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Species limits and English names in the genus Gygis (Laridae)

by H. Douglas Pratt

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Summary.—The alpha taxonomy of the genus *Gygis* is controversial, with limited molecular studies contradicting distributional and phenotypic evidence that two Pacific forms, larger candida and smaller microrhyncha are separate species. This paper reviews evidence from the subfossil record, morphology, distribution and hybridisation, and vocalisations to conclude that Gygis comprises three biological species, nominate alba in the Atlantic, and two Pacific species. It also reviews historical English vernacular names and proposes 'fairytern' as a group name for these members of the newly recognised subfamily Gyginae. This name maintains popular tradition but requires a minor exception to some current naming conventions. Proposed English names are Atlantic Fairytern, Common Fairytern, and Little Fairytern. The name White Tern should now apply only to the historical single species, and Fairy Tern remains for Sternula nereis.

The genus Gygis (Laridae) is distributed around the world in tropical and subtropical seas. It comprises three morphologically distinct populations: Atlantic alba; the Indo-Pacific candida group with several named subspecies; and microrhyncha, with a relictual distribution in the Marquesas Islands of the eastern tropical Pacific (Wingate & Watson 1974, del Hoyo & Collar 2014, Thibault & Cibois 2017). The genus is currently classified variously as comprising one (Yeung et al. 2009, Dickinson & Remsen 2013, Thibault & Cibois 2017, Scott 2018, Gill & Donsker 2019), two (Thomas et al. 2004, del Hoyo & Collar 2014) or three species (Olson 2005, Steadman 2006, Howell & Zufelt 2019). Yeung et al. (2009) studied two mitochondrial genes in search of differentiation among four Pacific Gygis taxa, three named subspecies of the candida group plus microrhyncha, and concluded that none of these populations was diagnosable even at the level of subspecies. They found significantly smaller size in microrhyncha, but classified all Pacific populations as a single monotypic species. Thibault & Cibois (2017) expanded the Yeung et al. (2009) dataset geographically but did not alter the conclusions. The eclectic study of Thomas et al. (2004), with a different molecular dataset, considered microrhyncha a species. Subsequently, Jackson et al. (2012) showed that molecular studies of Charadriiformes that depend entirely on mitochondrial DNA can be problematic and would profit from additional nuclear markers. No such study has yet been published. With no current consensus, and molecular studies at odds with other data, a thorough systematic review is timely. This analysis includes published subfossil evidence (Steadman 2006) along with new information from biogeography, evidence of ongoing hybridisation, and previously overlooked differences in vocalisations. It also reviews the history of English names in Gygis, and proposes new ones that reflect current understanding of the taxonomy and evolutionary position of the genus.

Archaeology

Steadman (2006) summarised the now quite extensive literature on subfossil remains from the Pacific and showed that *G. microrhyncha* and *G. candida* (by using the epithet candida,

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he tacitly acknowledged nominate alba as a third species) were broadly sympatric across the tropical Pacific, from the Marianas (Tinian) in Micronesia to several sites in south-eastern Polynesia (two sites in Tonga, one in Samoa, Mangaia in the Cook Islands, and Tahuata in the Marquesas) in geologically recent times. Bones of both forms were found together at several sites, with no intermediates reported, which would not have been possible if, as Cibois & Thibault (2009) suggested, a continuum in size existed, with the smaller bones assigned to microrhyncha. Unfortunately, Steadman (2006) did not specify his criteria for identifying bones of the two Pacific Gygis, but the fact that he cited Pratt et al. (1987) suggests that he was aware of and took into account qualitative, as well as quantitative, differences. Thibault & Cibois (2017: 247) later criticised Steadman's (2006) work as based solely on 'geographical and morphological evidence', without mentioning that the geographical evidence involved a vast prehistoric zone of sympatry. Given that, candida and microrhyncha meet the gold standard of the biological species concept, i.e. sympatry without (apparent) interbreeding. Allopatric alba presumably forms a third species but must be evaluated using the character comparisons discussed below.

Morphology

Pacific members of Gygis exhibit two strikingly different bill shapes (Wingate & Watson 1974, Olson 2005; Fig. 1; note that legends may refer to online images in the Internet Bird Collection + Macaulay Library www.macaulaylibrary.org). Widespread candida exhibits a uniquely wedge-shaped or dagger-like bill quite unlike those of its congeners or, indeed, most other terns. The wedge-shaped look is enhanced because the insertion of the maxilla forms, in profile, a nearly straight line at an acute angle to the tomia, with the feather insertion of the mandible also appearing straight but at a less acute angle. The insertion thus inscribes a straight line bent slightly at the tomia (Fig. 1a). The culmen does not indent the forehead, so that, viewed from above or in front (Fig. 2a), the insertion line forms an inverted V or Greek lambda. The gonydeal angle is at the midpoint, and the bill is notably rich cobalt-blue over approximately the basal third (Figs. 1a, 3). Perhaps because of the thicker bill, this species has a subtly more rounded head profile, with a more bulbous forehead, than its congeners (pers. obs.; Figs. 1a, 3).

G. alba and G. microrhyncha have more conventional tern bill shapes with the culmen and gonys roughly parallel, then tapering to a very sharp awl-like tip (sharper in microrhyncha; Figs. 1b, 3). The inconspicuous gonydeal angle is set further back on the mandible. The insertion line of the maxilla is deeply bowed downward rather than straight. In *microrhyncha*, the feathers may extend into the nasal groove, often to an acute point, but in alba the forward protrusion is rounded (Fig. 3). From above or from in front, these insertion lines inscribe a rounded, shallow letter W, with the midpoint indenting the forehead (Fig. 2b; see video ML 201638871 for alba). Similarly, the base of the mandible is indented by a forward protrusion of feathers rather than squared off. This bill shape is conspicuously different, even at a distance, from the dagger-like bill of candida (Pratt et al. 1987, Morris & Beaman 2017; Figs. 1, 5). In alba and microrhyncha, the bill is entirely black, sometimes with a 'trace of blue at base' (Pratt et al. 1987: 187) in microrhyncha (often difficult to discern in photographs because of problematic light conditions). Note, however, that blue bill colour in microrhyncha could result from hybridisation with candida as discussed below. Although the bills of alba and microrhyncha are similar in general shape (alba somewhat thicker at the base) they differ strikingly in size, with alba the largest and microrhyncha the smallest in the genus (Fig. 3). Both have concave forehead profiles.

The bill bases of downy Gygis chicks resemble each other more than their respective adults but are by no means identical (Figs. 3, 6h; for image of same age microrhyncha, see



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Figure 1. The two Pacific forms of Gygis: (a) candida and (b) microrhyncha perched showing characteristic bill shape and dark primary shafts; (c) candida and (d) microrhyncha in flight, with the latter appearing a more compact, goggle-eyed bird with shorter, more rounded wings and less deeply forked tail; Marquesas Islands, French Polynesia (© Pete Morris) For comparable images of Atlantic alba, see ML 144554051 (for a and b) and ML 205939691 (for c and d).

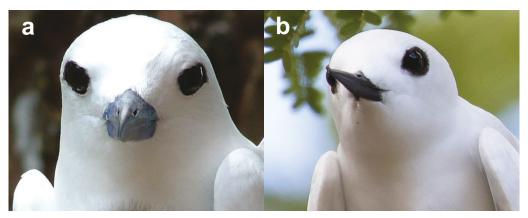
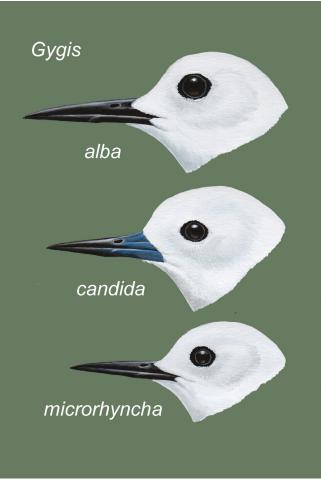


Figure 2. Head-on views of Pacific Gygis showing different bill insertion contours: (a) candida with inverted V or lambda-shaped basal contour, Honolulu, Hawaiian Islands (© Darcy Fiero); (b) microrhyncha with rounded or W-shaped contour, Nuku Hiva, Marquesas Islands (© Pete Morris). For comparable image of Atlantic G. alba, see ML 201638871.

ML 198094251; and for alba see video ML 201638871). By the time contour feathers start to emerge, the characteristic adult configuration of each species begins to take form, and adult base contour is achieved by the time juvenile plumage is complete (Fig. 4).

Certain plumage differences accompany the three Gygis bill morphotypes. In alba and candida, the shafts of the outer 3-4 primaries and the rectrices are darkly pigmented, sometimes on both surfaces. In microrhyncha, these feathers are immaculate or only the outermost primary has a dark shaft, and usually on the upper surface alone. All have black around the eye, thicker in front and behind it, the rest covering only about half of the feathered eye-ring, but the eyering of microrhyncha is broader, enhancing the endearing largeeyed appearance for which the genus is well known. The most noticeable morphological difference in flight is the shape



of the tail. In candida and alba, Figure 3. The three morphotypes of genus Gygis (H. Douglas Pratt, the tail is deeply forked, usually based on museum specimens and images of live birds)





Figure 4. Developmental stages of young Gygis candida, Kiritimati, Kiribati: above, young chick just beginning to grow contour feathers; below, full juvenile plumage with bill not fully grown, but showing adult insertion contour (© E. A. VanderWerf)

with the outermost rectrix longest (Fig. 5a). The tail fork is much shallower in microrhyncha with the outer two rectrices often shorter than the third, so that the fork disappears entirely when the tail is spread and it becomes almost spoon-shaped (Fig. 5b). In flight (Figs. 1c-d, 5) the wings of candida also look slightly longer and narrower than those of microrhyncha.





Figure 5. Gygis in overhead flight, showing differences in wing and tail shape, Marquesas Islands, French Polynesia: (a) candida with long narrow wings, deeply forked tail; (b) microrhyncha with shorter, slightly more rounded wings, rounded tail showing no fork in this configuration (© Pete Morris)

Yeung et al. (2009), Cibois & Thibault (2009), and Thibault & Cibois (2017) overlook, or dismiss as trivial, these qualitative differences among Gygis (Wingate & Watson 1974, Olson 2005) perhaps because bill shape in particular is not easily revealed by use of conventional bill measurements (Baldwin et al. 1931), nor did they consider the possibility that bill shape and colour can be important potential isolating mechanisms (Pratt et al. 1987: 185–186, Pratt 2010). Some of these phenotypic differences were the basis for splitting G. microrhyncha, but enigmatically not G. candida, from G. alba by del Hoyo & Collar (2014) employing the Tobias et al. (2010) scoring system. However, this taxonomy is untenable if Olson (2005) is correct that G. alba and G. microrhyncha are sister taxa, as morphology suggests.



Figure 6. Map of the Marquesas Islands showing the localities mentioned in the text.

Hybridisation and genetic swamping

Olson (2005) suggested that microrhyncha fell victim to a rapidly expanding candida that replaced it over vast areas by genetic swamping. S. L. Olson (unpubl. data; pers. comm.) examined a series of specimens in the US National Museum (USNM; Smithsonian Institution, Washington DC) of both Pacific taxa, including some with intermediate characters that may be hybrids, collected in the 1920s and 1930s from the Line and Phoenix Islands, where only candida apparently occurs today. I also examined these specimens but made no detailed notes. I have found evidence that genetic swamping is ongoing in the remaining relictual range of *microrhyncha*. Traditionally, *G. candida* and *G.* microrhyncha have been said to be parapatric within the Marquesas Islands (Fig. 6), with candida on the northernmost large island, Hatutaa (in most older literature referred to as Hatutu), and the relictual population of *microrhyncha* in the rest of the archipelago (Pratt et al. 1987). But the situation is more complex and dynamic than that. In 1983, I examined specimens at the American Museum of Natural History (AMNH; New York) collected in the Marquesas by the Whitney South Seas Expedition in 1921–22. I categorised each specimen as candida or microrhyncha based on the qualitative bill differences described above. Among seven specimens taken on Hatutaa, five were typical of candida, but two



Figure 7. A series of photographs of *Gygis* spp. taken on Hatutaa (Hatutu), Marquesas Islands, September 2013: (a) an individual very close to *G. candida*, but with a slightly thinner bill, reduced blue at the base, and shallow tail-fork; (b) another bird, also superficially like pure *candida*, but with no blue at the base of the bill; (c) a bird a with much thinner bill than typical *candida* but with a blue basal third and irregular margin to the maxilla, with white feathers intruding into the nasal groove as in *microrhyncha*; (d) a mated pair with dagger-shaped bills, both of which show evidence of mixed ancestry, with the left-hand bird showing some blue at the bill base but an irregular margin, and that on the right an all-black bill with margin that bows outward and only the outermost primary has a dark shaft; (e) a bird approaching the morphology of *G. microrhyncha*, but with a somewhat thicker blue bill base; (f) a bird that appears to be pure *microrhyncha*; (g) a bird in juvenile plumage (compare with Fig. 4) that appears to be *G. microrhyncha*; and (h) a juvenile bird just starting to lose its natal down, with a bill base typical of *microrhyncha* but with more blue tinge than usual for that species. Images (g) and (h) suggest that *G. microrhyncha* may still breed on Hatutaa, which island was long thought to harbour only *G. candida* (© David Sargeant)

(AMNH 194874 and 194888) were intermediate. Likewise, two (AMNH 220772 and 194881) of three specimens from neighbouring Eiao could not be identified by bill type. All other specimens from the Marquesas were typical microrhyncha (n = 39) except one specimen of candida (AMNH 194905) from Mohotani. Holyoak & Thibault (1984) reported that among 17 specimens (apparently including the seven I examined at AMNH) from Hatutaa, 13 were intermediate, three looked like candida, and one like microrhyncha. From nearby Eiao, the same authors found two intermediates and three typical microrhyncha. Ten specimens from Mohotani, much further south in the archipelago (Fig. 6), included three each resembling candida and microrhyncha and four intermediates. If their specimens included any collected after the early 1920s, those later specimens might provide evidence of progressive changes during the 20th century (or Holyoak & Thibault may simply have used different methods to categorise specimens).

In September-October 2013 a group of prominent birders visited both Hatutaa and Ua Huka (Sargeant 2013). Among their images from Hatutaa are several birds with intermediate bill structure, thicker than in typical microrhyncha but not as heavy as in candida, with a proximal border not as straight, and no blue at the base. These probably represent hybrids or intergrades. Sargeant himself obtained a heretofore unpublished series of images from Hatutaa that reveal a highly variable Gygis population on the island (Fig. 7). He photographed several birds that resemble typical candida but have all-black bills whose rear margins are not quite straight; one adult that approaches typical microrhyncha; and another adult, a juvenile, and a much younger chick that appear to be intermediate between the parental morphotypes. These images are the first photographic evidence of possible hybridisation and intergradation between candida and microrhyncha in the Marquesas. They reveal that a few G. microrhyncha may persist in nearly pure form on Hatutaa, and that many of the birds most observers would identify as G. candida there differ noticeably from typical members of that species.

G. candida appears to be slowly invading the Marquesas from north to south and displacing microrhyncha by hybridisation and genetic swamping (Todesco et al. 2016) as Olson (2005) suggested had occurred in the Line Islands. Thus, across the Pacific, the microrhyncha phenotype may have disappeared completely from previously inhabited islands, but left a trail of microrhyncha genes, a possibility not considered by molecular systematists. Importantly, such hybridisation does not necessarily imply that the two taxa are conspecific (e.g. Fowler et al. 2009, Lavretsky et al. 2015) but it may lead to the extinction of the species being genetically swamped (Todesco et al. 2016), which suggests that G. microrhyncha should probably be considered an endangered species. No one has suggested any obvious reason for the displacement of the formerly sympatric G. microrhyncha by G. candida, but it was broadly coincidental with human colonisation of the Pacific (Steadman 2006). The genetic interactions of G. candida and G. microrhyncha in the Marquesas are fertile ground for further research. The variations in Fig. 7 suggest that for most hybrids, traits are inherited in a blending, rather than mosaic, pattern. The fact that both parental types appear to persist in the zone of intergradation also suggests a non-random pattern of hybridisation. But these observations are mere speculation until further genetic and field studies can be undertaken.

Vocalisations

Although Yeung et al. (2009) did not study microrhyncha in the field, they claim that it and candida have 'no subspecific distinctions in behavior or vocalizations'. That statement overlooks Holyoak & Thibault's (1984) report that microrhyncha sounds different to the



ISSN-2513-9894 (Online) human ear, and that chicks in the Marquesas, presumably microrhyncha, utter a begging call not heard in other populations (which requires further investigation; apparently no recordings exist). I searched recordings of all forms of Gygis in the two major online archives: Macaulay Library (ML; www.macaulaylibrary.org; now incorporating the former Internet Bird Collection); and Xeno-canto (XC; www.xeno-canto.org). Both permit one to listen to a recording and simultaneously view its sonogram. Sound-recordings of candida are plentiful, but those of alba and microrhyncha are relatively few in these collections, and many more samples are required before firm conclusions can be drawn.

Vocalisations of G. candida are remarkably uniform throughout the Indo-Pacific (pers. obs.). Most frequently heard is a series of identical short raspy notes, yik-yik-yik...etc., c.5 per second, spanning 2 KHz to 10 KHz (e.g. ML 32673). These are contact notes that may be given by perched birds or groups flying over a colony. Sometimes these notes take on a more structured pattern that rises to a crescendo, then falls symmetrically (e.g. ML 32586 2:21–2:29). Another vocalisation, possibly used for chick defence because it is often uttered when humans approach, is a series of low-pitched twangy notes, consisting of a short sharp whistle followed very quickly by a more structured lower-pitched note or two such notes given in harmony (e.g. ML 5410, ML 96891). It recalls the sound of a stretched rubber band plucked near the ear. These notes may be interspersed with loud raspy upslurred notes, longer in duration than those of birds flying over (e.g. ML 94998 0:21-0:32), which indicate heightened alarm.

Only two recordings were available that I could confidently identify as pure G. microrhyncha, but they yielded some surprises. One (ML 203895301) of several birds includes a series of short, sharp rasps similar to flight calls of G. candida, plus a series of five two-syllable raspy notes, shi-dick, shi-dick,... quite unlike anything I have heard or found in archives for G. candida elsewhere in the Pacific. So distinctive are these calls that I question whether they were uttered by G. microrhyncha, but no other species is identified on the recording, and in the sonogram these calls appear to be continuous sounds from the same bird or birds giving more typical vocalisations. A recording from Hatutaa (ML 203895611) identified as G. microrhyncha sounds very much like typical G. candida and, as discussed above, could represent an intergrade. T. Mark recorded G. microrhyncha calls on Ua Huka (XC 75212) that are probably homologous to the 'rubber band' calls of G. candida. They have a similar twangy quality, but sound higher pitched, cover a narrower sound spectrum (2.5–10.0 KHz), and possess a simpler structure with an initial loud note followed by a faint but identical 'echo' that equates to the 'rubber band' effect.

The voice of Atlantic G. alba is even more distinctive. All of its vocalisations are strikingly lower pitched than those of either Pacific species, making homologies less obvious. The rapidly repeated notes (XC 431353) are much heavier sounding because they are sustained longer and are pitched at only 2-3 KHz. A structured rising and falling version (XC 14680) reaches no higher than 7 KHz. The 'rubber band' call is similarly low-pitched (1–8 KHz) and the individual notes possess a unique structure with only one 'echo' note that in a sonogram appears like a hook dangling from the initial note. Another low-pitched vocalisation (XC 431354) has long-sustained notes with a far more complex structure than anything uttered, as far as is known, by either Pacific species.

In summary, although homologies can be discerned, each species of Gygis appears to have a unique vocal repertoire easily distinguishable from the other two. Further recordings of G. alba and especially G. microrhyncha are a critical research requirement. The most obvious gap in sound collections are the reportedly distinctive begging calls of microrhyncha chicks (Holyoak & Thibault 1984).



Conclusions

Yeung et al. (2009) and Thibault & Cibois (2017) present a view, based on studies of two mitochondrial genes, that the genus *Gygis* has no genetic structure across the vast tropical Pacific Ocean. This paper summarises a large body of phenotypic and biogeographic evidence that suggests otherwise. The subfossil record demonstrates broad sympatry, the ultimate test of the biological species concept, of two Pacific species in pre-human times. Qualitative shape differences among the three species have been overlooked because standard measurements are not adequate to detect such differences. New and historical evidence of hybridisation, as G. candida continues its hypothesised range expansion and genetic swamping of G. microrhyncha, suggests a possible source of genetic bias. Striking vocal differences, described here for the first time, also suggest that Gygis comprises three species. Nevertheless, molecular systematists (Thibault & Cibois 2017) and list-makers (Gill & Donsker 2019) have seized upon the Yeung et al. (2009) study to make generalisations that dismiss other lines of evidence. However, the findings of Jackson et al. (2012) suggest that fresh research, including both nuclear and mitochondrial genes, is sorely needed in this complex before genetic data can be seriously weighed against seemingly overwhelming non-molecular evidence. For now, the only meaningful taxonomy is to regard G. alba, G. candida and G. microrhyncha as biological species.

English names redux

Readers have undoubtedly noticed that, until now, I have avoided using English names. Vernacular names in this genus have a long, highly controversial, and still unresolved history, in which I have been involved for several decades as a member and advisor to committees that led up to what was the International Ornithological Congress' committee on English names (Gill & Donsker 2019). Now, the split into three species and recent genetic studies of higher categories within the Laridae (see below) have fundamentally altered the discussion and require that we reconsider English names in this genus.

As an iconic single species, G. alba has long been popularly known as the fairy tern, a name that has served it well and is a difficult one to abandon, given the birds' popularity in areas where it is conspicuous to large human populations (Morgan 2007). Unfortunately, when Sternula (formerly Sterna) nereis, a little-known small tern restricted to temperate waters of Australia and New Zealand, was discovered in the 19th century, it was also called 'fairy tern'. Nevertheless, in much of the rest of the world, 'fairy tern' continued to be used for G. alba. Ornithologists began employing the rather insipid 'White Tern' for G. alba, which gained fairly wide acceptance, particularly among list compilers, but the general public was less easily persuaded (although see Scott 2018). To this day, ordinary folk and popular publications around the world know and love the 'Fairy Tern', and not in reference to S. nereis (e.g. Floyd 2019 and comments). Even when White Tern is used, it is usually followed by 'also known as Fairy Tern' or similar, or given as alternatives (White / Fairy Tern). In Honolulu, Hawaii, where the bird is a city icon (Morgan 2007, Scott 2018), the hybrid name 'White Fairy Tern' has taken hold (Yuen 2012, Allen 2019, Vollbrecht 2019). Pratt et al. (1987) offered a compromise that involved hyphenating 'fairy-tern' in the case of Gygis, while keeping 'Fairy Tern' for the austral bird, but current trends on the use of hyphens in bird names (Gill et al. 2009) make this problematic. However, the guidelines of the American Ornithological Society's checklist committee (Chesser et al. 2019) would still consider hyphenated fairy-tern viable.



Meanwhile, molecular systematists have been studying evolutionary relationships within the family Laridae, i.e. terns, gulls, jaegers and skuas, and skimmers. One important finding is that noddies (Anous, probably including Procelsterna; Cibois et al. 2016), traditionally thought to be terns, are a basal offshoot and sister to the rest of the Laridae, forming their own subfamily Anoinae (Bridge et al. 2005, Pons et al. 2005, Baker et al. 2007). Because a few narrower studies (Ödeen et al. 2010, Cibois et al. 2016) considered Gygis a sister group to noddies, Gill & Donsker (2019) prematurely proposed such names as 'White Noddy' or 'Fairy Noddy' for the then-single species. A consensus topology (Thibault & Cibois 2017: 246) now positions Gygis as an independent basal offshoot of Laridae forming its own subfamily Gyginae (grouping it with the noddies would render the Anoinae paraphyletic). However, the precise position of Gygis at the base of the larid tree remains unsettled (Jackson et al. 2012). Unfortunately, Howell & Zufelt (2019), whose book is likely to be very influential among birders, unwisely call the members of Gygis 'white noddies', a name that now appears to be misleading or wrong (Thibault & Cibois 2017).

Because these birds are neither noddies nor typical terns, the three species in the Gyginae need a name that will distinguish them as a group, which the unhyphenated 'white tern' fails to do. I propose the unhyphenated compound name 'fairytern' as a group name for Gygis (leaving Fairy Tern for Sternula nereis). That way, the Gyginae would be indexed under F, but S. nereis under T with other Sterninae. I understand that this name violates, slightly, one rule proposed by Gill & Donsker (2019) but I believe 'fairytern' should be granted an exception comparable to those made for such traditional names as 'goldfinch' and 'skylark'.

Use of 'fairytern' would allow non-professionals to maintain a beloved and widely used name without being scolded by pedants. Note that 'fairytern' has a subtly different pronunciation from 'fairy tern'. For the three species, Howell & Zufelt (2019) use the epithets Atlantic, Indo-Pacific, and Little. I suggest 'Common' in place of 'Indo-Pacific', which, although appropriate, is an unfamiliar construct among the general public. Common Fairytern is appropriate, despite 'Common' as a modifier of bird names being often denigrated (pers. obs.), because the bird is indeed common most places where it occurs, it is the species most people will see, and the epithet has been used by birders in the Pacific at least since publication of the Pratt et al. (1987) field guide, until recently the only such reference for the region. 'White Tern' should now be reserved for the monotypic species before it was split, as required by American Ornithological Society rules (Chesser et al. 2019). As for Sternula nereis, if an additional modifier is deemed necessary, 'Austral Fairy Tern' would suffice, but I do not advocate such a change.

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