ISSN 0738-9388

Volume: 54 THE FESTIVUS ISSUE 3

A putative inter-generic hybrid between *Harpago* Mörch, 1852 and *Solidistrombus* Dekkers, 2008 (Gastropoda: Neostromboidae; Strombidae) from Đảo Phú Quý Vietnam

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ABSTRACT This paper presents a new putative inter-generic *Harpago chiragra* x *Solidistrombus latissimus* hybrid from Đảo Phú Quý, Vietnam. Hybridisation is not uncommon with the Strombidae, with 12 inter-generic and 11 infra-generic hybrids known in the literature. Understanding the rates and extent of hybridisation within an organism complex facilitates a greater understanding of the potential for hybrid derived speciation in that complex.

KEYWORDS Đảo Phú Quý, *Harpago*, hybridisation, *Solidistrombus*, speciation, Vietnam.

INTRODUCTION

Hybridisation is a pathway to speciation and is known to occur between genetically and morphologically divergent groups (Hamilton and Johnson 2015). In organisms where there are multiple opportunities for hybridisation, such as secondary contact or sympatry, and evidence for high rates of hybridisation, introgression and fixation of traits is not to be unexpected (Parker *et al.* 2020). The introgression of characteristics into a complex may not indicate that divergence between two parental populations is occurring, but rather may signal the decline of one species through merging of species complexes (van Wky *et al*. 2019; Matute *et al.* 2020). Similarly, a hybridisation event may represent a random mating event with no fecundity in offspring resulting in no consequences for either parental stock.

Hybridisation may also lead to taxonomic errors in species recognition based on morphology (Costa *et al.* 2019). This has two implications. First, the recognition of hybridisation in species which are very similar morphologically where the hybridisation even leads to an organism with negligible morphological variation form the parental stock (Slager *et al*. 2020). Second, implications for deciphering the taxonomy of highly morphologically variable species complexes where phenotypical states for both parental species are discordant (Schweizer *et al.* 2019). The recognition of a species arising from the consequences of hybridisation needs evidence of morphological constancy and for that morphological form to be present through time (Maxwell *et al*. 2019).

The hybridisation of sympatric taxa is not uncommon and may occur in between localised populations being absent in a broader shared range (Natacha *et al.* 2020). This localised hybridisation is seen as a pathway towards genetic diversification through ongoing introgression and may lead to genetic diversification that may lead to the recognition of cryptic subspecies (Maxwell and Dekkers 2019; Everson *et al*. 2020; Maxwell *et al*. 2021).

In the family Strombidae, hybridisation is an ongoing process occurring between species at both the inter-generic and infra-generic level (for a synopsis of hybridisation in Strombidae, see Maxwell *et al.* 1999). This indicates that there is a level of tension in stromboidian species demarcation with a low degree of reproductive isolation even between genetically divergent taxon, although this level of reproductive isolation is not uncommon in nature between divergent taxa (Lu *et al*. 2020; McEntee *et al.* 2020; Pérea-Pedraza *et al*. 2021). Notwithstanding this high propensity and occurrence of hybridisation within the family, the Philippines being a particular hot spot, the majority of hybrids do not result in speciation events with most hybrids considered episodic (for a synopsis of hybridisation in Strombidae, see Maxwell *et al*. 1999). However, hybridisation between the Philippine stromboidian genera *Lambis* Röding, 1798 and *Millepes* Mörch, 1852 has resulted in at least one record of speciation, with the recognition of *Millepes achnoides* (Shikama, 1971) as having modern hybrid ancestry (Maxwell *et al*. 2019). In this paper, we present a novel example of episodic hybridisation between two different genera within Strombidae from Đảo Phú Quý, Vietnam, and this new hybrid highlights of hybridation potential of taxon with the family.

METHODS

During a trip to Đảo Phú Quý, off the southeast Coast of Vietnam, the second author was hunting during March 2020 for specimens of *Harpago chiragra* (Linné, 1758), known to fishermen as Ốc bàn tay (hand), and *Solidistrombus latissimus* (Linné, 1758), also known to locals as Ốc bàn ủi (flat iron), both being collected for consumption (Figure 1). Within the catch of returning fishermen, the second author noted an unusually formed specimen, and this was purchased for future study. This specimen was later brought to the attention of the first author, who recognised it as a putative hybrid between the two fished species of molluscs. The putative hybrid is described and compared with the proposed parents and illustrated along with examples of both species obtained from the same catch (Figure 2). The provided length of shell reflects the maximum length, including digitations.

SYSTEMATICS

Harpago Mörch, 1852

Type. *Strombus chiragra* Linné, 1758.

Diagnosis. The shell is large to very large, with six extended digitations. The last anterior digitation, the anterior canal, is reflected to the left of the shell axis. The second anterior canal forms an extension of the stromboidal lobe and is reflected to the right. The stromboidal sinus, which serves to allow the eye to extend when the shell is lying flat, is u-shaped and well defined. The final posterior digitation crosses the spire almost perpendicular to the axis and then is reflected posteriorly. The aperture is quadrate with the second and third posterior digitations arising from the corners of the aperture; the middle digitation arising near the halfway point along the aperture. The dorsum is crossed by strong wide ribs that have wide interspaces. The posterior canal is constricted. The aperture is constricted internally, and the columella is thickened anteriorly forming a long plate at the lower half.

Remarks. There are three species in the *Harpago* complex. *Harpago arthritica* (Röding, 1798) from the African coasts has a distinctively lirate aperture within the aperture. The Coral Sea atoll species, *Harpago rugosa* (Sowerby, 1842), is a more delicate species with a deep red aperture. The most widespread species within the complex is *Harpago chiragra*, ranging throughout the tropics from India to

ISSN 0738-9388

French Polynesia. It varies in rarity, being uncommon in Queensland, but collected commercially in the central and northern Pacific (Figure 1). *Harpago chiragra* is the only member of the genus to come from Đảo Phú Quý. Members of the *Harpago* do not show a great deal of diversity in form other than the occasional extra digitation.

Solidistrombus Dekkers, 2008

Type. *Strombus sinuatus* Humphrey, 1786.
Original Diagnosis. "Shell large to very large, solid to very thick walls, medium weight to heavy weight shells. The form of the shell is not triangular (as in *Tricornis*), but rather oval. Spire tall columella and aperture smooth outer lip very thick, broadly flared with striking posterior expansions in the form of a flap or finger-like digitations. Outer lip has a striking sharp ridge or a thickened ridge (without the sharp ridge) which readily characterises the genus. Body whorls decorated with knobs, sometimes large and mostly on or around the broad shoulder. Stromboid notch is present, mostly large" (Dekkers 2008, p. 45).
Remarks. The genus is restricted to the central and western Pacific into Indonesia, with two member species coming from the Đảo Phú Quý, *Solidistrombus latissimus* and *S. sinuatus* (Lightfoot, 1786). While rare in other parts of their range (such as Queensland), these two species are regularly encountered in the northern range where they are targeted for eating by local fishermen (Figure 1). The attractive *S. taurus* (Reeve, 1857) is known from islands in the central Pacific where it forms colonies and is periodically collected for the specimen trade and is not hunted commercially. The rarest of the complex, *S. theristies* (Swainson, 1822), is known form the Coral Sea and surrounding reef systems, and Japan. Members of the *Solidistrombus* have a stable form varying little across their range.

***Harpago chiragra* (Linné, 1758) x *Solidistrombus latissimus* (Linné, 1758)**

Description. The shell is large and heavy with an ovate shape with a fringed outer lip and a few rudimentary formed digitations. The dorsum has raised broad spiral ribs with interspecies that contain finer spiral threads. The teleoconch is triangulate, with sightly concave whorls with moderate nodulations. The anterior canal forms the last digitiation which is short but distinctly reflected to the left. The aperture is primarily smooth and white internally, with a moderate constriction that is tinged with red within; the posterior outer lip is forming a broad, thin flange that is marginally coloured russet. The central outer lip is thickened, and the anterior lobe is broad and does not have a digitation. The stromboidal sinus is well defined. The columella is well defined and smooth. The posterior canal is open. Maximum length 14.5 cm (Figure 2A)
Remarks. There are distinctive features found in the putative hybrid that is unique to its parents (Figure 2B-C). The dorsum carries a similar form to *Harpago chiragra*, with broad raised ribs with interspaces that contain two or three finer raised spiral threads, both features absent in *Solidistrombus*. Similarly, the teleoconch follows after *H. chiagra* being more triangulate and nodulous than *S. latissimus*. The ventral side is more akin to *S. latissimus*; there is the broad ovate flaring lip, with a thickening mid-length typical of that species. While there are rudimentary legs and a general spininess to the outer lip margin found in *H. chiragra*, these are rudimentarily formed. Most striking is the reflected and extended anterior canal of the hybrid. The lack of digitation extending out of the stromboidal lobe typically is a trait closer to *S. latissimus* than to *H. chiragra*. The hybrid aperture colour is typical of *S. latissimus,* being orange toward the outer lip with a white inner,

unlike the nearly uniform red to pink interior typical of *H. chiragra.*

DISCUSSION

There are literary records for both putative intra-generic and inter-generic hybridisation between *Solidistrombus* and other members of the *Neoaligerinae*, the *Lambis* and *Harpago* in particular (Maxwell *et al.* 2019). While intra-generic hybridisation between *Solidistrombus taurus* and *S. sinuatus* and inter-generic hybrids between *Lambis lambis* (Linné, 1758) and *Solidistrombus latissimus* are recorded (Kronenberg, 2008), this is the first record of a hybrid between *Solidistrombus* and *Harpago.* Given that this the first recorded example of hybridising of these two sympatric species and that there is no evidence for the establishment of a population, the hybridisation event is to be considered episodic (Maxwell *et al.* 2019).

While the hybridisation event presented in this paper is episodic, when it is contextualized with the wider potential for stromboidian hybridisation (see Maxwell *et al*. 2019), and the frequency of those hybrids, it cannot be dismissed that the stromboidians have entered a stage of hybrid driven speciation. It is to be expected that as our knowledge of the family grows, and more samples come to hand, that novel taxa with a hybrid ancestry will be described (Maxwell *et al.* 2019). The level of hybridisation within the family has resulted in the blurring not only of some species boundaries in terms of morphology creating taxonomic inconstancies.

This morpholocal bluring caused by hybrids in turn may have led to the aggregating genera, such as *Millepes* with *Lambis* (Dekkers 2008), although Dekkers (2008) did not offer any rationale the decision to merge the genera. In this case, there is enough morphological justification for the reinstatement of the genus *Millepes* (see Abbott 1961) irrespective of the level of hybridisation with sister genera (Maxwell *et al.* 2019). The use of reproductive barriers as basis for genera would lead to the collapse of much of the stromboidian taxonomy, resulting in large aggregations of species within a genus. In addition to the example presented in this paper where the two genera are untenable under a reproductive isolation model, a great many other genera, such as *Conomurex* Fisher, 1884 and *Gibberulus* Jousseaume, 1888 (Dekkers and Maxwell 2018), would have to be merged. This despite their significant anatomical differences (Maxwell and Rymer 2021). The flow-on of such a theoretical approach would create chaos for the systematics across diverse phyla and result in a great loss of relational meaning between taxa that is implicit within the nomenclature (Oyebanji *et al.* 2020; Akita *et al.* 2021). Therefore, the use of reproductive isolation as means of assessing taxonomic validity is crude and should be avoided being grounded in what is to be considered blunt and anachronistic speciation theory (Maxwell *et al*. 2020).

CONCLUSION

This paper presents the first example of inter-generic hybridisation within Strombidae between *Harpago chiragra* and *Solidistrombus latissimus*. The high propensity for hybridisation within this family gives rise for opportunistic introgression and the fixation of traits. This can make the discernment of species boundaries problematic between species where hybridisation is common. Given the high rates of hybridisation with the family, particularly inter-generic, it is problematic to hybrids as a basis to argue for taxonomic division, or validity of genera, without risking the potential collapse of the entire nomenclature into a mono-generic system, not dissimilar to the revision of

Abbott (1960). Furthermore, the high rates of hybridisation also increase the propensity for such mating to result in new species.

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Cite as:

Maxwell S.J. and K. Ocean. 2022. A putative inter-generic hybrid between *Harpago* Mörch, 1852 and *Solidistrombus* Dekkers, 2008 (Gastropoda: Neostromboidae; Strombidae) from Đảo Phú Quý Vietnam. The Festivus 54(3):196-203 http://doi:10.54173/F543196

ISSN 0738-9388

Figure 1. Đảo Phú Quý off the southeast coast of Vientam **(A)**, and the historical remnants of prior fishing trips to collect mollusca for food showing mounds of *Harpago chiragra* (Linné, 1758), **(B-D)**, and the fresh catch, including *Solidistrombus latissimus* (Linné, 1758), **(E)** (map: GoogleEarth accessed 13/10/2021; images of middens: by Khang Ocean, 03/2020).

ISSN 0738-9388

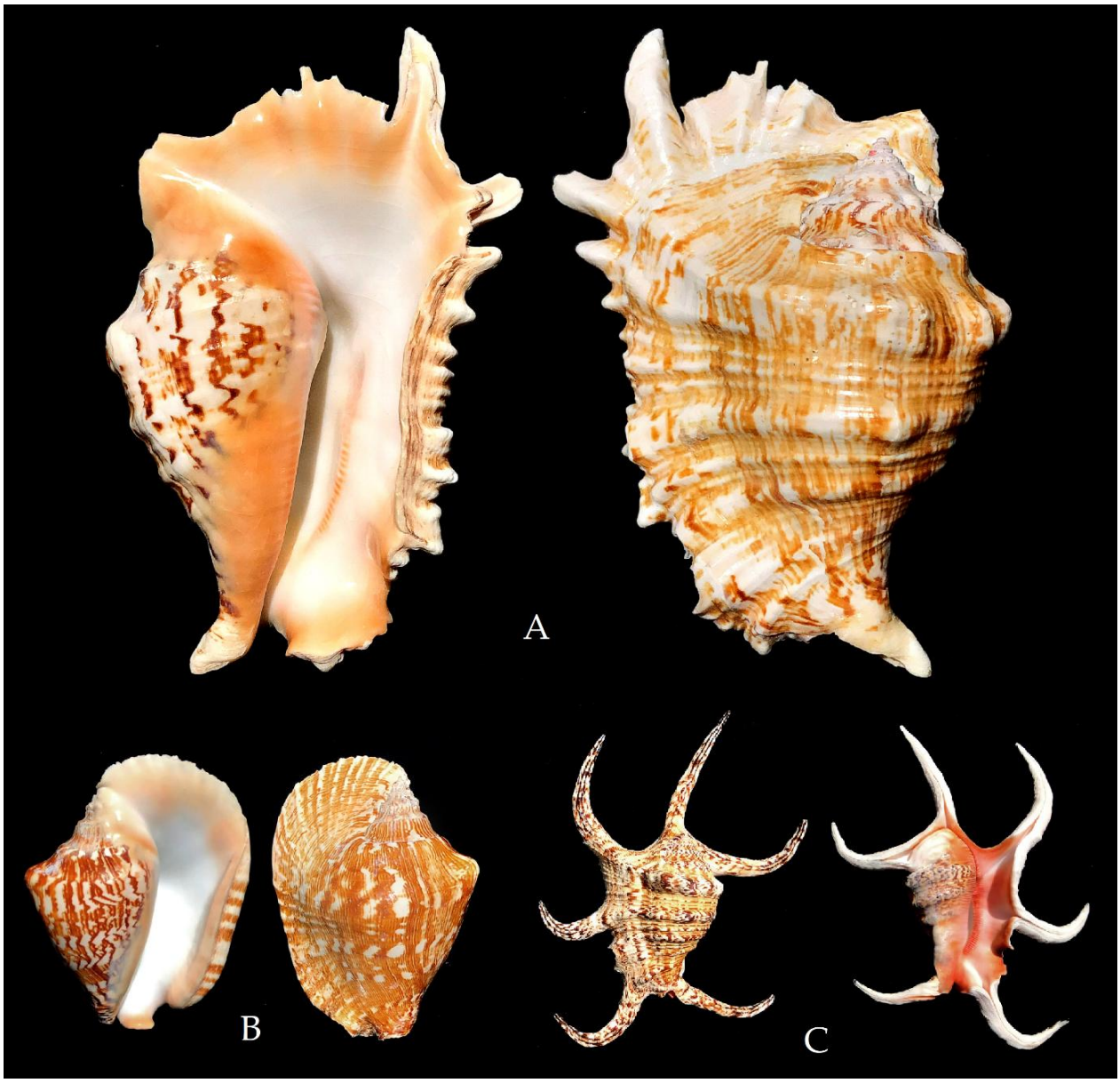

Figure 2. The hybrid showing its parental species all from Đảo Phú Quý, Vietnam: **A=** putative hybrid between *Harpago chiragra* (Linné, 1758) and *Solidistrombus latissimus*, 14.5 cm (Collection of Khang Ocean); **B=** *Solidistrombus latissimus* (Linné, 1758) 16.0 cm (Collection of Khang Ocean); **C=** *Harpago chiragra* 25.0 cm (Collection of Khang Ocean).