only 1.3% divergent from *H. reidi* (Silveira *et al.* 2014; Casey *et al.* 2004; Teske *et al.* 2004; BOLD 2016), but is here retained as a valid separate species due to the geographic distance between the West African and Brazilian coasts (see Discussion for further explanation). Further research is needed to determine the level of connectivity and gene exchange between the two populations. Synonymies were confirmed by examination of all type specimens (Lourie *et al.* 1999).



**FIGURE 3.** Range map for *Hippocampus algiricus*. Note the location that the holotype was reported from (Algeria). As no further specimens of *H. algiricus* have occurred in the Mediterranean, we restrict the range to West Africa and presume the holotype locality to possibly have been mislabelled. See Figure 2 caption for further details.

### *H. angustus* Günther 1870

**English common names.** Narrow-Bellied Seahorse, Western Australian seahorse, western spiny seahorse.

**Syntypes.** BMNH 1858.12.27.97-103 (7).

**Type locality.** Freycinet Harbour, Western Australia.

**Synonyms.** *H. grandiceps* Kuitert 2001; *H. hendriki* Kuitert 2001; *H. multispinus* Kuitert 2001; *H. erinaceus* Günther 1870.

**Distribution.** Australia (north and northwest).

**Notes.** Differences of opinion exist as to the number of spiny, striped-snouted, reticulated brown-patterned seahorse species in northern Australia. Morphologically and meristically there is a lot of overlap among the specimens and there are no clear morphological distinctions (Appendix B). Based on our measurements of many of the same specimens that were used to describe *H. grandiceps*, *H. hendriki*, and *H. multispinus* (Kuitert 2001), we find inconsistencies between our counts, and our counts do not uphold the very slight modal differences among the putative species described in Kuitert (2001). Even these differences disappear when all the specimens measured by SL (including ones not measured in Kuitert 2001) are divided regionally, and we therefore treat them as a single, morphologically variable species with the name *H. angustus*. Eleven barcode sequences are available for specimens from this group (six of which are publicly available): one from Rockingham, south of Perth (identified as *H. subelongatus*), one from Shark Bay (identified as *H. angustus*), two from the northwest coast of Western Australia (identified as *H. angustus*), one from Misool, West Papua (identified as *H. cf barbouri*) and five from the Torres Strait (identified as *H. hendriki* and not publicly available). BOLD separates them into three BINs (Barcode Index Number groups): i) *H. subelongatus* and *H. angustus* (Shark Bay) (identical sequences), ii) two northwest *H. angustus* (maximum genetic distance within this group is 0.61%) and iii) *H. cf barbouri* and *H. hendriki* (maximum genetic distance within this group is 0.92%). The genetic distance among the groups is 1.28–1.44%, which is below

the 2% threshold We have adopted for this revision. If further study suggests that spiny seahorses from Shark Bay (the type locality of *H. angustus*) are indeed the same as *H. subelongatus*, *H. angustus* has chronological priority. If the spiny northern seahorses turn out to be a single species, and distinct from *H. angustus*, but conspecific with *H. erinaceus*, the name *H. erinaceus* would have priority over new species names (those from Kuitert 2001). That said, although the meristic data of *H. erinaceus* match those of other northern spiny species, it is a much smaller specimen with a relatively short snout. If the northern seahorses turn out to be more than one species, *H. erinaceus* should be one of the names. See additional notes under *H. subelongatus*.



FIGURE 4. Range map for *Hippocampus angustus*. See Figure 2 caption for further details.

### *H. barbouri* Jordan & Richardson 1908

**English common names.** Barbour's Seahorse, zebra-snout seahorse.

**Holotype.** USNM 61683. **Paratypes:** CAS-SU 20205 (2).

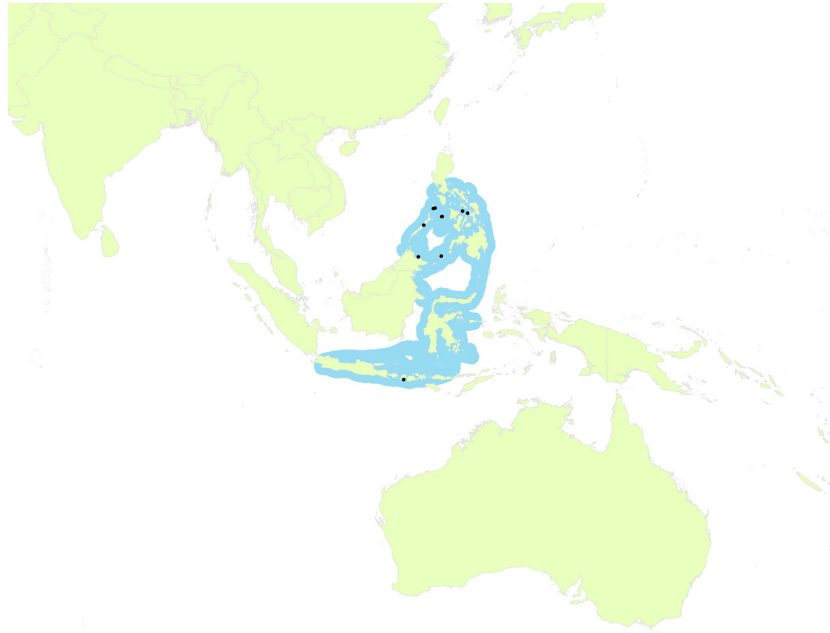
**Type locality.** Cuyo, Philippines.

**Synonyms.** *H. arnei* Roule 1916 (in part) (and its misspellings *H. aimei* and *H. airnei*).

**Distribution.** Indonesia (Java, Sulawesi and Borneo), Malaysia (Sabah), Philippines.

**Notes.** *H. arnei* is synonymized, in part, with *H. barbouri* on the basis of the original morphological description, illustrations, and photographs of the type specimens (Lourie *et al.* 1999). Note that the specimens of *H. arnei* are both female, and apparently of two different species, and are not male and female as Roule indicates. Genetic variation (648 bp, CO1) within *H. barbouri* is approximately 1.1% while the distance to the closest members of the *H. angustus* clade (from the Torres Strait) is approximately 6.1% (BOLD 2016).





**FIGURE 5.** Range map for *Hippocampus barbouri*. See Figure 2 caption for further details.

***H. bargibanti* Whitley 1970**

**English common names.** Bargibant's Pygmy Seahorse, pygmy seahorse.

**Lectotype.** AMS I.15418-001. **Paralectotypes:** AMS I.15418-002.

**Type locality.** Nouméa, New Caledonia.

**Synonyms.** None.

**Distribution.** Australia, Indonesia, Japan (Izu, Ogasawara and Ryukyu Islands), Malaysia (Borneo), New Caledonia, Palau, Papua New Guinea, Philippines, Solomon Islands, Vanuatu.

**Notes.** *H. bargibanti* exists in two different colour morphs: grey with pink tubercles, and yellow with orange tubercles.



**FIGURE 6.** Range map for *Hippocampus bargibanti*. See Figure 2 caption for further details.

***H. breviceps* Peters 1869**

**English common names.** Short-head Seahorse, knobby seahorse, short-headed seahorse, short-snouted seahorse.

**Holotype.** ZMB 7082 (missing in 2001).



**FIGURE 7.** Range map for *Hippocampus breviceps*. See Figure 2 caption for further details.

**Type locality.** Adelaide, South Australia.

**Synonyms.** *H. tuberculatus* Castelnau 1875.

**Distribution.** Australia (south and west, Tasmania).

**Notes.** Kuitert (2001) recognizes separate species to the west (*H. tuberculatus*) and east (*H. breviceps*) of the Great Australian Bight. Our data do not show the meristic differences that Kuitert cites in support of this separation (see Appendix C), and there are no genetic data yet available to shed light on the question. Further molecular work is needed to determine whether there exist sufficient differences between these two disjunct populations of *H. breviceps* to warrant the validity of *H. tuberculatus* as a distinct species. For now we accept the validity of a single species only.

***H. camelopardalis* Bianconi 1854**

**English common names.** Giraffe Seahorse.

**Type specimen.** Unknown (but see BMNH 1920.12.6.2).

**Type locality.** Mozambique.

**Synonyms.** *H. subcoronatus* Günther 1866 (in Playfair & Günther 1866).

**Distribution.** Mozambique, South Africa, Tanzania.

**Notes.** The name *H. subcoronatus* has barely been used except in Günther's original description. We synonymize it with *H. camelopardalis* based on the description, illustration, and our examination of the type specimen.



**FIGURE 8.** Range map for *Hippocampus camelopardalis*. See Figure 2 caption for further details.

***H. capensis* Boulenger 1900**

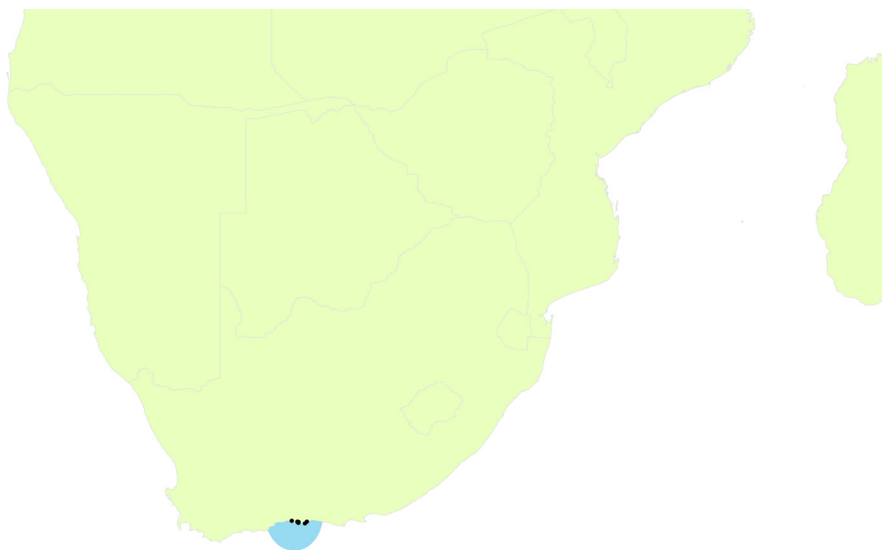
**English common names.** Knysna Seahorse, Cape seahorse.

**Holotype.** BMNH 1898.12.17.3.

**Type locality.** Knysna Harbour, South Africa.

**Synonyms.** None.

**Distribution.** South Africa (Knysna, Keurbooms, and Swartvlei Estuaries).



**FIGURE 9.** Range map for *Hippocampus capensis*. See Figure 2 caption for further details.

**Notes.** Meristics and genetic evidence (Teske *et al.* 2005, 2007a; BOLD 2016) suggest that *H. capensis* is a member of the *H. kuda* complex. We conservatively retain its status as a distinct species based on the distinctive morphological and ecological characteristics it exhibits and the substantial threats facing these populations (Lockyear *et al.* 2006; Teske *et al.* 2007b). The species is the only seahorse known to exclusively inhabit estuaries, and the populations within these estuaries all exhibit genetic differences that warrant them being treated as separate management units (Teske *et al.* 2003). See the Discussion for further explanation.

### *H. colemani* Kuitert 2003

**English common names.** Coleman's Pygmy Seahorse.

**Holotype.** AMS I41181-001. **Paratypes:** AMS I41181-002.

**Type locality.** Lord Howe Island, Australia.

**Synonyms.** None.



**FIGURE 10.** Range map for *Hippocampus colemani*. See Figure 2 caption for further details.

**Distribution.** Australia (Lord Howe Island).

**Notes.** The original description of *H. colemani* was based only on the two type specimens (Kuitert 2003) and contained errors (corrected in Lourie & Kuitert 2008). Two additional specimens from Milne Bay, Papua New Guinea, are housed in the NMV and tentatively assigned to *H. colemani*. However, they are substantially smaller and have body proportions more similar to *H. pontohi* (Lourie & Kuitert 2008). Given the relative isolation of Lord Howe Island, the paucity of specimens available for comparisons, and their many shared features, it is possible that the specimens described as *H. colemani* represent a population of a more widespread species that was subsequently, erroneously, described as *H. pontohi*. If this were the case (genetic data would be helpful to resolve this question), *H. colemani* would be the species name retained based on the Principle of Priority (Article 23, International Code of Zoological Nomenclature).

### *H. comes* Cantor 1849

**English common names.** Tiger-tail Seahorse, tiger-tailed seahorse.

**Holotype.** BMNH 1982.6.17.9 [ex 1860.3.19.532].

**Type locality.** Penang, Malaysia.

**Synonyms.** None.

**Distribution.** India (Andaman Islands), Indonesia, Malaysia, Philippines, Singapore, Thailand, Viet Nam.

**Notes.** BOLD (2016) data suggest that *H. comes* is most closely related to *H. angustus* and *H. subelongatus* from Shark Bay, Western Australia, with a divergence of 2.73%.



**FIGURE 11.** Range map for *Hippocampus comes*. See Figure 2 caption for further details.

### ***H. coronatus* Temminck & Schlegel 1850**

**English common names.** Crowned Seahorse.

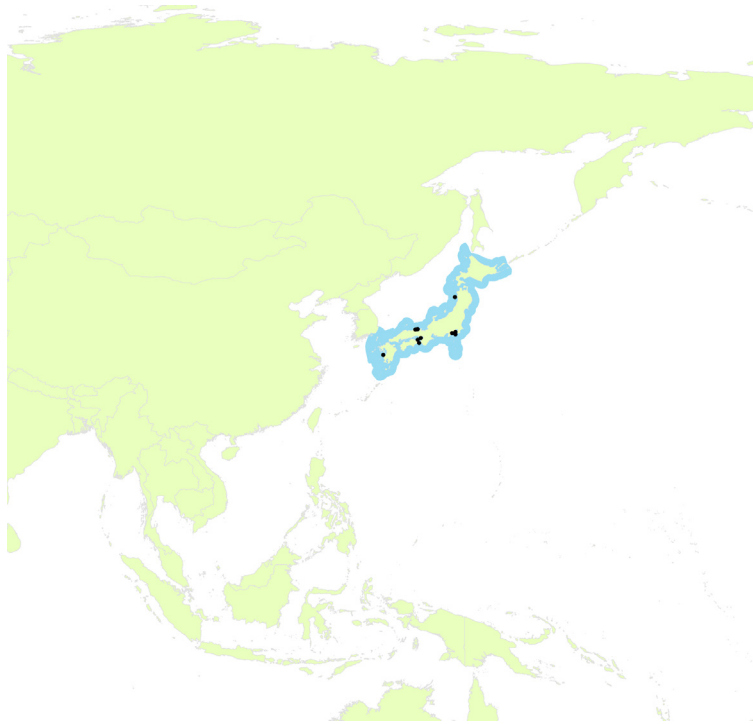
**Lectotype** (designated by Boeseman (1947:195–196)): RMNH D1543 (dry). **Paralectotype:** RMNH D1541-42 (2, dry), D1544 (1, dry).

**Type locality.** Nagasaki, Japan.

**Synonyms.** None.

**Distribution.** Japan, South Korea (southeast).

**Notes.** Mukai *et al.* (2000) assessed the mtDNA 12S rRNA divergence of specimens from Sagami Bay, Japan that they identified as *H. coronatus*. They concluded the samples represented two different taxonomic units, 4.4–4.6% divergent from one another. It is possible that the samples were misidentified and may in fact be *H. coronatus* and *H. sindonis* (this is likely based on the photographs in the paper). The paper did not mention *H. sindonis*. Morphological examination of the seahorses from Sagami Bay is needed.



**FIGURE 12.** Range map for *Hippocampus coronatus*. See Figure 2 caption for further details.

***H. dahl* Ogilby 1908**

**English common name.** Lowcrown Seahorse.

**Holotype.** QM I.788.



**FIGURE 13.** Range map for *Hippocampus dahl*. See Figure 2 caption for further details.

**Type locality.** Moreton Bay, Noosa, southern Queensland, Australia.

**Synonyms.** None.

**Distribution.** Northern and Eastern Australia.

**Notes.** Morphological data for the type specimen of *H. dahli* have been lost. Specimens from northeast Australia that are classified as *H. dahli* by Kuitert (2001) are meristically indistinguishable from *H. trimaculatus* from elsewhere in their range (Appendix D), although they apparently lack the three spots characteristic of *H. trimaculatus* (data for Lourie *et al.* 1999). Genetic data (648bp, CO1) from a single specimen identified as *H. dahli* (not publicly available) suggests a 4.86% divergence between this specimen and others from India to Taiwan, Province of China, Indonesia and the Philippines (BOLD 2016). Further investigation is warranted.

### ***H. debelius* Gomon & Kuitert 2009**

**English common name.** Softcoral Seahorse.

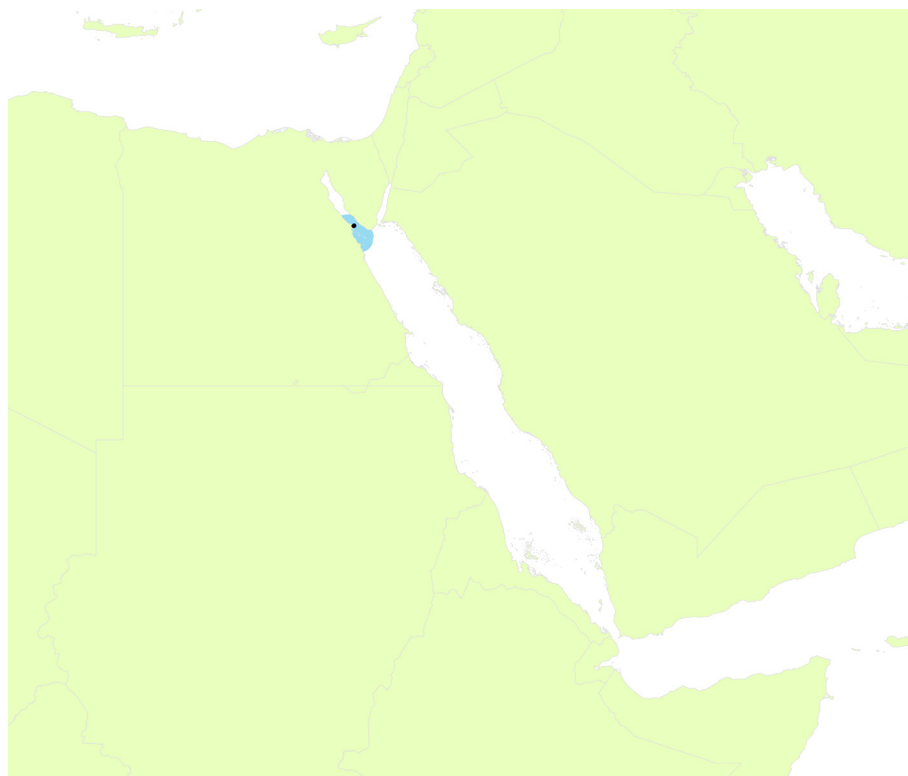
**Holotype.** NMV A 29864-001.

**Type locality.** Red Sea, Hurghada, Erg Camel, Egypt.

**Synonyms.** None.

**Distribution.** Egypt (Red Sea).

**Notes.** This species is clearly distinguishable from all other seahorses based on morphology and meristic data, but is known from very few specimens/observations. Further research is needed.



**FIGURE 14.** Range map for *Hippocampus debelius*. See Figure 2 caption for further details.

### ***H. denise* Lourie & Randall 2003**

**English common names.** Denise's Pygmy Seahorse.

**Holotype.** MZB 10920. **Paratypes:** BPBM 38955 (3); MZB 10921; USNM 368872-73 (1, 3), 370526.

**Type locality.** Banta Island, Indonesia (holotype, and one paratype); Palau (other paratypes).

**Synonyms.** None.

**Distribution.** Australia (northeast), Indonesia, Malaysia (Borneo), Marshall Islands, Federated States of Micronesia, Palau, Papua New Guinea, Philippines, Solomon Islands, Vanuatu.

**Notes.** Some specimens of *H. denise* from West Papua are red with large white tubercles. It is unclear whether these represent a separate species as specimens have yet to be collected. Further research is needed to understand the range boundaries of this species.



**FIGURE 15.** Range map for *Hippocampus denise*. See Figure 2 caption for further details.

### *H. erectus* Perry 1810

**English common names.** Lined Seahorse, northern seahorse, spotted seahorse.

**Neotype.** USNM 223087

**Type locality.** ‘American seas, coasts of Mexico and West Indies’ (presumably Atlantic coasts). Neotype from Florida (Gulf of Mexico), USA.

**Synonyms.** *H. hudsonius* DeKay 1842, *H. punctulatus* Guichenot 1853, *H. marginalis* Kaup 1856, *H. fascicularis* Kaup 1856, *H. laevicaudatus* Kaup 1856, *H. villosus* Günther 1880, *H. stylifer* Jordan and Gilbert 1882, *H. brunneus* Bean 1906, *H. kincaidi* Townsend and Barbour 1906, *Syngnathus caballus* Larranaga 1923.

**Distribution.** Anguilla, Antigua and Barbuda, Aruba, Azores Islands (though possibly as a vagrant or of anthropogenic origin—see Woodall *et al.* 2009), Bahamas, Barbados, Belize, Bermuda, Brazil, British Virgin Islands, Canada, Cayman Islands, Colombia, Costa Rica, Cuba, Curaçao, Dominica, Dominican Republic, French Guiana, Grenada, Guadeloupe, Guatemala, Guyana, Haiti, Honduras, Jamaica, Martinique, Mexico, Montserrat, Netherlands Antilles, Nicaragua, Panama, Puerto Rico, St. Kitts and Nevis, St. Lucia, St. Vincent and the Grenadines, Suriname, Trinidad and Tobago, Turks and Caicos, USA, US Virgin Islands, Venezuela.

**Notes.** No type specimen is associated with the original description of *H. erectus*, and its type locality was not specific, but we here designate a neotype from the centre of its range. Vari (1982) revised the western Atlantic seahorses and made the synonymies, however the morphological variation, particularly in terms of spine development among some specimens, is relatively large. The Brazilian *H. erectus* forms a genetically distinct clade (648bp, CO1), separate from the Caribbean specimens, however the genetic distance between these clades (1.6%, Silveira *et al.* 2014) is below the 2% threshold employed in this revision. Boehm *et al.* (2015) indicate that *H. erectus* from the Gulf of Mexico to Long Island exist as three genetic subpopulations (based on 11,708 single nucleotide polymorphisms), although an earlier study based on 3840bp (mtDNA *cytb*, CO1, CR) and five nuclear loci (aldolase, myh6, rhodopsin, Tmo4c4, S7 intron) gave no evidence to support a distinction on either side of



Cape Hatteras (Boehm *et al.* 2013). Boehm *et al.* (2015) have recently demonstrated that this species is resident as far north as Long Island. Many records of the species exist from over the Scotian shelf off the east coast of Canada—further research is needed to determine whether they are resident there or if they are vagrant drifters on the Gulf Stream.

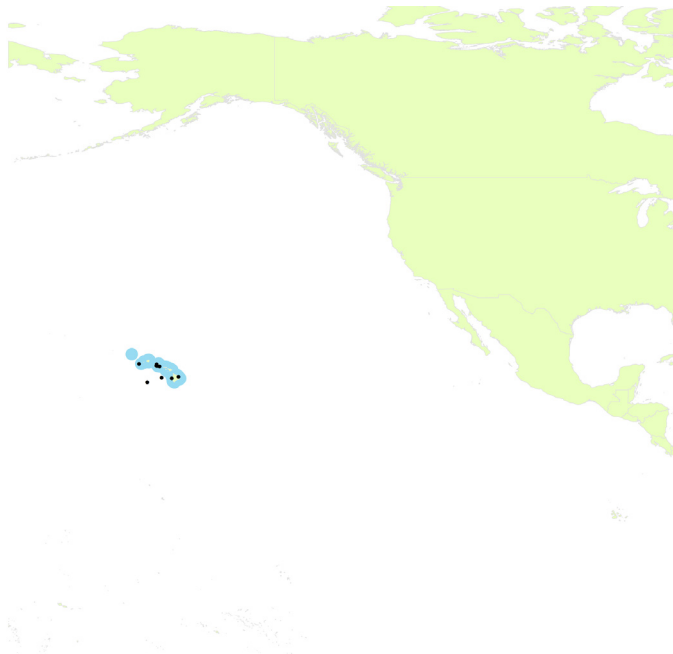


**FIGURE 16.** Range map for *Hippocampus erectus*. See Figure 2 caption for further details.

***H. fisheri* Jordan & Evermann 1903**

**English common names.** Fisher's Seahorse.

**Synonyms.** None.



**FIGURE 17.** Range map for *Hippocampus fisheri*. See Figure 2 caption for further details.

**Holotype.** USNM 50625. **Paratypes:** BPBM 1687, FMNH 3946, MCZ 168879 (never received), CAS-SU 7450, USNM 126534 [ex USBF 1058/USFC 2700].

**Type locality.** Kailua, Hawaii (holotype); Hilo, Hawaii (paratypes).

**Distribution.** USA (Hawaii).

**Notes.** Szabó *et al.* (2011) confirm the presence, and distinctness, of *H. fisheri* as a Hawaiian endemic using genetic and morphometric methods. It is >5% divergent from *H. kuda* (696bp, *cytb*) (Szabó *et al.* 2011). Specimens that were formerly tentatively assigned to *H. fisheri* from New Caledonia and Lord Howe Island (Lourie *et al.* 1999, 2004) have subsequently been described as *H. jugumus* and *H. pusillus* (Kuiter 2001; Fricke 2004).

### *H. guttulatus* Cuvier 1829

**English common names.** Long-snouted Seahorse, spiny seahorse, maned seahorse.

**Synonyms.** *H. guttulatus multiannularis* Ginsburg 1937, *H. hippocampus microcoronatus* Slastenenko 1938, *H. hippocampus microstephanus* Slastenenko 1937, *H. longirostris* Schinz 1822.

**Neotype:** MNHN-IC 2016-0023.

**Type locality.** Nice, France.

**Distribution.** Azores Islands, Bulgaria, Channel Islands, Croatia, Cyprus, France, Georgia, Greece, Isle of Man, Italy, Malta, Montenegro, Morocco, Netherlands, Portugal, Romania, Russia, Spain, UK, Ukraine.



**FIGURE 18.** Range map for *Hippocampus guttulatus*. See Figure 2 caption for further details.

**Notes.** The name *H. ramulosus* has frequently been used for the European Long-snouted Seahorse, but see *Species Inquirenda* below. Schinz (1822) proposed the name *H. longirostris* (~long-snouted seahorse) for this species in opposition to his *H. brevirostris* (~short-snouted seahorse). *Hippocampus longirostris* is given here in synonymy despite its earlier date (as in Lourie *et al.* 1999), following Ginsburg (1937) who called for its suppression and support of *H. guttulatus* ‘in accordance with universal usage’. This has been challenged by Vasil’Eva (2007), however, we continue to support Ginsburg’s concept (see also notes under *H. hippocampus*). *Hippocampus bicuspis* is similar meristically (Appendix E, and different from the other known species from the region, *H. algericus*), but it was found far outside the species’ typical range (in Senegal) and is here treated as a *Species Inquirendum*. Based on genetic data (991bp *cyt b* and CR, and five microsatellites) there are four distinct

subpopulations of *H. guttulatus* throughout Europe (Eastern Atlantic, Iberian Peninsula, Mediterranean Sea and Black Sea) (Woodall *et al.* 2015). The most common mtDNA haplotypes were found in all sampled locations, and the average genetic distance among populations was only 0.65%, supporting the conclusion that this is still a single species even though there is likely no current gene flow between the Black Sea and the Mediterranean. That said, even the Black Sea population is only 1.06% different from the furthest population in the Bay of Biscay (Woodall *et al.* 2015).

### *H. hippocampus* (Linnaeus 1758)

#### English common names. Short-snouted Seahorse.

**Synonyms.** *Gasterosteus equus* Cabrera, Pérez, and Haenseler 1817, *Syngnathus hippocampus* Linnaeus 1758, *H. heptagonus* Rafinesque 1810, *H. antiquorum* Leach 1814, *H. vulgaris* Cloquet 1821, *H. brevirostris* Schinz 1822, *H. antiquus* Risso 1827, *H. europaeus* Ginsburg 1937; *H. pentagonus* Rafinesque 1810.

**Distribution.** Algeria, Albania, Azores, Croatia, France, The Gambia, Greece, Guinea, Guinea-Bissau, Italy, Malta, Montenegro, Netherlands, Portugal, Senegal, Slovenia, Spain (including the Canary Islands), Turkey, UK, Western Sahara.



FIGURE 19. Range map for *Hippocampus hippocampus*. See Figure 2 caption for further details.

**Neotype:** BMNH 1872.2.6.3 (but see notes about Linnaeus' specimens).

**Type locality.** Spain/Portugal, eastern Atlantic.

**Notes.** Linnaeus had two seahorses in his collection, one of which is the European Short-snouted Seahorse, the other is a distinctly spiny species of unknown identity (SL *pers. obs.*, Maclaine 2015). Linnaeus himself made no distinction between different species of seahorse and gave them only a single name, *Syngnathus hippocampus*. This species name has been used extensively with the revised generic name for seahorses—*Hippocampus*) for the Short-Snouted Seahorse over the years, and is consistent with one of Linnaeus' specimens. Vasil'Eva (2007) however, suggests the use of *H. hippocampus* for the long-snouted European seahorse based on (some of) the meristic data in Linnaeus' original descriptions. This action would be extremely disruptive to European seahorse nomenclature. We follow CF (Eschmeyer & Fricke 2016) and Maclaine (2015) in recommending that Vasil'Eva's publication, its

neotype designation, and its nomenclatural conclusions be suppressed. *Hippocampus hippocampus* consists of three distinct genetic units (921 bp *cyt b* and CR) in the English Channel/Bay of Biscay, the Mediterranean/Atlantic Europe, and West Africa (Woodall *et al.* 2011). *Hippocampus europaeus* does not exhibit meristic or morphological characteristics that distinguish it (Appendix F). The average distance among the populations in the Mediterranean and Atlantic Europe is 0.89%, while the average distance of the West African populations is 1.90% from the above populations (Woodall *et al.* 2011), and these do tend to have distinctively large coronets (Lourie *et al.* 1999).

### ***H. histrix* Kaup 1856**

**English common names.** Thorny Seahorse, longspine seahorse, spiny seahorse.

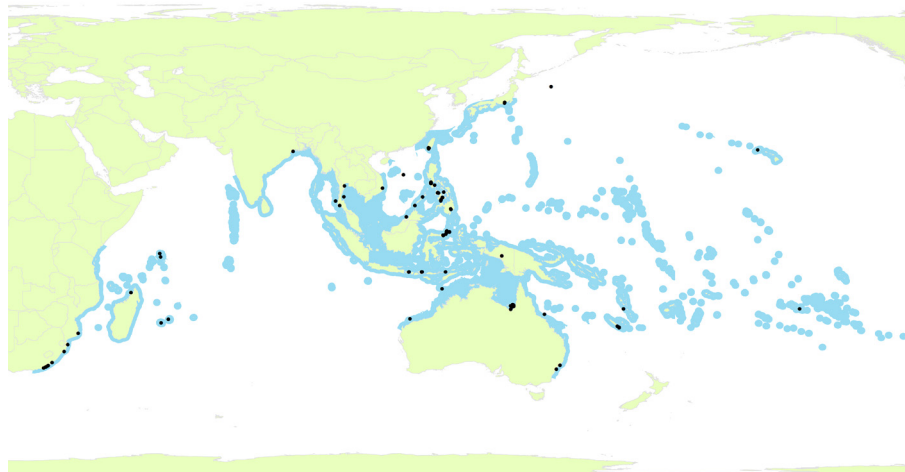
**Synonyms.** *H. curvicauspis* Fricke 2004 (in part), *H. hystrix* Kaup 1856.

**Distribution.** Australia, China (including Province of Taiwan), French Polynesia, Guam, Hawaii, India, Indonesia, Japan, Malaysia, Mauritius, Mozambique, Micronesia, New Caledonia, Palau, Papua New Guinea, Philippines, Reunion, Samoa, Seychelles, South Africa, South Korea, Tahiti, Tanzania, Thailand, Tonga, Viet Nam.

**Syntypes.** MNHN A-0906, RMNH 1537.

**Type locality.** Japan.

**Notes.** Five of the eleven specimens used by Fricke (2004) to describe *H. curvicauspis* were examined previously by the first author who did not find the cited morphological and meristic distinctions that purportedly separate these specimens from *H. histrix* (Lourie *et al.* 1999; Appendix G). In addition, one specimen (AMS IB.4155) in the type series appeared to be a member of a different species (*H. spinosissimus*) (SL *pers. obs.*). The wide geographic range of *H. histrix* (from east Africa to Japan) warrants further investigation, as Song & Mabuchi (2014) suggest that the genetic distance between Indian and Pacific *H. histrix* is 6.6–6.7% (CO1) and this is also suggested by BOLD (2016) which indicates a 6.13% distinction between specimens from Mozambique/India versus Viet Nam/Japan (648bp CO1). This high degree of divergence indicates the presence of at least one cryptic species across the range. There are no genetic data currently available for *H. jayakari*, which is morphologically very similar to but replaces *H. histrix* in the Red Sea and Arabian Gulf.



**FIGURE 20.** Range map for *Hippocampus histrix*. See Figure 2 caption for further details.

## *H. ingens* Girard 1858

**English common names.** Pacific Seahorse, Giant seahorse.

**Synonyms.** *H. gracilis* Gill 1862, *H. ecuadorensis* Fowler 1922, *H. hildebrandi* Ginsburg 1933.

**Distribution.** Colombia, Costa Rica, Ecuador (including the Malpelo, Cocos and Galapagos Islands), El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, USA (California).

**Lectotype:** USNM 982. **Paralectotypes:** MCZ 35914 [ex USNM 982], UMMZ 118063, USNM 214485 [ex USNM 982] (2).

**Type locality.** San Diego, USA.

**Notes.** See Fritzsche (1980) for refutations of all three synonyms. Anecdotal reports exist of *H. ingens* individuals being seen by fishers as far north as Barkley Sound, British Columbia (W. Harstad, *pers. comm.* 2014; A. Vincent, *pers. comm.* 2014). Genetic studies indicate low overall diversity within this species relative to other seahorses based on mtDNA *cytb* (587 bp, 0.8% Tamura-Nei distance) and control region (340 bp, 1.2% Tamura-Nei distance) and tRNA-pro and control region (428 bp, 0.39% nucleotide diversity ( $q_p$ ) sequences (Sanders *et al.* 2008; Saarman *et al.* 2010).



**FIGURE 21.** Range map for *Hippocampus ingens*. See Figure 2 caption for further details.

## *H. jayakari* Boulenger 1900

**English common names.** Jayakar's Seahorse.

**Synonyms.** None.

**Holotype.** BMNH 1900.5.23.1.

**Type locality.** Muscat, Oman.

**Distribution.** Israel (Red Sea), Oman, Pakistan.

**Notes.** This species may be closely related to *H. histrix*. No genetic data are currently available.



**FIGURE 22.** Range map for *Hippocampus jayakari*. See Figure 2 caption for further details.

***H. jugumus* Kuiter 2001**

**English common names.** Collar Seahorse, collared seahorse.

**Synonyms.** None.

**Holotype.** AMS IA.2424.

**Type locality.** Lord Howe Island, Australia.

**Distribution.** Australia (Lord Howe Island).

**Notes.** This species was described on the basis of a single specimen, however since then a second specimen has been collected from Lord Howe Island (from the gut of a kingfish *Seriola lalandi* Valenciennes 1833), and is now deposited at the Australian Museum in Sydney. *Hippocampus jugumus* looks superficially similar to the species described as *H. pusillus* and *H. fisheri*, however the meristics do not agree (Lourie *et al.* 1999; Kuiter 2001; Fricke 2004). Additional research is required to determine the relationships among these three species.



**FIGURE 23.** Range map for *Hippocampus jugumus*. See Figure 2 caption for further details.

## *H. kelloggi* Jordan & Snyder 1901

**English common names.** Great Seahorse, Kellogg's seahorse, offshore seahorse.

**Holotype.** CAS-SU 6521.

**Type locality.** Kagoshima, Japan.

**Synonyms.** *H. suezensis* Duncker 1940.

**Distribution.** Australia (northeast), China (Hong Kong SAR and Province of Taiwan), Egypt, India, Indonesia, Japan, Malaysia, New Caledonia, Oman, Papua New Guinea, Pakistan, Philippines, Thailand, Tanzania, Viet Nam.

**Notes.** Jawad *et al.* (2011) conclude there are morphological differences between *H. kelloggi* and specimens from Oman (potentially *H. suezensis*), however the crucial table containing distinguishing characteristics is missing from that paper and could thus not be evaluated for this current revision. The specimens that we have examined do not show meristic differences (Appendix H). One of the paratype specimens identified as *H. alatus* appears to be a specimen of *H. kelloggi* (Appendix N), as are several specimens identified by Kuitert (2001) as *H. tristis*.



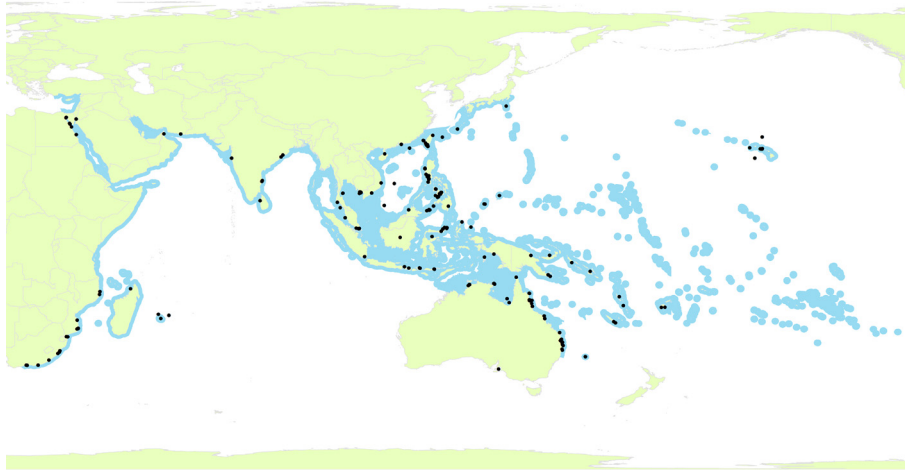
**FIGURE 24.** Range map for *Hippocampus kelloggi*. See Figure 2 caption for further details.

## *H. kuda* Bleeker 1852

**English common names.** Spotted Seahorse, common seahorse, estuarine seahorse, estuary seahorse, oceanic seahorse, yellow seahorse.

**Synonyms.** *H. aterrimus* Jordan and Snyder 1902, *H. borboniensis* Duméril 1870, *H. chinensis* Basilewsky 1855, *H. fuscus* Rüppell 1838, *H. hilonis* Jordan and Evermann 1903, *H. horai* Duncker 1926, *H. melanospilos* Bleeker 1854, *H. moluccensis* Bleeker 1852, *H. novaeheburum* Fowler 1944, *H. polytaenia* Bleeker 1854, *H. raji* Whitley 1955 (= *H. kuda multiannularis* Raj 1941), *H. rhynchomacer* Duméril 1870, *H. taeniops* Fowler 1904, *H. taeniopterus* Bleeker 1852, *H. tristis* Castelnau 1872

**Syntypes.** (2) RMNH 5167 (1 of several), BMNH 1867.11.28.360 (see also Bleeker specimens: NMV 46227-28 (2)).



**FIGURE 25.** Range map for *Hippocampus kuda*. See Figure 2 caption for further details.

**Type locality.** Singapore

**Distribution.** Australia (northern), Bahrain, Cambodia, China (including Hong Kong SAR and Province of Taiwan), Comoros, Cyprus, Djibouti, Egypt, Eritrea, Fiji, France (Réunion), India, Indonesia, Iran, Israel, Japan, Kenya, Kuwait, Lebanon, Malaysia, Madagascar, Mauritius, Mozambique, Federated States of Micronesia, New Caledonia, Oman, Pakistan, Papua New Guinea, Philippines, Qatar, Saudi Arabia, Seychelles, Singapore, Solomon Islands, Somalia, South Africa (eastern), Sri Lanka, Sudan, Syria, Tanzania, Thailand, Tonga, Turkey, United Arab Emirates, USA (Hawaii), Viet Nam.

**Notes.** *Hippocampus kuda* is a very widespread species (or species-complex) that exhibits localized haplotypes, phylogeographic structuring (Lourie 2004; Teske *et al.* 2005), and variable morphology. BOLD (2016) separates the 54 sequenced specimens into four BINS (Barcode Identification Numbers) although they only differ from one another by 1.28–2.25% (648 bp, CO1), and two of the three BINS with more than a single specimen contain members of more than one purported species. Furthermore, overlapping meristics, parphyly among purported species, genotypes from different clades (BINS) in the same populations, and lack of diagnostic morphological differences mean that, pending further research, we are unable to uphold purported species as valid in this revision. The global ‘*H. kuda*-clade’ includes *H. kuda*, *H. fuscus*, *H. borboniensis*, *H. capensis*, *H. algiricus*, and *H. reidi* (Casey *et al.* 2004; Silveira *et al.* 2014; Teske *et al.* 2005; BOLD 2016). We have here synonymized *H. fuscus* and *H. borboniensis* due to a lack of distinguishable morphological, genetic, or geographic differences from *H. kuda* proper (from Southeast Asia). Note that this implies that *H. kuda* is in fact a Lessepsian migrant, meaning that it has passed through the Suez Canal and into the Mediterranean Sea (Golani & Fine 2002). We retain *H. reidi* and *H. algiricus* based on their subtly distinctive coronets, longer snouts, but mostly their large geographic separation (see Discussion). Further studies are needed to determine whether gene flow occurs across the Atlantic, as these two species appear to be very close genetically (1.3% divergence in 1141bp, *cytb*, according to Casey *et al.* 2004 and 1.6% divergence in 652bp, CO1, according to Silveira *et al.* 2014). We also conservatively retain *H. capensis* based on its distinctive coronet, noticeably and consistently smaller size, ecological considerations (it appears to be one of the most brackish-water tolerant seahorses and has only been found in estuaries—Lockyear *et al.* 2006), and conservation status (it is the only seahorse listed as Endangered on the IUCN Red List—Czembor & Bell 2012). Comparisons of *cyt b* sequences of present-day specimens identified as *H. kuda* from Hawaii with the type specimen of *H. hilonis* revealed the same unique haplotype and led the authors to classify them as a subspecies *H. kuda hilonis* (Szabó *et al.* 2011). That said, the Hawaiian haplotype differs from Taiwanese and Philippines haplotypes by only one and two bases, respectively. Thus we do not support the acceptance of subspecific classification. The synonymization of *H. melanospilos* and *H. taeniopterus* with *H. kuda* was likely Bleeker’s own (according to manuscript notes to complete Bleeker’s Atlas of Ichthyology by Popta 1895). Lourie *et al.* (1999) followed Popta’s synonymy and we do here as well. According to Kuitert (2009), the type specimens of *H. moluccensis* are housed at the Museum of Victoria, although this identification is tentative. Kuitert further identifies



them as a spiny species, however after examination of a photograph of one of the specimens we conclude that it is not spiny and more strongly conforms to *H. kuda* (SL *pers. obs.*). The type description of *H. moluccensis* also repeatedly mentions ‘low tubercles’ and nothing about spines. The original description of *H. tristis* only mentions a single specimen (Castelnau 1872), however there are two type specimens in MNHN. Castelnau’s paper chiefly deals with fish from the Melbourne fish market and he gives no indication as to the origin of the specimens. The specimen labels however, suggest they are from ‘Swan River, Australia’. Both Melbourne and Swan River are outside the range of *H. kuda* and it is possible that the specimens came from elsewhere. Morphologically they conform to *H. kuda*. Other names that we synonymise, based on our examination of the type material, morphologically conform to *H. kuda* (e.g. *H. aterrimus*, *H. novaeheburum*, *H. polytaenia*—see also notes under *H. spinosissimus*, *H. rhynchomacer*, *H. taeniops*) (Appendix I). Remaining names lack type specimens, or we were unable to examine the types, and are synonymised based on the original morphological descriptions (e.g. *H. chinensis*, *H. horai*, *H. raji* and *H. taeniopterus*).

### ***H. minotaur* Gomon 1997**

**English common names.** Bullneck Seahorse.

**Synonyms.** None.

**Distribution.** Australia (southeast).

**Holotype.** NMV A192. **Paratypes:** AMS IA.3509, IA.3560, NMV A14161.

**Type locality.** Eden, Australia (holotype), New South Wales and Bass Strait, Australia (paratypes).

**Notes.** *Hippocampus minotaur* is known only from four specimens (Gomon 1997).



**FIGURE 26.** Range map for *Hippocampus minotaur*. See Figure 2 caption for further details.

### ***H. mohnikei* Bleeker 1853**

**English common names.** Japanese Seahorse.

**Synonyms.** *H. japonicus* Kaup 1856.

**Distribution.** Cambodia, China (including Province of Taiwan), India (eastern), Japan, Malaysia, Singapore, South Korea, Thailand, Singapore and Viet Nam (see Aylesworth *et al.* 2016).

**Holotype.** RMNH 7259.



**FIGURE 27.** Range map for *Hippocampus mohnikei*. See Figure 2 caption for further details.

**Type locality.** Kaminoseki Island, Japan.

**Notes.** Both *H. mohnikei* and *H. japonicus* were described from Japan and examination of their type specimens shows them to be the same species (Appendix J). Specimens from elsewhere in the Indo-Pacific morphologically conform to *H. mohnikei*, and differ genetically (e.g. Japanese and Vietnamese specimens differ by an average of 2.25%—648 bp, CO1, BOLD 2016), indicating that there is the possibility of cryptic species within what we know as *H. mohnikei*. Zhang *et al.* (2014) found an overall nucleotide diversity of 0.35% between the two populations sampled from northern China (780 bp, *cyt b*).

***H. paradoxus* Foster & Gomon 2010**

**English common names.** Paradoxical Seahorse.

**Synonyms.** None.



**FIGURE 28.** Range map for *Hippocampus paradoxus*. See Figure 2 caption for further details.

**Holotype.** SAMA F10490.

**Type locality.** SW of Esperance, Australia.

**Distribution.** Australia (southwest).

**Notes.** This species is known only from the holotype. It is closely related to *H. minotaur* (Foster & Gomon 2010).

### ***H. patagonicus* Piacentino & Luzzatto 2004**

**English common names.** Patagonian Seahorse.

**Synonyms.** None

**Distribution.** Argentina, Brazil (south), Uruguay.

**Holotype.** MACN 8806. **Paratypes:** MACN 8807, 8808, 8809.

**Type locality.** Río Negro, San Antonio Oeste, Bahía, Argentina.

**Notes.** Molecular research amply supports the diagnosis of *H. patagonicus* as a species separate from *H. erectus* (Casey *et al.* 2004; González *et al.* 2014; Silveira *et al.* 2014). It is 6.13% divergent from Brazilian *H. erectus* (648 bp, CO1, BOLD 2016) which in turn is 1.29% divergent from North American and Caribbean *H. erectus*.



**FIGURE 29.** Range map for *Hippocampus patagonicus*. See Figure 2 caption for further details.

### ***H. planifrons* Peters 1877**

**English common names.** Flatface Seahorse, false-eye seahorse, false-eyed seahorse.

**Synonyms.** *H. biocellatus* Kuitert 2001.

**Distribution.** Australia (Shark Bay and Exmouth Gulf).

**Holotype.** ZMB 9387.

**Type locality.** Naturalist's Channel, Australia.

**Notes.** The type specimen of *H. planifrons* is bleached and eye spots cannot be discerned. The limited number of specimens examined by Kuitert (2001) for descriptions of *H. biocellatus* (6) and *H. planifrons* (4) did not display distinguishing characteristics when re-examined by SL (see Appendix K), aside from *H. biocellatus* having a deeper body (potentially confounded by ontogeny and sex differences among the specimens examined) and spot

markings that are split (that again may reflect ontogenetic differences) and cannot be seen on the type specimen of *H. planifrons*. The name *H. planifrons* has chronological precedence, thus subsuming *H. biocellatus* as a junior synonym.



**FIGURE 30.** Range map for *Hippocampus planifrons*. See Figure 2 caption for further details.

***H. pontohi* Lourie & Kuitert 2008**

**English common name.** Pontoh's Pygmy Seahorse  
**Synonyms.** *H. severnsi* Lourie and Kuitert 2008.



**FIGURE 31.** Range map for *Hippocampus pontohi*. See Figure 2 caption for further details.

**Distribution.** Indonesia, Fiji, Papua New Guinea, Philippines, Solomon Islands, USA (Northern Mariana Islands).

**Holotype:** MZB 13593. **Paratypes:** MZB 13596, 13597.

**Type locality.** Bunaken, North Sulawesi, Indonesia.

**Notes.** *H. severnsi* is considered a synonym based on the fact that its original description (Lourie & Kuitert 2008) does not include distinct morphological characters (colour only) (Appendix L). Recent genetic analyses confirm this synonymy (H. Hamilton, *in litt. to SL and RP, 13 Feb 2015*).

### ***H. pusillus* Fricke 2004**

**English common names.** Pygmy Thorny Seahorse, Dwarf thorny seahorse.

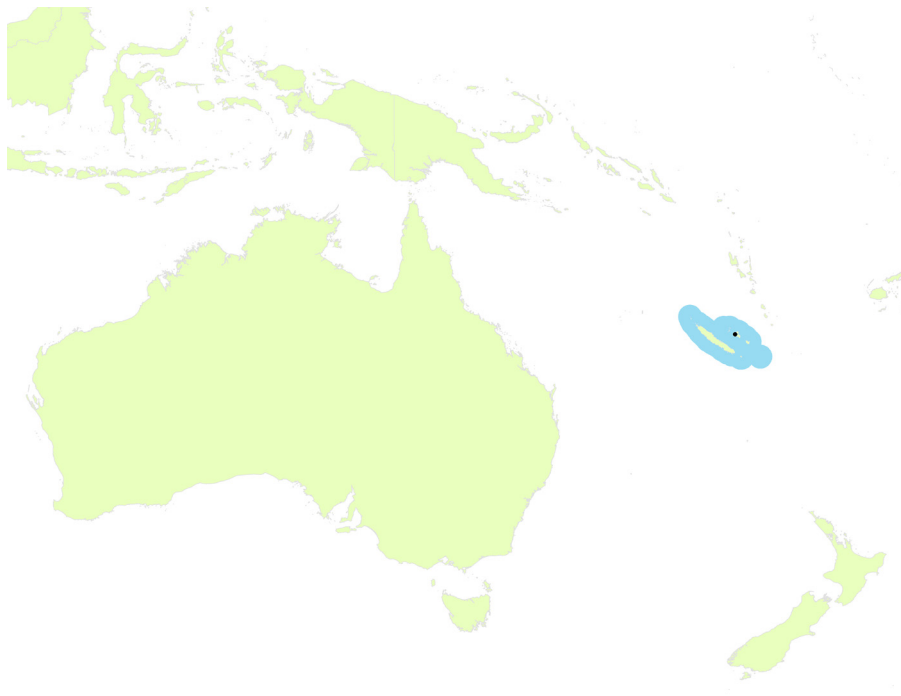
**Synonyms.** None.

**Holotype.** MNHN 2004-2029. **Paratypes:** MNHN 2002-3234, SMNS 23384.

**Type locality.** Loyalty Islands (holotype), Loyalty Islands and Province Nord, Grand Terre, New Caledonia (paratypes).

**Distribution.** France (New Caledonia).

**Notes.** This species is known only from the holotype and two paratypes. It very closely resembles *H. jugumus* although the meristic data do not agree. Further investigation is warranted.



**FIGURE 32.** Range map for *Hippocampus pusillus*. See Figure 2 caption for further details.

### ***H. reidi* Ginsburg 1933**

**English common names.** Slender Seahorse, Brazilian seahorse, longsnout seahorse, long-snout seahorse.

**Synonyms.** *H. obtusus* Ginsburg 1933, *H. poeyi* Howell and Riviero 1934.

**Distribution.** Bahamas, Barbados, Belize, Bermuda, Brazil, Cayman Islands, Colombia, Cuba, French Guiana, Grenada, Haiti, Honduras, Jamaica, Mexico, Nicaragua, Panama, Puerto Rico, St. Lucia, Suriname, Turks and Caicos Islands, Trinidad and Tobago, USA (North Carolina to Texas), Venezuela, Virgin Islands (US and UK).



**FIGURE 33.** Range map for *Hippocampus reidi*. See Figure 2 caption for further details.

**Holotype.** USNM 86590. **Paratypes:** USNM 223673.

**Type locality.** Grenada, West Indies.

**Notes.** Both *H. obtusus* and *H. poeyi* are juvenile specimens that conform to *H. reidi* meristically and morphologically, and are hence synonymised. *Hippocampus reidi* is thought to be part of the *H. kuda* complex (Teske *et al.* 2005), and is very closely related to *H. algiricus* (Casey *et al.* 2004; Silveira *et al.* 2014). Indeed the Barcode of Life places them both in the same BIN group, with an average within-group divergence of 1.28% (BOLD 2016). Research is needed to determine whether gene flow across the Atlantic Ocean takes place between *H. reidi* and *H. algiricus*, but we retain them both as valid species here due to the large geographic distance and entire ocean basin between the two populations.

### ***H. satomiae* Lourie & Kuitert 2008**

**English common names.** Satomi's Pygmy Seahorse.

**Synonyms.** *H. waleananus* Gomon and Kuitert 2009.

**Distribution.** Brunei, Indonesia (Kalimantan), Malaysia (Sabah).

**Holotype.** NMV A25420-001. **Paratype:** NMV A25420-002.

**Type locality.** Derawan Island, Kalimantan, Indonesia.

**Notes.** *Hippocampus waleananus* was described based on a single specimen. Differences cited included tail rings (32 vs. 27–28 for *H. satomiae*) and dorsal fin rays (12 versus 13–14), however a lack of other differences, and its apparent distribution entirely encompassed within the distribution of *H. satomiae*, lead us to synonymize it under *H. satomiae* (Appendix M). Further surveys and molecular studies in the region are needed to confirm this.



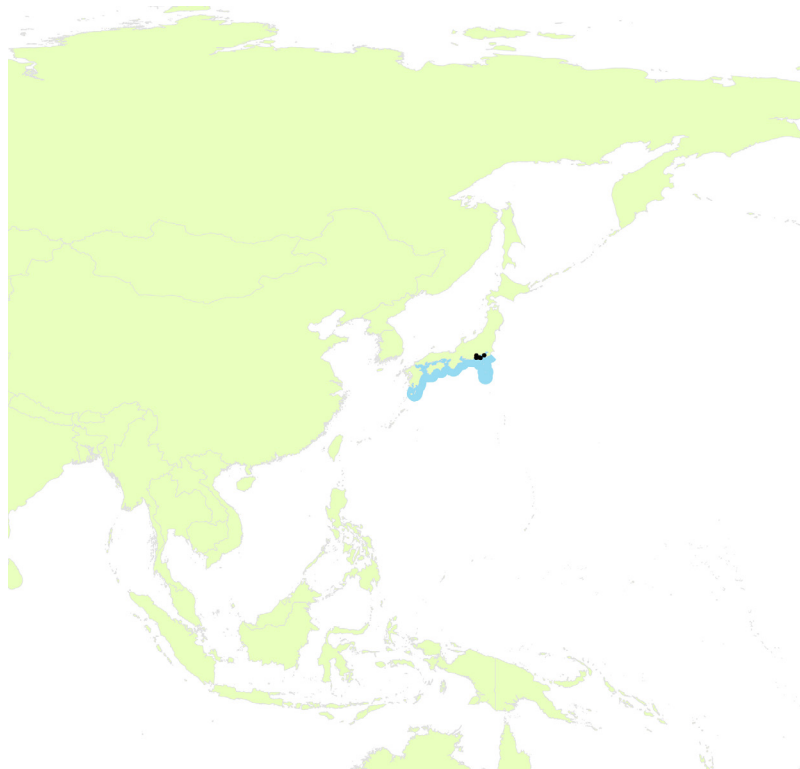
**FIGURE 34.** Range map for *Hippocampus satomiae*. See Figure 2 caption for further details.

***H. sindonis* Jordan & Snyder 1901**

**English common names.** Sindo's Seahorse, Shiho's seahorse.

**Synonyms.** None.

**Holotype.** USNM 47930.



**FIGURE 35.** Range map for *Hippocampus sindonis*. See Figure 2 caption for further details.

**Type locality.** Totomi Bay, off Hamamatsu, Japan.

**Distribution.** Japan.

**Notes.** Genetic data (714bp, 12S rRNA) from specimens identified by Mukai *et al.* (2000) as *H. coronatus* from Sagami Bay, Japan, separated into two distinct clades that differed by 4.4–4.6%. Photographs from that same paper, however, appear to be *H. sindonis* and *H. coronatus*, which would explain the observed genetic divergence.

### *H. spinosissimus* Weber 1913

**English common names.** Hedgehog Seahorse.

**Synonyms.** *H. alatus* Kuitert 2001, *H. arnei* Roule 1916 (in part), *H. curvicuspis* Fricke 2004 (in part), *H. queenslandicus* Horne 2001, *H. semispinosus* Kuitert 2001.

**Syntypes.** ZMA 104.665 (2).

**Type locality.** Sapeh Strait, Indonesia.

**Distribution.** Australia (north), Cambodia, India, Indonesia, Malaysia, Myanmar, Philippines, Singapore, Sri Lanka, Taiwan, Province of China, Thailand, Viet Nam.



**FIGURE 36.** Range map for *Hippocampus spinosissimus*. See Figure 2 caption for further details.

**Notes.** The type specimens of *H. spinosissimus* are surprisingly small, yet they are males with fully developed pouches. They also have clear nose spines, double cheek spines, and all body spines are approximately equally developed. A third specimen labelled as ‘type’ (ZMA 114.473) had single cheek spines. Lourie *et al.* (1999) used this name to refer to spiny seahorses from across Southeast Asia, even though the latter frequently lacked a nose spine. No genetic data are available from the type specimens. Morphological and genetic data do not support the distinctness of *H. queenslandicus* nor *H. semispinosus* from what is understood as *H. spinosissimus* by Lourie *et al.* (1999) (Teske *et al.* 2007c; BOLD 2016; Appendix N; see also Zhang *et al.* 2014). Admittedly there exists variation in spine development and colour pattern among *H. spinosissimus* specimens and genetic data indicate that haplotype diversity is high, with three major lineages, two of which are broadly sympatric and one that is restricted to the central Philippines (Lourie *et al.* 2005). However, the genetic divergence among specimens of *H. spinosissimus* examined from Australia, Malaysia and the Philippines is only 0.82% (648bp, CO1) (BOLD 2016), and the average cytochrome *b* sequence divergence among 172 specimens from 29 populations is only 1.3%



(Lourie *et al.* 2005). At present we suggest that the variation represents polymorphism within a single species, rather than different species, however further investigation is warranted. Kuitert (2009) and Allen & Erdmann (2012) identify spiny Southeast Asian seahorses variously as *H. arnei* (see comments under *H. barbouri*), *H. alatus*, *H. moluccensis* (see comments under *H. kuda*), and *H. polytaenia*. The illustration of *H. polytaenia* (Bleeker, 1983) does show markings and moderately developed spines that are reminiscent of *H. spinosissimus*, however the type specimens conform to *H. kuda* (SL *pers. obs.*). *Hippocampus alatus* is tentatively synonymised here on the basis of morphological similarity, pending further work (especially genetics) (see Appendix N).

### ***H. subelongatus* Castelnau 1873**

**English common names.** West Australian Seahorse, tiger snout seahorse.

**Synonyms.** *H. elongatus* Castelnau 1873.



**FIGURE 37.** Range map for *Hippocampus subelongatus*. See Figure 2 caption for further details.

**Paratypes:** MNHN A-4535, MNHN A-4536, MNHN A-4552 (according to Kuitert 2001) MNHN A-4535 is probably the holotype of *H. subelongatus*, and A-4536 is probably the holotype of *H. elongatus*.

**Type locality.** Swan River, Western Australia.

**Distribution.** Australia (southwest).

**Notes.** Meristic data largely overlap between *H. subelongatus* and *H. angustus* (Appendix B). Genetic divergence between *H. subelongatus* from Rockingham and *H. angustus* from Cape Bossut is 1.99% (652bp, CO1) (Harasti 2014), which is just about at the cut-off that we set for species distinctions for this revision. However the same specimen from Rockingham had an identical haplotype to a specimen of *H. angustus* from Denham, Shark Bay (BOLD 2016). Further investigation is warranted. In the meantime we continue to recognize *H. subelongatus* as a species separate from *H. angustus*. In support of this decision, *H. subelongatus* specimens do have distinctive, very tall and rounded coronets, and are not at all spiny, unlike their northern congeners that are distinctly spiny.

***H. trimaculatus* Leach 1814**

**English common names.** **Three-spot Seahorse**, flat-faced seahorse, longnose seahorse, low-crowned seahorse, smooth seahorse, three-spotted seahorse.

**Synonyms.** *H. kamylotrachelos* Bleeker 1854, *H. manadensis* Bleeker 1856, *H. mannulus* Cantor 1849, *H. takakurae* Tanaka 1916.

**Syntypes.** BMNH 1982.6.17.42, BMNH 1982.6.17.43 (designated here as **lectotype**), BMNH 1982.6.17.44-45 (2), BMNH 1982.6.17.46-47 (2).

**Type locality.** China Seas.



**FIGURE 38.** Range map for *Hippocampus trimaculatus*. See Figure 2 caption for further details.

**Distribution.** Cambodia, China (Hong Kong SAR and Province of Taiwan), France (Tahiti), India, Indonesia, Japan, Malaysia, Myanmar, Philippines, Singapore, Thailand, Viet Nam.

**Notes.** The syntype series labeled as *H. trimaculatus* is actually a mixture of species: BMNH 1982.6.17.42 is *H. barbouri* (larger specimen) and *H. mohnikei* (smaller specimen); BMNH 1982.6.17.43 is *H. trimaculatus*, and is hereby designated as a lectotype; BMNH 1982.6.17.44–45 are *H. trimaculatus*; BMNH 1982.6.17.46–47 are *H. spinosissimus*. The type specimen of *H. kamylotrachelos* matches *H. trimaculatus* morphologically and meristically, as does the single specimen, which is in poor condition and was found among nesting birds that Kuitert (2001) used to resurrect the species name. Both *H. mannulus* and *H. manadensis* are considered synonyms based on their type descriptions, and for *H. manadensis* examination of the holotype. Genetic data suggest there is a deep division between *H. trimaculatus* specimens from west and east of Wallace’s Line (2.9%, K2P distance, 696 bp cyt *b*, Lourie & Vincent 2004a; 1.93%, 648 bp, CO1, BOLD 2016). There is some morphological evidence (slight difference in modal counts of tail rings and pectoral fin rays) to support this division as well (Appendix D). However, the difference is only retained for pectoral fin rays when Australian specimens are included and may not represent species distinctions. That said, we are currently treating Australian specimens in this group as a separate species, *H. dahli* (see above). Further research is needed to understand exactly where the changeover occurs and if there is a zone of overlap. Some specimens of *H. trimaculatus* have a zebra-striped pattern. Morphology, meristics and genetics identify these specimens as an unusual colour-morph of *H. trimaculatus* and not a separate species.

***H. tyro* Randall & Lourie 2009**

**English common names.** Tyro Seahorse.

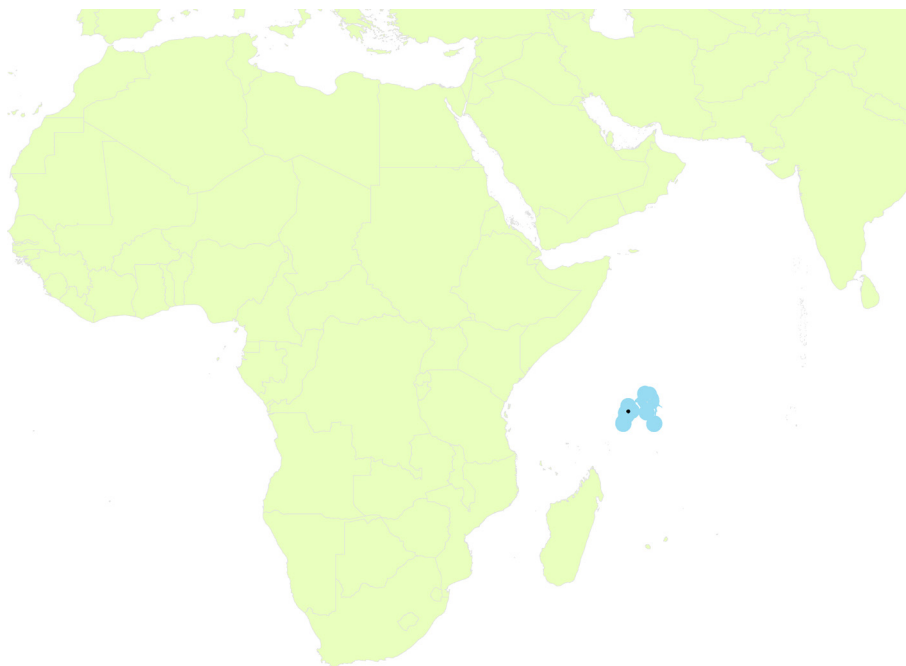
**Holotype.** BPBM 35555.

**Type locality.** Poivre Atoll, Seychelles.

**Synonyms.** None.

**Distribution.** Seychelles.

**Notes.** This species is only known from a single specimen collected from a deep-water dredge in 1992.



**FIGURE 39.** Range map for *Hippocampus tyro*. See Figure 2 caption for further details.

***H. whitei* Bleeker 1855**

**English common names.** White's Seahorse, common seahorse, New Holland seahorse, Sydney seahorse.

**Synonyms.** *H. novaehollandiae* Steindacher 1866; *H. procerus* Kuitert 2001.

**Neotype:** I.40831-018.

**Type locality.** Sydney Harbour, New South Wales, Australia.

**Distribution.** Australia (east), Solomon Islands.

**Notes.** Meristic and morphological data do not separate purported *H. procerus* from *H. whitei* (Appendix O), nor do genetics. Four specimens from Moreton Bay (the type locality for *H. procerus*) included three haplotypes, each of which was identical to a haplotype from Sydney Harbour (type locality for *H. whitei*) (H. Hamilton, *in litt.* to SL and RP, 13 Feb 2015).



**FIGURE 40.** Range map for *Hippocampus whitei*. See Figure 2 caption for further details.

***H. zebra* Whitley 1964**

**English common names.** Zebra Seahorse.

**Synonyms.** *H. montebelloensis* Kuitert 2001

**Holotype.** AMS IB.6015. **Paratype:** AMS IB.2819.

**Type locality.** Gillett Cay, Swain Reefs, Queensland, Australia.



**FIGURE 41.** Range map for *Hippocampus zebra*. See Figure 2 caption for further details.

**Distribution.** Australia.

**Notes.** Some specimens of *H. trimaculatus* have zebra-stripes, however these can be separated from *H. zebra* on the basis of meristic counts (Appendix D) and their less distinct coronet (Lourie *et al.* 2004). Note that the paratype of *H. zebra* is one such misidentification. Specimens from the west coast of Australia described as *H. montebelloensis* by Kuitert (2001) have identical meristic data, and underwater photographs show distinct zebra-striped specimens supporting synonymization. No genetic data are yet available.

### *H. zosterae* Jordan & Gilbert 1882

**English common names.** Dwarf Seahorse.

**Synonyms.** *H. rosamondae* Borodin 1928, *H. regulus* Ginsburg 1933.

**Syntypes.** MNHN 1887-0515, CAS-SU 1671 (2), USNM 30852 (2 or 1, not found in 1980).

**Type locality.** Laguna Grande, Pensacola, Florida.

**Distribution.** Bahamas, Mexico, USA (Gulf of Mexico).

**Notes.** The type specimen of *H. lichtensteinii* is thought to possibly be *H. zosterae* and to have been mistakenly labelled as being from the Red Sea (Kaup 1856—See Appendix P and *Species Inquirenda* below). Although populations throughout the Floridian portion of the species' range exhibit gene flow, mtDNA evidence (1,450 bp, ND4, D-loop, CO1) suggests four distinct subpopulations (overall  $F_{ST} = 0.47$ , average nucleotide diversity within populations = 0.49%) (Fedrizzi *et al.* 2015).



**FIGURE 42.** Range map for *Hippocampus zosterae*. See Figure 2 caption for further details.

### Species Inquirenda

*Hippocampus bicuspis* Kaup 1856 (meristically similar to *H. guttulatus* but collected from far outside the known range, no further specimens have been discovered in the area or elsewhere); *H. lichtensteinii* Kaup 1856 (type specimen locality originally given as ‘Red Sea?’, with no more recent specimens; morphology and meristic data coincide with those of *H. zosterae* or potentially a thus-far unnamed species in Japan (see photos

labelled *H. lichtensteinii* in Kuitert 2009, Appendix P). *H. ramulosus* Leach 1814 (type specimen has an unknown locality—many authors have listed this species as a synonym of *H. guttulatus* however the type specimen is very different).

### Nomina nuda

The following species names appear in publications or on museum labels, without accompanying descriptions and are therefore considered 'nomina nuda': *H. atrichus* De la Pylaie 1835; *H. fasciatus* Kaup 1853; *H. filamentosus* Duméril 1870; *H. gigas* Gill 1862; *H. jubatus* De la Pylaie 1835; *H. lenis* De Vis 1908; *H. nuda*; *H. obscurus* Hemprich and Ehrenberg 1856; *H. pilosus*; *H. pygmaeus*; *H. ringens* Jordan and Evermann 1905; *H. rondeletii* Yarrell 1836; *H. rosaceus* Risso 1826; *H. sexmaculatus* Kaup 1856; *H. titicacaensis* Posnansky 1911; *H. valentini* Bleeker 1859.

### Other Invalid Names

*Hippocampus foliaceus* Richardson 1843—synonym of the seadragon *Phyllopteryx taeniolatus* (Lacepède 1804); *H. foliatus* Perry 1810—synonym of *P. taeniolatus*; *H. gracilissimus* Temminck and Schlegel 1850—synonym of the pygmy pipehorse *Acentronura gracilissima* (Temminck & Schlegel 1850).

### Discussion

This global revision of 41 seahorse species meets its goal of using the best available morphological, genetic, and geographic information to provide a pragmatic account of all currently valid seahorse species. We have been conservative in our recognition of species, aiming for the requirement that they have clear diagnostic morphological features and/or clear genetic divergence from nearest neighbours. The vast majority of species—35—recognized as valid in this revision meet one or both of these criteria. A further six required further consideration in order to determine their validity. Three of these (bringing the tally to 38) are very closely related to *H. kuda* while three others (for a total of 41) are somewhat ambiguous.

For two species we took into account the extent of their geographic separation from other valid species that are morphologically and genetically similar—this was essential in order to meet our goal of a revision in support of seahorse conservation and management. *Hippocampus algiricus* and *H. reidi* overlap meristically with *H. kuda*, and available genetic evidence does not separate them out as species, but instead combines *H. algiricus* with *H. reidi*; the group differs by less than the 2% divergence to qualify as species under our criterion. They do have some morphological differences—mostly related to shape of coronet—but overall the available evidence in support of keeping them as valid species is weak, as was the case with the now synonymized *H. borboniensis* and *H. fuscus*. Unlike *H. borboniensis* and *H. fuscus*, however, *H. algiricus* and *H. reidi* have considerable geographic separation from each other, and from *H. kuda* which is found in the Indo-Pacific: *H. algiricus* is known only from the coast of West Africa, and *H. reidi* is distributed along the east coasts of North and South America. These species should therefore be considered as separate in conservation and management terms—even if they are actually isolated populations of *H. kuda*.

For *H. capensis* we took into account geography, but also its threatened status on the IUCN Red List. *Hippocampus capensis* overlaps meristically with *H. kuda*, and available genetic evidence does not separate it out as a species, but instead combines it with *H. kuda* (from East Africa to Papua New Guinea) with an average within-BIN divergence of 1.61%, less than the 2% divergence to qualify as species under our criterion. *Hippocampus capensis* is, however, known from just three estuaries in South Africa—in which there have been very few, and no recent, reported sightings of *H. kuda* (SAIAB 2016). Most critically, *H. capensis* is considered the world's most threatened seahorse—listed as Endangered on the IUCN Red List (Czembor & Bell 2012). We risk losing current impetus for localized conservation and management efforts for this species if we subsume it under *H. kuda*, and so have put the burden of proof on its synonymization rather than on its validity as a separate species.

Evidence in support of three other species was ambiguous, but again we have retained their validity until further research can be undertaken. The first, *H. dahli*, has the same morphology as *H. trimaculatus*, but genetic information from a single specimen labelled as *H. dahli* available on BOLD suggests it to be a distinct species (5% divergence from *H. trimaculatus*, BOLD 2016). The second, *H. pontohi*, overlaps meristically with *H. colemani*, and there is little geographic and no known genetic information to distinguish it from *H. colemani*—the main reported difference is size and body proportions. Finally, *H. subelongatus* overlaps with *H. angustus* meristically although other morphological features are somewhat divergent (the former having a medium-sized spiny coronet and some body spines—the latter with a tall, rounded coronet and smooth body), the two species adjoin one another in distribution, and available genetic information is ambiguous (suggesting a shared haplotype between Perth and Shark Bay, yet 1.99% difference between Rockingham and Cape Bossut, BOLD 2016; Glenn Moore *pers. comm.*). Further genetic analysis for each of these species is needed to confirm or refute their validity.

Our focus on distinguishable species has multiple advantages, not least the tractability of species identification by non-specialists (such as Customs officers and citizen scientists) who may have to make identifications with limited background knowledge. This is true even for *H. algericus*, *H. capensis* and *H. reidi*—Customs officers, divers and researchers should not have to struggle to assign species names to specimens from this group given they originate in such distinct locations from *H. kuda* and each other. Challenges will come, however, in markets or in shipments that are unreported or illegal, where species are mixed together and the point of origin is not known. In this case coronet shape can be used as a defining feature but it must be considered that species labelled as *H. kuda* could be one of the other three species, and vice versa.

Geographic separation should also help in the case of *H. dahli* in the absence of any means for genetic identification. Specimens of *H. dahli* are morphologically indistinguishable from *H. trimaculatus*, with the possible exception of spot markings, although genetic evidence from one specimen suggests them to be two species. Retaining *H. dahli*, which is distributed in Australia, means that *H. trimaculatus*' distribution is now limited to Asia. The exact region of changeover is not known. Geography also helps in the case of keeping *H. subelongatus* separate from *H. angustus*, which combined with other unique morphological characteristics warrant them being retained as separate species until new evidence suggests otherwise. In the case of *H. pontohi* we have too little information about *H. colemani* to make a clear statement about geographic ranges.

Efforts to discover more about seahorse ranges and population sizes will be affected positively by the changes to seahorse taxonomy we have made with this revision. Divers will be better equipped to distinguish seahorse species because there are fewer species with nearby or overlapping ranges that do not differ substantially in terms of morphology (for instance the northern Australian spiny species, which are now subsumed under *H. angustus*). Observations of previously-recognized species such as *H. severnsi* will now fall under their parent species (*H. pontohi* in this case), simplifying field and photograph identification and contributing to appropriate monitoring and conservation efforts for the valid species.

While making a positive difference in seahorse conservation and management going forward, the taxonomic changes suggested here will have limited impact on the IUCN Red List of Threatened Species, CITES or iSeahorse as they currently stand. *Hippocampus borboniensis* and *H. fuscus*, both currently listed as Data Deficient (DD) on the IUCN Red List (Project Seahorse 2003a; b) will now be subsumed under *H. kuda*, which is assessed as Vulnerable (VU, Aylesworth 2014). The addition of these populations will not change *H. kuda*'s threatened status; it has been documented to be in decline elsewhere throughout its range (Aylesworth 2014). *Hippocampus hendriki*, currently listed as DD on the IUCN Red List (Fritzsche *et al.* 2010), will now be subsumed under another species (*H. angustus*, also DD, Project Seahorse 2002). However several other synonyms hitherto recognized by the IUCN, but not yet evaluated, will no longer require assessments.

Fourteen seahorse species considered valid by CITES (at the time of writing, UNEP-WCMC (Comps.) 2016) are not considered valid species in this revision, but only five of these are reported in the CITES trade database, each in small volumes (UNEP-WCMC 2015): *H. fuscus* (now *H. kuda*)—a total of 1459 individuals reportedly exported from 2005-2014; *H. procerus* (now *H. whitei*)—90 individuals reportedly exported in 2010; *H. borboniensis* (now *H. kuda*)—50 individuals reportedly exported in 2005 and 1 in 2008; *H. biocellatus* (now *H. planifrons*)—50 individuals reportedly exported in 2011; *H. queenslandicus* (now *H. spinosissimus*)—8 individuals reportedly exported in 2012. A further three species will need to be added to the CITES list of seahorses (*H. dahli*, *H. planifrons* and *H. pusillus*).

Nine species currently recognized by iSeahorse at the time of writing (iSeahorse 2016), are not considered valid in this revision—but sightings have been reported for only three: 10, 14 and 12 sightings reported for *H. borboniensis* (now *H. kuda*), *H. fuscus* (now *H. kuda*) and *H. severnsi* (now *H. pontohi*), respectively. *Hippocampus dahl*, *H. paradoxus* and *H. planifrons* will need to be added to the iSeahorse list of valid species.

Although the focus of this revision has been clarifying seahorse species in support of research, conservation, and management, we should note that it is ideal (although not often pragmatic) to consider a species' phylogeographic structure when considering management or conservation scenarios. It has been shown that many seahorse species do exist as a patchwork of geographically localized genetic subunits—e.g. *H. erectus* (Boehm *et al.* 2015), *H. guttulatus* (Woodall *et al.* 2015), *H. hippocampus* (Woodall 2009; Woodall *et al.* 2011), *H. ingens* (Saarman *et al.* 2010), *H. kuda* (Lourie *et al.* 2005; Teske *et al.* 2005; Szabó *et al.* 2011)—that some authors might consider separate subspecies. These subunits could be indicative of barriers to dispersal and/or poor colonizing ability (e.g. Saarman *et al.* 2010; Boehm *et al.* 2013; Woodall *et al.* 2015). On the other hand, intraspecific diversity can render locally adapted seahorse populations vulnerable to more localized environmental or anthropogenic disturbances and extirpation (e.g., population fluctuations of *H. capensis* in the Swartvlei Estuary, Lockyear *et al.* 2006), and can also play a key role in species persistence in the face of environmental changes (Schindler *et al.* 2010). Where the capacity exists, we encourage local and regional monitoring and conservation action to take into account and actively pursue the discovery of evolutionarily distinct subpopulations in order to conserve biodiversity at the genetic as well as the species level (Fraser & Bernatchez 2001; Palsbøll *et al.* 2007; Reiss *et al.* 2009; Bradbury *et al.* 2013; Mee *et al.* 2015). This would be particularly important, for example, should further research ever determine that any of *H. algericus*, *H. capensis*, or *H. reidi* is indeed *H. kuda*.

**Recommendations for further taxonomic research.** Although the foregoing revision of 41 seahorse species is our best assessment of the current situation with regards to seahorse taxonomy, it is highly likely that this will be improved with further integrative taxonomic work. In this light, we turn to a discussion of some of the more salient issues that were encountered during this study—those that most urgently require further research.

1) **The genetic definition of seahorse species**—Seahorse identification is challenging as a result of the limited basic morphological variation across the genus, the overlap of meristic and other morphological features, and the individual variation in colour, spininess, and dermal appendages. It is unsurprising, therefore, that there has been much confusion over the years. It would be ideal to base the division on integration between genetics and morphology which should be less ambiguous—but what should the genetic cut-off be? Is a 2% divergence in mitochondrial DNA, as used here, appropriate? And how much hybridization occurs among seahorse species, complete with mitochondrial transfer (as has been demonstrated for *H. hippocampus* and *H. algericus* in Gran Canaria; Otero-Ferrer *et al.* 2015)? Carvalho & Craig (2011), and other papers in the same volume, provided numerous examples of the debate regarding the use of integrated morphology and genetics for taxonomic questions. The average genetic variability (648bp CO1) within seahorse species and across the *Hippocampus* genus (1.57 and 10.54%, respectively, BOLD 2016) is similar to, or greater than, that seen in other fish taxa (Ward *et al.* 2009). The most divergent species sequenced (*H. pontohi*) differs from congeners by 18–21% (H. Hamilton, *in litt. to SL and RP, 13 Feb 2015*). Species or species complexes for which limited genetic data exist should be a priority for further research (e.g. *H. colemani*, *H. jayakari*), as should a further understanding of the geographic variation within species. At a species level, BOLD serves an excellent purpose as a reference database; however, it is currently marred by a large number of incorrectly identified sequences. Finally, most of the molecular studies carried out thus far on seahorses focus on mitochondrial DNA and COI (but see Teske *et al.* 2004; Teske & Beheregaray 2009), and so there is a need for more diverse genetic data. Relationships among species should be clarified by genetic markers from both mitochondrial and nuclear DNA. The nascent field of genomics is accelerating and should provide further insight into the evolutionary relationships within the genus.

2) **The potential for cryptic species**—Previously unknown deep divergences have been elucidated within some species (e.g. 6% in *H. histrix*, 2.25% in *H. mohnikae*, BOLD 2016), suggesting the possible existence of additional cryptic species yet to be described. The vast geographic range of *H. histrix* in particular warrants further investigation. The species has been recorded from South Africa to Hawaii, with a large disjunction between the Horn of Africa and India (Lourie *et al.* 1999). Casey *et al.* (2004) showed little divergence (1.1%) in the cytochrome *b* gene between Japan and Viet Nam, whereas Song & Mabuchi (2014) and BOLD (2016) data



both indicate a divergence greater than 6% in CO1 between Japan and India, and between Viet Nam and Mozambique respectively. Further sampling and genomic work could reveal populations with geographic barriers to gene flow that are in need of species designation and description (and should therefore be the subject of management and conservation efforts). Further studies are also needed between the Horn of Africa and the Gulf of Mannar, including the Red Sea and Arabian Gulf, to determine the evolutionary relationship between *H. histrix* and *H. jayakari*, where their populations end and begin, and what, if any, geographic overlap exists.

**3) The *H. kuda* complex**—The range of the *H. kuda* complex is similar to that of *H. histrix*. However, variable morphology and meristic data have spurred the designation of several species names over the years: *H. capensis* in South Africa; *H. borboniensis* in Reunion, Madagascar, and East Africa from Kenya to South Africa; and *H. fuscus*, which was described from the Red Sea but specimens that look like *H. fuscus* occur in India (described as *H. brachyrhynchus*), and Africa (described as *H. natalensis*). Only the first three of these are considered valid on CF, and we here suggest that there are insufficient distinguishing features and lack of genetic support to uphold at least two of them as separate species from *H. kuda*—*H. borboniensis* and *H. fuscus*. That said, the lower range of dorsal and fin ray counts of purported *H. fuscus* specimens is less than those of *H. kuda* elsewhere in its range; further research is needed to better understand species diversity in the Western Indian Ocean. We have, however, retained three species (*H. algiricus*, *H. capensis* and *H. reidi*) as valid; although they overlap meristically, and are genetically closely related to *H. kuda* (Casey *et al.* 2004; Teske *et al.* 2005; Silveira *et al.* 2014), they are sufficiently separated geographically to suggest their isolation if not completed speciation (as explained above in the Discussion). Further field and molecular studies are needed, however, to pinpoint geographic barriers to gene flow, areas of range disjunction and overlap, and to further elucidate the evolutionary and spatial relationships among these species. More sampling of *H. kuda* should also be conducted in the Pacific to ensure no further cryptic but isolated species exist within the complex. Indeed studies have indicated that the entire *H. kuda* complex (now *H. algiricus*, *H. capensis*, *H. reidi* and *H. kuda*)—together spanning the majority of the Pacific, and all of the Indian and Atlantic Oceans—is very closely related to *H. ingens* in the eastern Pacific, making the group eligible for study as a circumglobal lineage (Teske *et al.* 2007a). Such studies have been undertaken of other syngnathiform taxa including the pipefish *Microphis brachyurus* (Dawson 1979) and the trumpetfishes of the genus *Aulostomus* (Bowen *et al.* 2001).

**4) Northern Australia spiny species**—Further research is needed to establish the evolutionary relationship between *H. angustus* and *H. subelongatus*, and further assess the putative species divisions proposed by Kuitert (2001). Field and molecular work should be carried out in order to determine the nature of small variations among the northern Australian spiny specimens and whether this represents a cline, localized or individual variation, or the presence of cryptic species.

**5) Pygmy seahorses**—Effort should also be put forward to compare the pygmy seahorses to their larger congeners, as morphological and early genetic data seem to support their designation as a separate genus (Lourie & Randall 2003; Teske *et al.* 2004; Smith 2010).

**6) Dedicated surveys for poorly-known species**—Many of the seahorse species included here are known only from a few specimens (or less). Further surveys, collections, and genetic samples are needed from these species in order to assess their status, and conserve them where needed. Dedicated field surveys—using SCUBA but also fisheries sampling—in and around type localities are needed in order to establish range limits and to elucidate evolutionary relationships between these and other better-known species. Species in need of such further inquiry include: *H. colemani*, *H. coronatus*, *H. debelius*, *H. fisheri*, *H. jayakari*, *H. jugumus*, *H. minotaur*, *H. paradoxus*, *H. planifrons*, *H. pontohi*, *H. pusillus*, *H. satomiae*, and *H. tyro*.

The 41 members of the genus *Hippocampus* outlined in our comprehensive treatment is the first attempt at taxonomic clarity for the group since the onset of the genomic age of biology, and many improvements upon this work are likely in the near future. While anticipating inevitable future updates to seahorse taxonomy, overall we trust that this global revision of currently valid species will help bring some clarity to seahorse nomenclature, and a stable platform on which to base future efforts in seahorse research, management, and conservation. We hope such efforts will lead to the ongoing persistence of all seahorse species and their irreplaceable ocean habitats.

**TABLE 3.** Diagnostic morphological characteristics for 41 seahorse species (*Hippocampus* spp.) considered valid in this revision.

<i>Hippocampus</i> species	Standard common name	Tail rings (TaR)	Pectoral fin rays (PF)	Dorsal fin rays (DF)	Body spines	Cheek spines	Eye spines	Coronet	Max. recorded height (cm)
<i>abdominalis</i>	Bigbelly Seahorse	47 (45–48)	15 (15–17)	27–28 (25–33)	Low, rounded bumps	1	1	Low, triangular wedge	35 <sup>a</sup>
<i>algricus</i>	West African Seahorse	36 (35–37)	16–17 (15–17)	17–18	Low, rounded bumps	1–2	1–2	Relatively low and overhanging at the back	19 <sup>b</sup>
<i>angustus</i>	Narrow-Bellied Seahorse	33–34 (32–35)	16–17 (15–19)	18 (17–19)	Well-developed with blunt or sharp tips	2	1	Medium height with five well-developed spines	16 <sup>c</sup>
<i>barbouri</i>	Barbour's Seahorse	34–35 (33–36)	17–18 (15–20)	19 (16–22)	Well-developed, usually sharp eye spine; first dorsal trunk spine much longer than others and curved backwards; tail spines of different lengths in a regular series (e.g., long, short, long, short)	2	1	Medium-high, five sharp spines	15 <sup>c</sup>
<i>bargibanti</i>	Bargibant's Pygmy Seahorse	31–32 (31–33)	10 (10–11)	14 (13–15)	Irregular bulbous tubercles scattered over body and tail; single, prominent rounded eye spine; single, low rounded cheek spine	1	1	Rounded knob	2.4 <sup>d</sup>
<i>breviceps</i>	Short-head Seahorse	40 (39–43)	14–15 (13–15)	20–21 (19–23)	Mostly low, some prominent rounded tubercles	1	1	Tall and columnar	10 <sup>e</sup>
<i>camelopardalis</i>	Giraffe Seahorse	38	17–18	19–22	Low rounded, prominent eye spine and pre-coronet spine	0	1	Very high, inclined backwards with a rounded top	10 <sup>c</sup>
<i>capensis</i>	Knysna Seahorse	34 (32–37)	15 (14–17)	17 (16–18)	None	0	0	None	12 <sup>f</sup>
<i>colemani</i>	Coleman's Pygmy Seahorse	28–30	10	14	Relatively smooth, occasional small tubercles	0	0	Low and rounded with tentacle-like dermal appendage	2.2 <sup>g</sup>
<i>comes</i>	Tiger-tail Seahorse	35–36 (34–37)	17 (16–19)	18 (17–19)	Variable - knob-like and blunt to well-developed and sharp	2	1–2	Small and low with five rounded knobs	18.7 <sup>h</sup>

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TABLE 3. (Continued)

<i>Hippocampus</i> species	Standard common name	Tail rings (TaR)	Pectoral fin rays (PF)	Dorsal fin rays (DF)	Body spines	Cheek spines	Eye spines	Coronet	Max. recorded height (cm)
<i>coronatus</i>	Crowned Seahorse	39 (38–40)	12	14	Irregular but mostly lacking. Some long, thin and blunt-tipped spines	1	1	Extremely tall, turned backward with a fluted tip	12.7 <sup>l</sup>
<i>dahlhi</i>	Lowcrown Seahorse	41 (40–42)	17 (17–18)	21 (21–22)	Low	1–2	1	Low with three short backward-pointing spines	14 <sup>j</sup>
<i>debelius</i>	Softcoral Seahorse	28	10–11	14	Very few, but those present are long, sharp	1	1–2	Low, angular ridge with two sharp spines	3.5 <sup>k</sup>
<i>denise</i>	Denise's Pygmy Seahorse	28–29	10 (10–11)	14	Smooth or with occasional tubercles	0	0	None, rounded hump	2.1 <sup>l</sup>
<i>erectus</i>	Lined Seahorse	36 (34–39)	15–16 (14–18)	18–19 (16–20)	Variable, better developed on trunk rings (TrR) 1,3,5	1–2	1	Variable; usually wedge- or ridge-like, or raised with sharp edges or spines	19 <sup>c</sup>
<i>fisheri</i>	Fisher's Seahorse	37–38 (36–39)	15 (13–16)	17–18	Small, sharp	1	1–2	Slightly raised with five tiny sharp points	8 <sup>c</sup>
<i>guttulatus</i>	Long-snouted Seahorse	37–39 (35–40)	17 (16–18)	19–20 (17–20)	Medium-well developed with blunt tips	1	1	Low but distinct with five rounded knobs and long plate in front, not joined smoothly to neck	18 <sup>m</sup>
<i>hippocampus</i>	Short-snouted Seahorse	37 (35–38)	14 (13–15)	17 (16–19)	Low	0–2	0–2	Narrow and ridge-like, large and angular in W. African specimens	15 <sup>n</sup>
<i>histrix</i>	Thorny Seahorse	35 (34–37)	18 (17–20)	17 (15–18)	Extremely long and sharp	1	1	Medium with four or five long sharp spines	17 <sup>o</sup>
<i>ingens</i>	Pacific Seahorse	39 (38–40)	16 (15–17)	19 (18–21)	Variable - low rounded bumps to well-developed and blunt-tipped	1	1–2	Medium-high and tilted backward with five well-defined points or flanges at top	31 <sup>p</sup>

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TABLE 3. (Continued)

<i>Hippocampus</i> species	Standard common name	Tail rings (TaR)	Pectoral fin rays (PF)	Dorsal fin rays (DF)	Body spines	Cheek spines	Eye spines	Coronet	Max. recorded height (cm)
<i>jayakari</i>	Jayakar's Seahorse	38–39	17–18	18–19	Long and sharp, alternate tail spines low or lacking	2	1	Low-medium with four long sharp spines	14 <sup>g</sup>
<i>jugumus</i>	Collar Seahorse	38	16	21	Medium, sharp, longer on 1st, 4th, 7th and 11–12th trunk rings	1	2	Low with 6–7 short spines, larger head spine in front of coronet	4.4 <sup>t</sup>
<i>kelloggi</i>	Great Seahorse	40 (39–41)	18 (17–19)	18 (17–19)	Low and rounded	1	1	Medium-high with five short spines and high plate in front	28 <sup>s</sup>
<i>kuda</i>	Spotted Seahorse	36 (30–38)	16 (14–18)	17 (14–19)	Low, rounded bumps	1–2	0–1	Low-medium, overhanging at the back	17 <sup>c</sup>
<i>minotaur</i>	Bullneck Seahorse	41	11	7	None	0	0	Low mound	5 <sup>c</sup>
<i>mohnikei</i>	Japanese Seahorse	38 (37–40)	13 (12–14)	15–16	Low	2	0	Low ridge-like crest	8 <sup>c</sup>
<i>paradoxus</i>	Paradoxical Seahorse	41	11	N/A (type lacks dorsal fin)	None	0	0	Not visible, mound-like head	6.5 <sup>t</sup>
<i>patagonicus</i>	Patagonian Seahorse	37 (35–38)	14 (13–15)	18 (16–18)	Low	1	1	Variable; usually ridge-like but sometimes with sharp spines	15.5 <sup>s</sup>
<i>planifrons</i>	Flatface Seahorse	39 (39–41)	17 (16–18)	23 (21–23)	Low or none.	1	1	Five tiny points, slightly raised	11.6 <sup>c</sup>
<i>pontohi</i>	Pontoh's Pygmy Seahorse	26–28	9–10	14	Scattered tubercles on trunk and tail; branching filaments (usually red in life) attached to the fifth trunk ring	0	1	Raised, angular	1.7 <sup>t</sup>
<i>pusillus</i>	Pygmy Thorny Seahorse	34	12–13	15	Moderately well-developed, enlarged on 1st, 4th, 7th, 11th–13th trunk rings	1	2	Raised with six groups of 1–6 spines each	3.9 <sup>f</sup>

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TABLE 3. (Continued)

<i>Hippocampus</i> species	Standard common name	Tail rings (TaR)	Pectoral fin rays (PF)	Dorsal fin rays (DF)	Body spines	Cheek spines	Eye spines	Coronet	Max. recorded height (cm)
<i>reidi</i>	Slender Seahorse	35 (31–39)	16 (15–17)	17 (16–19)	None or low, rounded tubercles	1–2	1–2	Low and rounded or convoluted	17.5 <sup>c</sup>
<i>satomiae</i>	Satomi's Pygmy Seahorse	27–28	9	13	Spines all over body, enlarged on 1st, 2nd, 5th, 8th trunk rings, 4th, 8th, 11th and 14th tail rings	1	2	Raised with flanges (H-shaped when viewed from above)	1.1 <sup>t</sup>
<i>sindonis</i>	Sindo's Seahorse	37 (36–38)	12 (12–14)	12 (11–15)	Well-developed, blunt-tipped, irregular	1	2	Medium, angular	8 <sup>c</sup>
<i>spinosissimus</i>	Hedgehog Seahorse	36 (32–39)	17 (14–19)	18 (13–19)	Well-developed, either blunt or sharp, often longer on 1st, 4th, 7th, 11th trunk rings	1–2	1	Low-medium with four or five sharp spines	17.2 <sup>u</sup>
<i>subelongatus</i>	West Australian Seahorse	34 (33–36)	17 (16–18)	18 (16–20)	Low, rounded bumps	2	1	High-very high, with an expanded, rounded top	20 <sup>c</sup>
<i>trimaculatus</i>	Three-spot Seahorse	40–41 (38–43)	17–18 (16–19)	20 (18–22)	Low or slightly raised	1	1	Low with five tiny points	17 <sup>n</sup>
<i>tyro</i>	Tyro Seahorse	38	14–15	15	Low, rounded bumps (enlarged on 3rd, 7th trunk rings, 4th, 8th, 11th tail rings)	1	1	Crested ridge	6.1 <sup>v</sup>
<i>whitei</i>	White's Seahorse	35 (32–36)	16–17 (15–18)	18 (16–20)	Variable	1–2	1	High, inclined backwards, with seven small points	16.2 <sup>w</sup>
<i>zebra</i>	Zebra Seahorse	38–39	15–16	17	Low and sharp or none	1	1	Medium, conical with five to six tiny points	9.4 <sup>x</sup>
<i>zosteræ</i>	Dwarf Seahorse	31–32	11–12	12	Low, rounded bumps	0	0	High, columnar	2.5 <sup>c</sup>

<sup>a</sup>Francis (1988); <sup>b</sup>Cisneros-Montemayor *et al.* (2015); <sup>c</sup>Lourie *et al.* (1999); <sup>d</sup>Gomon (1997); <sup>e</sup>Kuiter (1997); <sup>f</sup>Lockyear *et al.* (1997); <sup>g</sup>Kuiter (2003); <sup>h</sup>Meeuwig *in litt.*; <sup>i</sup>Kaup (1856); <sup>j</sup>Kuiter (2009); <sup>k</sup>Gomon & Kuiter (2009); <sup>l</sup>Lourie & Vincent (2006); <sup>m</sup>Curtis and Vincent (2006); <sup>n</sup>Dawson (1986); <sup>o</sup>Masuda *et al.* (1984); <sup>p</sup>Miller & Lea (1972); <sup>q</sup>Kuiter (2000); <sup>r</sup>Kuiter (2001); <sup>s</sup>Diego and Luzzatto (2004); <sup>t</sup>Lourie and Kuiter (2008); <sup>u</sup>Nguyen and Do (1996); <sup>v</sup>Randall and Lourie (2009); <sup>w</sup>Harasti (2014); <sup>x</sup>Whitley (1964).

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**APPENDIX A.** Meristic data for *H. abdominalis* and putative species synonymized. Species names in parentheses are not currently recognized by us as valid. **Valid species and representative counts are highlighted in bold.** *N* = number of specimens examined. TaR = number of tail rings (modal value, with range in parentheses). PF = pectoral fin rays. DF = dorsal fin rays. ‘SL/RK matched’ = SL’s counts for specimens that both she and Kuitert (2001) have measured, RF = R. Fricke (2004).

Putative Species	N	TaR	PF	DF	Reference
<i>H. abdominalis</i>	6	44–45	15–16	25–28	(Kuitert 2001)
( <i>H. bleekeri</i> )	7	44–48	14–16	27–30	Kuitert (2001)
<b><i>H. abdominalis</i></b>	<b>18</b>	<b>47(45–48)</b>	<b>15(15–17)</b>	<b>27–28(25–33)</b>	<b>Lourie <i>et al.</i> (2004)</b>

**APPENDIX B.** Meristic data for *H. angustus* and putative species synonymized. See Appendix A for other abbreviations.

Putative Species	N	TaR	PF	DF	Reference
<i>H. angustus</i>	11	31–32	17 (15–20)	18–19	Kuitert (2001)
( <i>H. multispinus</i> )	8	35 (30–35)	17 (16–18)	18	Kuitert (2001)
( <i>H. grandiceps</i> )	10	33 (32–33)	18 (17–18)	18	Kuitert (2001)
( <i>H. hendriki</i> )	7	34	16–17	18 (17–18)	Kuitert (2001)
<i>H. angustus</i>	10	34 (32–34)	17 (15–19)	18 (17–19)	SL/RK matched
( <i>H. multispinus</i> )	7	31 (31 <sup>a</sup> –34)	18 (16–18)	18 (17–18)	SL/RK matched
( <i>H. grandiceps</i> )	10	33 (33–35)	16 (16–18)	18 (18–19)	SL/RK matched
( <i>H. hendriki</i> )	7	35 (33–35)	17 (16–18)	18 (18–19)	SL/RK matched
<b><i>H. angustus</i></b>	<b>54</b>	<b>33–34 (32–35)</b>	<b>16–17 (15–19)</b>	<b>18 (17–19)</b>	<b>Lourie <i>et al.</i> (1999)</b>
<b><i>H. subelongatus</i></b>	<b>23</b>	<b>34 (33–36)</b>	<b>17 (16–18)</b>	<b>18 (16–20)</b>	<b>Lourie <i>et al.</i> (1999)</b>
<i>H. subelongatus</i> (TYPE)	1	34	18	18	Paratype specimen, <i>Data for</i> Lourie <i>et al.</i> (1999)
Divided regionally according to Kuitert’s (2001) division between species					Data for Lourie <i>et al.</i> (1999) and SL unpublished data.
- W Australia (= <i>H. angustus</i> )	34	33 (32–35)	17 (15–19)	18 (17–19)	
- N Australia (= <i>H. angustus</i> )	14	34 (31–35)	16 (15–18)	18 (17–19)	
- NE Gulf Carpentaria (= <i>H. angustus</i> )	15	33 (33–35)	16–17 (16–19)	18 (17–19)	
- NE Australia (= <i>H. angustus</i> )	14	33–34 (33–35)	17 (16–18)	18 (17–20)	
<i>H. angustus</i> (TYPE)	6	34 (33–34)	16 (15–17)	19 (18–20)	SL unpublished data

<sup>a</sup>One specimen identified by RK as *H. multispinus* had only 29 TaR but it this may have been damaged.

**APPENDIX C.** Meristic data for *H. breviceps* and putative species synonymized. See Appendix A for other abbreviations.

Putative Species	N	TaR	PF	DF	Reference
<i>H. breviceps</i>	4	38–42	13–14	22 (21–22)	Kuiter (2001)
( <i>H. tuberculatus</i> )	12	36–37	15	20–21	Kuiter (2001)
( <i>H. tuberculatus</i> )	7	40 (39–40)	15 (14–15)	20 (19–20)	SL/RK matched
<b><i>H. breviceps</i></b>	<b>40</b>	<b>40 (39–43)</b>	<b>14–15 (13–15)</b>	<b>20–21 (19–23)</b>	<b>Lourie <i>et al.</i> (1999)</b>
<i>H. breviceps</i>					Data for Lourie <i>et al.</i> (1999)
- eastern specimens only	7	39 (37–44)	15	20 (19–21)	(= <i>H. breviceps</i> )
- western specimens only	20	40 (39–43)	15 (13–15)	21 (19–23)	(= <i>H. tuberculatus</i> )
- northwestern only	7	40 (38–40)	15 (14–15)	20 (19–21)	(= <i>type Z</i> <sup>a</sup> )
( <i>H. tuberculatus</i> ) (TYPE)	1	37	15	19	Data for Lourie <i>et al.</i> (1999)

<sup>a</sup>These specimens were included in Lourie *et al.* (1999) as *H. breviceps*, however they had had a distinctly more slender snout than other specimens.

**APPENDIX D.** *H. dahli*, *H. planifrons*, *H. trimaculatus*, *H. zebra* and putative species synonymize. See Appendix A for other abbreviations.

Putative Species	N	TaR	PF	DF	Reference
<i>H. dahli</i>	17	39 (37–40)	17 (17–18)	21 (21–22)	Kuiter (2001)
<b><i>H. trimaculatus</i> (all specimens)</b>	<b>56</b>	<b>40–41 (38–43)</b>	<b>17–18 (16–19)</b>	<b>20 (18–22)</b>	<b>Lourie <i>et al.</i> (2004)</b>
<i>H. trimaculatus</i> (no Australian specimens)	41	41 (38–43)	17 (16–19)	20 (18–21)	Lourie <i>et al.</i> (1999)
<i>H. trimaculatus</i> (west of Wallace’s Line)	33	41 (38–43)	18 (17–19)	20 (18–21)	Lourie <i>et al.</i> (1999)
<i>H. trimaculatus</i> (east of Wallace’s Line, no Australians)	8	39 (39–41)	17 (16–18)	19 (19–21)	Lourie <i>et al.</i> (1999)
<b><i>H. dahli</i></b>	<b>15</b>	<b>41 (40–42)</b>	<b>17 (17–18)</b>	<b>21 (21–22)</b>	<b>Data for Lourie <i>et al.</i> (1999)</b>
<b><i>H. planifrons</i> (= <i>H. biocellatus</i>)</b>	<b>9</b>	<b>39 (39–41)</b>	<b>17 (16–18)</b>	<b>23 (21–23)</b>	<b>split-spot <i>H. trimaculatus</i>, Data for Lourie <i>et al.</i> (1999)</b>
<i>H. trimaculatus</i> (zebra– striped form)	5	41 (40–42)	18 (17–19)	21 (20–21)	zebra-striped, Data for Lourie <i>et al.</i> (1999) (Viet Nam & Australia)
<b><i>H. zebra</i></b>	<b>3</b>	<b>38–39</b>	<b>15–16</b>	<b>17</b>	<b>Lourie <i>et al.</i> (2004)</b>
<i>H. zebra</i>	2	37–39	15–16	17–18	Kuiter (2001)
( <i>H. montebelloensis</i> )	2	38–39	15–16	18–19	Data for Lourie <i>et al.</i> (1999), SL/RK matched
( <i>H. montebelloensis</i> )	2	37	15–16	18–19	Kuiter (2001)

<sup>a</sup>See also appendix of *H. planifrons* (Appendix K) and putative species synonymized.

**APPENDIX E.** Meristic data for *H. guttulatus* and *H. bicuspis*. Although *H. bicuspis* was originally questionably synonymized with *H. guttulatus* due to meristic similarities (Lourie *et al.* 1999), we here treat it as a *species inquirendum* due to the distance of the type locality from extant known populations of that species. See Appendix A for other abbreviations.

Putative Species	N	TaR	PF	DF	Reference
<i>H. guttulatus</i>	<b>46</b>	<b>37–39 (35–40)</b>	<b>17 (16–18)</b>	<b>19–20 (17–20)</b>	<b>Lourie <i>et al.</i> (2004)</b>
( <i>H. bicuspis</i> ) (TYPE)	1	39	18	20	Data for Lourie <i>et al.</i> (1999)

**APPENDIX F.** Meristic data for *H. hippocampus* and putative species synonymized. See Appendix A for other abbreviations.

Putative Species	N	TaR	PF	DF	Reference
<i>H. hippocampus</i>	<b>35</b>	<b>37 (35–38)</b>	<b>14 (13–15)</b>	<b>17 (16–19)</b>	<b>Lourie <i>et al.</i> (1999)</b>
( <i>H. europaeus</i> )	14	36–37 (35–38)	14 (13–15)	18 (17–19)	Data for Lourie <i>et al.</i> (1999)

**APPENDIX G.** Meristic data for *H. histrix* and putative species synonymized. See Appendix A for other abbreviations.

Putative Species	N	TaR	PF	DF	Reference
( <i>H. curvicauspis</i> )	11	37 (35–37)	18 (17–18)	17	Fricke (2004)
( <i>H. curvicauspis</i> ) <sup>a</sup>	5	35 (35–36)	18 (17–18)	17 (15–17)	SL/RF matched
<i>H. histrix</i>	<b>22</b>	<b>35 (34–37)</b>	<b>18 (17–20)</b>	<b>17 (15–18)</b>	<b>Lourie <i>et al.</i> (1999)</b>
<i>H. histrix</i> (TYPE)	2	34–35	-	16–18	Syntype specimens. Data for Lourie <i>et al.</i> (1999)
<i>H. histrix</i>					Data for Lourie <i>et al.</i> (1999)
- Indian Ocean only	3	35 (35–36)	17–18	17	
- Pacific Ocean only	21	35 (34–37)	18 (17–20)	17 (16–18)	

<sup>a</sup>Does not include data for AMS IB.4155 which appears to be a different species (*H. spinosissimus*?) and has the following meristics: TaR = 37, PF = 17?, DF = ? and much less developed spines and a column-like coronet without long spines.

**APPENDIX H.** Meristic data for *H. kelloggi* and putative species synonymized. See Appendix A for other abbreviations. Note that Kuiter's (2001) *H. tristis* comprises specimens of more than one species. The types of *H. tristis* are a primary synonym of *H. kuda*, however some of the specimens that Kuiter identifies as *H. tristis* are in fact *H. kelloggi*.

Putative Species	N	TaR	PF	DF	Reference
<i>H. kelloggi</i>	<b>22</b>	<b>40 (39–41)</b>	<b>18 (17–19)</b>	<b>18 (17–19)</b>	<b>Lourie <i>et al.</i> (1999)</b>
( <i>H. tristis</i> )	12	35–37	18–19	18–19	Kuiter (2001)
( <i>H. tristis</i> )					
- 'Australian kelloggi'	4	39–40 (39–41)	19 (17–19)	18 (18–19)	SL/RK matched
- 'Australian kuda'	2	37	16	16–17	SL/RK matched
<i>H. kelloggi</i> (TYPE)	1	40	17	17	Holotype specimen, Data for Lourie <i>et al.</i> (1999)
( <i>H. suezensis</i> )	4	40 (38–40)	18 (17–18)	18	Lourie <i>et al.</i> (1999)
( <i>H. suezensis</i> )	1	40	??	20	Jawad <i>et al.</i> (2011)



**APPENDIX I.** Meristic data for *H. kuda* and putative species synonymized. See Appendix A for other abbreviations.

Putative Species	N	TaR	PF	DF	Reference
<i>(H. hilonis)</i> (TYPE)	1	35	16?	16	Holotype specimen, Data for Lourie <i>et al.</i> (1999)
<b><i>H. kuda</i></b>	<b>280</b>	<b>36 (30–38)</b>	<b>16 (14–18)</b>	<b>17 (14–19)</b>	<b>All specimens including those newly synonymized</b>
<i>H. kuda</i>	235	36 (34–38)	16 (15–18)	17 (17–18)	Lourie <i>et al.</i> (2004)
<i>H. kuda</i> (TYPE)	11	37 (35–37)	16 (15–17)	17 (16–18)	Syntype specimens from BMNH and RMNH, Data for Lourie <i>et al.</i> (1999) and SL (unpublished)
<i>(H. taeniopterus)</i>	6	34–35	16 (16–18)	17–18	Kuiter (2001)
<i>(H. taeniopterus)</i>	4 <sup>a</sup>	36–37 (one 30)	16	17–18	SL/RK matched
<i>(H. tristis)</i> (TYPE)	2	35–36	16	17	Syntype specimens, Data for Lourie <i>et al.</i> (1999)
<i>(H. natalensis)</i> (TYPE)	1	34	18	18	von Bonde (1924)
<i>(H. borboniensis)</i>	19	35–36 (34–38)	15–16	17 (16–18)	Lourie <i>et al.</i> (1999)
<i>(H. fuscus)</i>	21	34 (33–37)	15 (14–16)	16 (14–17)	Lourie <i>et al.</i> (1999)

<sup>a</sup>one specimen was tiny and may represent a new species. It had the following counts: TaR = 38, PF = 16?, DF = 15?

**APPENDIX J.** *H. mohnikei* and putative species synonymized. See Appendix A for other abbreviations.

Putative Species	N	TaR	PF	DF	Reference
<b><i>H. mohnikei</i></b>	<b>14</b>	<b>38 (37–40)</b>	<b>13 (12–14)</b>	<b>15–16</b>	<b>Lourie <i>et al.</i> (1999)</b>
<i>H. mohnikei</i> (TYPE)	3	39 (38–39)	12–13	15	Holotype and paratype specimens, Data for Lourie <i>et al.</i> (1999)
<i>(H. japonicus)</i> (TYPE)	5	39 (38–40)	13 (12–14)	16 (15–17)	Syntype specimens, Data for Lourie <i>et al.</i> (1999)

**APPENDIX K.** Meristic data for *H. planifrons* and putative species synonymized. See Appendix A for other abbreviations.

Putative Species	N	TaR	PF	DF	Reference
<i>H. planifrons</i>	4 <sup>a</sup>	37–38	18–19	23 (23–24)	Kuiter (2001)
<i>H. planifrons</i>	3	39	18 (16–18)	21–23	SL/RK matched
<i>(H. biocellatus)</i>	6	36 (36–38)	16 (16–18)	22 (22–23)	Kuiter (2001)
<i>(H. biocellatus)</i>	4	39 (39–41)	17	23 (22–23)	SL/RK matched
<b><i>H. planifrons</i></b>	<b>9</b>	<b>39 (39–41)</b>	<b>17 (16–18)</b>	<b>23 (21–23)</b>	<b><i>split-spot trimaculatus</i>, Data for Lourie <i>et al.</i> (1999)</b>
<i>H. planifrons</i> (TYPE)	1	39	18	22	Holotype specimen, data for Lourie <i>et al.</i> (1999)

<sup>a</sup>one specimen examined was only a photo that SL provided.

**APPENDIX L.** Meristic data for *H. pontohi* and putative species synonymized. See Appendix A for other abbreviations.

Putative Species	N	TaR	PF	DF	Reference
<b><i>H. pontohi</i></b>	<b>3</b>	<b>27 (26–28)</b>	<b>10(9–10)</b>	<b>14</b>	<b>Lourie and Kuiter (2008)</b>
<i>(H. severnsi)</i>	3	27	10	14	Lourie and Kuiter (2008)

**APPENDIX M.** Meristic data for *H. satomiæ* and putative species synonymized. See Appendix A for other abbreviations.

Putative Species	N	TaR	PF	DF	Reference
<i>H. satomiæ</i>	<b>2</b>	<b>27–28</b>	<b>9</b>	<b>13</b>	<b>Lourie and Kuitert (2008)</b>
( <i>H. waleananus</i> )	1	32	9	12	Gomon and Kuitert (2009)

**APPENDIX N.** Meristic data for *H. spinosissimus* and putative species synonymized. See Appendix A for other abbreviations.

Putative Species	N	TaR	PF	DF	Reference
<i>H. alatus</i>	7	34–36	17 (16–18)	17 (15–18)	Kuitert (2001)
( <i>H. alatus</i> <sup>a</sup> )	5	36 (34–36)	17 (16–17)	17 (14–17)	SL/RK matched
( <i>H. polytaenia</i> ) (TYPE)	1	36	16	17	Syntype specimen, Data for Lourie <i>et al.</i> (1999)
( <i>H. queenslandicus</i> )	18	35–36	17–18 (16–19)	17 (17–18)	Kuitert (2001)
( <i>H. queenslandicus</i> )	10	36–37 (36–38)	17 (16–18)	17 (17–18)	SL/RK matched
<b><i>H. spinosissimus</i></b>	<b>195</b>	<b>36 (32–39)</b>	<b>17 (14–19)</b>	<b>18 (13–19)</b>	<b>All specimens including those newly synonymized</b>
<i>H. spinosissimus</i>	53	36 (33–39)	17 (16–19)	17–18 (16–20)	Lourie <i>et al.</i> (2004)
( <i>H. spinosissimus</i> ) (TYPE)	2	35–36	16	17	Syntype specimens, Data for Lourie <i>et al.</i> (1999)
( <i>H. semispinosus</i> )	2	35–36	16–17	18	Kuitert (2001)
( <i>H. semispinosus</i> )	2	36–37	17	18	SL/RK matched

<sup>a</sup>SL counts do not include those for MWA S10959-001 which was designated as a paratype by Kuitert (2001) but is clearly a different species (likely *H. kelloggi*). Data for this specimen are: TaR = 40, DF = 19, PF = 18.

**APPENDIX O.** Meristic data for *H. whitei* and putative species synonymized. See Appendix A for other abbreviations.

Putative Species	N	TaR	PF	DF	Reference
<b><i>H. whitei</i></b>	<b>31</b>	<b>35 (32–36)</b>	<b>16–17 (15–18)</b>	<b>18 (16–20)</b>	<b>Lourie <i>et al.</i> (1999)</b>
( <i>H. procerus</i> )	10	34–35	16–18	17–19	Kuitert (2001)
( <i>H. procerus</i> )	4	35	16	18 (18–19)	SL/RK matched
<i>H. whitei</i>					
- north eastern specimens only	21	35 (32–36)	16–17 (16–18)	18 (16–19)	Data for Lourie <i>et al.</i> (1999)
- southeastern specimens only	13	35 (32–36)	16 (15–17)	17–18 (16–20)	

**APPENDIX P.** *H. zosteræ* and putative species synonymized. See Appendix A for other abbreviations.

Putative Species	N	TrR <sup>a</sup> + TaR	PF	DF	Reference
( <i>H. lichtensteinii</i> ) (TYPE)	1	10 + 31	12	11	Syntype specimen, Data for Lourie <i>et al.</i> (1999)
<b><i>H. zosteræ</i></b>	<b>17</b>	<b>9–10 + 31–32</b>	<b>11–12</b>	<b>12</b>	<b>Lourie <i>et al.</i> (2004)</b>
<i>H. zosteræ</i> (TYPE)	1	10 + 31	12?	12?	Syntype specimen, Data for Lourie <i>et al.</i> (1999)

<sup>a</sup>Note that trunk rings are also given because they differ from the normal number of 11 for the genus.