

An intergeneric hybrid (Gastropoda: Caenogastropoda: Strombidae) with remarks on the subdivision of Indo-Pacific *Tricornis*

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A supposed hybrid of the strombid genera *Sinustrombus* and *Lambis* is reported upon. It is compared with the supposed parental species. Based on literature records, a list of reported hybrids within the family Strombidae is provided. Some recently described genus level taxa within the Strombidae are briefly addressed.

Key words: Gastropoda, Strombidae, *Tricornis*, *Lambis*, hybridisation.

DEDICATION

About 25 years ago I had contact with Dr. Edi Gittenberger for the first time. This was when I had the opportunity to examine the collection of Strombidae at the Rijksmuseum van Natuurlijke Historie, then still in the old building at the Raamsteeg in Leiden. At that moment I would never have believed that 20 years later I had the honour to serve in the EDI-torial board of Vita Malacologica together with Dr. Gittenberger.

But before that I had to suffer from his editorial pen. One of these occasions was after submitting a paper for Vita Marina (Kronenberg, 1993). As that paper was on a supposed hybrid of two species of the genus *Lambis* Röding, 1798, it seems appropriate to dedicate this contribution, also on a supposed hybrid, to Dr. Gittenberger, commemorating his retirement from active duty in the very same museum where we first met.

INTRODUCTION

Before viable hybrids are born or hatched, a lot of barriers have to be crossed, see Dubois (1988). This must also be true for molluscs. Yet, supposed hybrids within Mollusca have been reported in literature (Kronenberg, 1993 and references therein); not only limited to the Recent fauna but probably also in the fossil record e.g. for *Melanopsis* (Cerithoidea) (Geary, 1992) -and still occurring (Heller et al., 2005). Hybridisation is probably not restricted to gastropods. For instance Voskuil & Onverwagt (1990) reported on a possible hybrid in *Acanthocardia* (Bivalvia, Cardiidae). Hybrid offspring can be fertile (see e.g. Owen *et al.*, 1971; and Mello-Silva *et al.*, 1998).

The first to report a possible hybrid within the family Strombidae was Wolfe (1974) on a presumed hybrid of *Lambis crocata crocata* (Link, 1807) × *L. scorpius scorpius* (Linnaeus, 1758). Since that paper, Kronenberg (1993) discussed specimens with characters intermediate between *L. millepeda* (Linnaeus, 1758) and *L. truncata sebae* (Kiener, 1843). These had earlier been described as *L. arachnoides* Shikama, 1971, and were at that time better known as *L. wheelwrighti* Greene, 1978. In that paper Kronenberg concluded that there was no proof of hybridisation, but that data strongly suggested the possibility of hybridisation. Since that paper a large number (far over 500) of this supposed hybrid have become known, and they appear rather frequently on the commercial market, so reproduction with fertile offspring may also occur among these possible hybrids. This matter requires

Hybrid	Alias	Source	#
<i>Doxander vittatus</i> × <i>D. campbelli</i>		Man in 't Veld & Visser, 1993: pl. 3 figs 6, 6a	1
<i>Euprotomus bulla</i> × <i>E. chrusostomus</i>		Liverani, 2002	2
<i>Euprotomus bulla</i> × <i>E. vomer</i>	<i>E. hirasei</i>	Kuroda, 1942 Kronenberg, 1999 Kronenberg, 2002	3
<i>Euprotomus bulla</i> × <i>E. aratrum</i>		J.P. Barbier, pers. comm. Photograph seen	1
<i>Harpago c.chiragra</i> × <i>Lambis lambis</i>		De Turck et al., 1999: pl. 30 fig. 2 Kronenberg, 2008: 530, pl. 210	4
<i>Lambis c. crocata</i> × <i>L. s. scorpius</i>	<i>Lambis gaspardi*</i>	Wolfe, 1974 Springsteen & Leobrera, 1986: 69, pl. 16, fig. 7 De Turck et al., 1999: pl. 31 figs 1, 2 Thach, 2007 : 18, fig. 38 Kronenberg, 2008: 534, pl. 212	>100
<i>Lambis c. crocata</i> × <i>L. lambis</i>		De Turck et al., 1999 : pl. 30 fig. 1 Thach, 2007 : 18, fig. 37 Kronenberg, 2008: 532, pl. 211	?
<i>Lambis lambis</i> × <i>L. millepeda</i>		Kronenberg, 1993: 54, pl. 3 figs 5a, 5b De Turck et al., 1999: pl. 32 fig. 3 Kronenberg, 2008: 530, pl. 210	> 100
<i>Lambis lambis</i> × <i>L. s. indomaris</i>	<i>Lambis christinae</i>	Bozzetti, 1999 Bozzetti, 2006	4
<i>Lambis lambis</i> × <i>L. s. scorpius</i>		De Turck et al., 1999: pl. 30 fig. 4 Thach, 2007 : 18, fig. 36 Kronenberg, 2008: 536, pl. 213	?
<i>Lambis millepeda</i> × <i>L. truncata sebae</i>	<i>L. millepeda</i> Kurz, 1970 (non Linnaeus, 1758) <i>L. arachnoides</i> ; <i>L. wheelwrighti</i>	[Kurz, 1970] Shikama, 1971 Gary, 1974 Greene, 1978 Collins, 1980 Leobrera, 1980 Springsteen & Leobrera, 1986: 69, pl. 16, fig. 2 Kronenberg, 1993 De Turck et al., 1999: pl. 32 Kronenberg, 2008: 528, pl. 209	> 500
<i>Lambis millepeda</i> × <i>L. s. scorpius</i>		De Turck et al., 1999: pl. 31 fig. 3 Kronenberg, 2008: 536, pl. 213	?
<i>Lentigo lentiginosus</i> × <i>L. pipus</i>		Kronenberg, 2008: 564, pl. 227	1
<i>Sinustrombus latissimus</i> × <i>S. sinuatus</i>		Thach, 2007: 18, fig. 35 Kronenberg, 2008: 544, pl. 217	± 5
<i>Sinustrombus sinuatus</i> × <i>S. taurus</i>		Bob Abela, Guam, pers. comm. Photograph seen	1
<i>Lambis lambis</i> × <i>Sinustrombus latissimus</i>		Herein	1

more research.

Since the Kronenberg (1993) paper, some more presumed hybrids within the family Strombidae were reported upon. Bozzetti (1999 and 2006, as *L. christinae*, but the illustrations show a specimen with characters intermediate between *L. scorpius indomaris* Abbott, 1962 and *L. lambis* (Linnaeus, 1758)); De Turck et al. (1999); Kronenberg (1999 and 2002); Liverani (2002); and more recently Thach (2007); and Kronenberg *in* Poppe (2008), discussed, or illustrated specimens of supposed hybrid origin.

An overview of supposed strombid hybrids known (taken from literature) is presented in table 1. So far thirteen of these hybrids have been reported upon in literature, most of them only by images. Another supposed hybrid, *Euprotomus aratum* (Röding, 1798) × *Doxander vittatus apicatus* (Man in 't Veld & Visser, 1993) (Thach, 2007: 18, fig. 39) is not recognised here, as this specimen only appears to be an aberrant, high spired specimen of *E. aratum*. Only the hybrids *Euprotomus bulla* (Röding, 1798) × *E. chrysostomus* (Kuroda, 1942) reported by Liverani (2002); *E. bulla* × *E. vomer* (Röding, 1798), first described as *Strombus hirasei* Kuroda, 1942 reported by Kronenberg (1999); *Lambis millepeda* × *L. truncata sebae*; and *L. lambis* × *L. scorpius indomaris* (Bozzetti, 1999) have been discussed in detail.

Soon after the publication by Thach (2007) the present author became aware of another possible hybrid within the family Strombidae. Subsequently Dr. Thach made this specimen available for study. This specimen is described and discussed herein. During the preparation of this paper the author became aware two more supposed hybrids (pers. comm. Jean-Pierre Barbier and Bob Abela), totalling the number of supposed hybrids within Strombidae to sixteen.

During the preparation of this paper, two papers (Bandel, 2007 and Dekkers, 2008) were published that described genus level taxa that were to be addressed briefly in this paper. As names for these taxa, from both Bandel (2007) and Dekkers (2008) are available now, these genus level taxa are discussed further below.

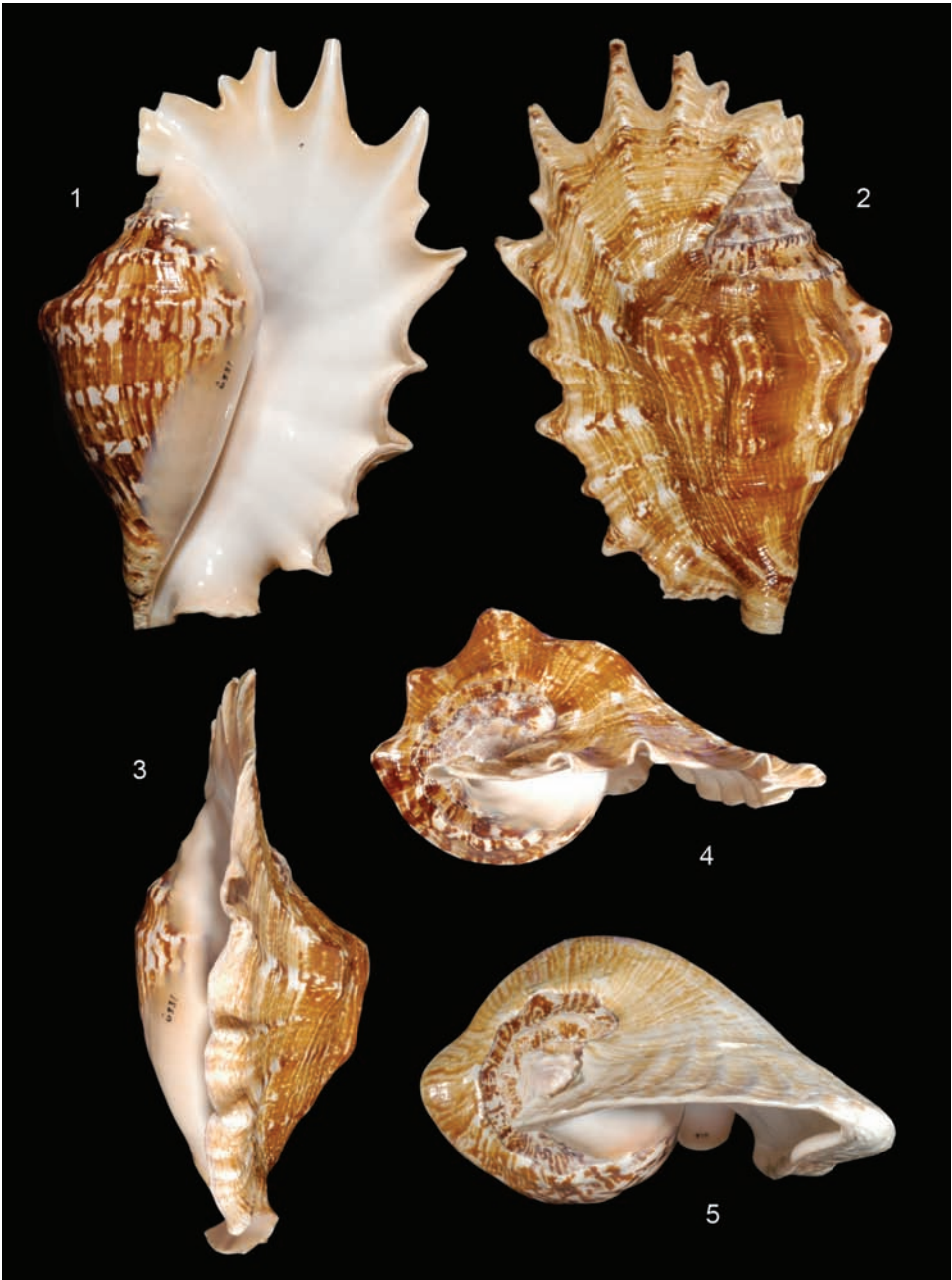
DESCRIPTIVE PART

Lambis lambis (Linnaeus, 1758) × *Sinustrombus latissimus* (Linnaeus, 1758) (figs 1-4)

Description. — Shell large, length including digits and anterior canal 184.4 mm. Protoconch worn off. Teleoconch with about 9 whorls, spire regularly coiled, not truncated. Spire on adapertural side largely covered by callous. First teleoconch whorl not covered, angled at shoulder, with calcareous deposit on it. Second whorl with close spaced axial folds, on the fourth whorl gradually transformed into, initially indistinct, shoulder knobs. From fourth whorl onward whorls concave. Fifth whorl with eight shoulder knobs discernable on half of whorl, other half covered by callus, subsuturally with numerous fine spiral lines, also present on shoulder knobs, suture of subsequent whorl running over shoulder knobs, just abapical of shoulder. Indistinct subsutural cord present from fifth whorl onward. Shoulder knobs gradually increasing in size, numbering six on sixth whorl at 50% of whorl covered by callus, eight on seventh whorl, visible on three quarters of a whorl. On the eighth whorl suture of last whorl set slightly adapical of shoulder knobs at

◀ Table 1. Records of (supposed) hybrids within Strombidae, taken from literature, with an estimate of numbers of hybrids known (#). The supposed hybrid *Euprotomus aratum* × *Doxander vittatus* (Thach, 2007: 18, fig. 39) is omitted, as this specimen appears to be a malformed *E. aratum* (Röding, 1798). Names of supposed hybrids appearing in literature are included.

* The name *Lambis gaspari* is a nomen nudum and has appeared only on the Conch-L discussion site.



Figs 1-5. 1-4, supposed hybrid *Lambis lambis* (Linnaeus, 1758) x *Sinustrombus latissimus* (Linnaeus, 1758) Vietnam, Binh Thuan province, approx. 250 km south of Nha Trang, by local fishermen at 15 – 20 m, summer 2007. Actual length, including digits and anterior canal 184.4 mm, author's collection reg. no. 6331; 1. Apertural view; 2. Dorsal view; 3 Lateral view; 4. Apical view. 5. *Sinustrombus latissimus* (Linnaeus, 1758) Philippines, no further data. Actual width 128.8 mm. Note adcolumnellary strongly bent outer lip, visible as a gutter in photograph. Photographs by Jeroen Goud.

adapertural side of the spire. The eighth whorl also shows marks of a large injury, just adapical of the suture of the last whorl. On the last whorl the adapertural side of the shell with four rather large but low shoulder knobs, penultimate knob highest, last one being very low. Abapically of the shoulder, also at the adapertural side two more rows of knobs, the adapical one with three knobs, the last one of that row connected with the penultimate one of the shoulder knobs, the abbasal one with would better be referred to as a very low indistinct cord with two very low knoblets. Indistinct spiral cords present all over the dorsal side of the shell.

Outer lip widely dilating with 12 projections (digits), first two broken off due to thinness of that part of the outer lip, third very short seemingly from the same starting point as the fourth. The third digit has rather an open, lobe-like character as a (closed) digit-like character. This lobe-like character is supposed to be present in the first two projections as well. With the fourth digit the process of forming a tube (to be subsequently filled by the animal with inner shell material) is becoming visible. Fourth, fifth and sixth digit projecting abbasal, (almost) parallel with the shell's axis. Tip of fourth digit broken off, fifth digit longest. Seventh digit very small, hardly developed. From the eighth digit onward, digits become more solid. Eighth digit still an open tube, but digits nine to twelve, that are very short, at stages of closing the tubes. Especially digit eleven is very short. Strombid notch deep and broad with three, obsolete, rounded triangular projections, flange between strombid notch and anterior canal with four, even less developed triangular projections. Anterior canal distinct but short, no traces of parts being broken off. Adapertural side of outer lip and columellar callus smooth with no traces of plicae.

Colour of shell white with collabral, sometime slightly wavy, lines of brown. These brown lines are irregularly interrupted just abapical of the suture on the spire whorls till about half way the last whorl. Four more such broad spiral white lines are visible on the last whorl, the three most adapical ones running towards the shoulder knobs, but the idea of the broad line disappears just after crossing the first knob. The abbasal one runs towards what is to become the strombid notch, but the white line appearance has faded before reaching the strombid notch. Towards the rim of the outer lip, the idea of white lines reappears, each white line leading towards the tip of a digit. Adapertural side of outer lip white. Towards the rim of the outer lip, especially the apical side between the digits and the strombid notch and flange between this notch and anterior canal, of a light pinkish orange colour. Within the aperture the colouring is very light salmon. Columellar and parietal callus rather thin, only where spire is embedded the callus is thick, whitish, abaperturally with the same light pinkish orange, slightly darker at columellar callus. On parietal area callus very thin, pattern of last whorl shining through.

Operculum and soft parts unknown

Locality data. — Vietnam, Binh Thuan province, approx. 250 km south of Nha Trang, by local fishermen at 15 – 20 m, summer 2007.

The specimen is kept in the author's collection reg. No. 6331, and will be deposited in Nationaal Natuurhistorisch Museum, Leiden, The Netherlands, at some point in the future.

As names of hybrids are excluded from the International Code of Zoological Nomenclature (Art. 1.3; see also Art. 17.2 and Art. 23.8 for the availability of *Strombus hira-sei*, *Lambis arachnoides*, *L. wheelwrighti* and *L. christinae*) no name is proposed for the specimen reported herein.

	<i>Lambis lambis</i>	supposed hybrid	<i>Sinustrombus latissimus</i>
size	92* - 280 mm	184.4 mm	111 - 220 mm
number of digits on outer lip	6	12	0
Columella	smooth	smooth	smooth
Aperture	smooth	smooth	smooth
Apex	pointed	pointed	pointed
Lateral hump on shoulder of last whorl, opposite of aperture	absent or clearly smaller as next (adlabial) knob in row	present, slightly larger as next (adlabial) knob in row	present, large
knobs on dorsum	present, well developed	present, well developed	absent
anterior canal	elongated	short	extremely short, merely a notch
parietal and columellar callus	abapical of shoulder broad but relatively thin, absent on shoulder	abapical of shoulder intermediate and thin, absent on shoulder	narrow but rather thick
colour pattern outer shell	Very variable, cream with light or dark brown maculation, spotted or mottled with purplish to blackish wavy narrow to broad lines	see description herein, very close to <i>T. latissimus</i>	See description of hybrid specimen discussed herein; colour lighter on abapertural side of last whorl
colour pattern aperture	Cream, tan, sometimes pinkish to orange rose, towards rim of outer lip often light purplish	White, peach/salmon towards rim of outer lip	White, peach/salmon towards rim of outer lip
colour pattern columellar and parietal callus	Cream, tan, or light purplish	White, peach/salmon towards rim of outer lip, not as dark as in <i>T. latissimus</i>	White, peach/salmon towards rim of outer lip

*The measurement of 92 mm corresponds with typical *L. Lambis*. Extreme malformed dwarfs, measuring to as little as 45 mm of *L. lambis* have been named *L. adamii* Bozzetti & Cossignani, 2003.

Table 2. Comparison of *Lambis lambis* (Linnaeus, 1758), *Sinustrombus latissimus* (Linnaeus, 1758) and the supposed hybrid specimen. Characters of *L. lambis* and *S. latissimus* based on literature records and personal observations.

DISCUSSION

At first glance this specimen could be mistaken for a malformed species of *Lambis* Röding, 1798 (type species *Strombus lambis* Linnaeus, 1758). Such malformations are quite

common in *Lambis* spp. (e.g. Walls, 1980: 62, top figs; De Turck et al., 1999: pl. 14, fig. 2, pl. 25 fig. 2, pls. 34, 35; Thach, 2007: pls 82 – 86).

However, in *Lambis* spp. the digits grow at approximately the same speed and once their full length is reached, the rims of these digits curl inwards, forming a conical tube, which is subsequently filled with nacreous material, thus forming a solid digit. This process is going on simultaneously in all digits, i.e. all digits are in the same growth phase. An exception to this is *Lambis violacea* (Swainson, 1821) and, to a lesser extent, *L. digitata* (Perry, 1811), where the bifid first digit is lobed in *L. violacea* and slightly open in *L. digitata* in adult specimens. Within the specimen here discussed the most adapical digits are not or barely starting to form the conical tube, while the lateral, most abapical digits are already completely formed, or even closed. Moreover, these lateral digits are extremely short, not characteristic of any species of *Lambis*. The anterior canal within species of *Lambis* (with the exception of *Harpago* Mörch, 1852 (type species *Lambis harpago* Röding, 1798 [= *Strombus chiragra* Linnaeus, 1758]), which is, based on morphological grounds, considered here as a genus rather than a subgenus of *Lambis*) is very much elongated. This is not the case in this specimen.

These overall differences with *Lambis* spp. strongly suggest that this specimen is not a *Lambis*, but of a hybrid origin, suggesting that one of the parental species is a *Lambis*.

The overall habitus with the large and more robust shape of the specimen suggest that the other parental species should be allocated in what was until recently named *Tricornis* Jousseaume, 1886 (type species *Strombus tricornis* Lightfoot, 1786), *Tricornis* used here in the restricted sense, i.e. only applicable to Indo-Pacific species, see Kronenberg & Vermeij (2002) and Kronenberg & Lee (2007).

As this specimen was found off the Vietnamese coast, I assume that both parental species live off the Vietnamese coast. This would eliminate *L. violacea*; *L. digitata*; and *L. truncata truncata* ([Lightfoot], 1786) as possible parental species, as these species live in the Indian Ocean (Abbott, 1961; Walls, 1980; Kronenberg & Berkhout, 1984; De Turck et al., 1999) as well as *L. robusta* (Swainson, 1821) restricted to the Society Islands and Tuamotu Archipelago. It would also eliminate *T. tricornis* (Lightfoot, 1786) and *T. oldi* (Emerson, 1965) as both these species are restricted to the Red Sea and adjacent part of the Indian Ocean, resp. Oman and Somali coasts (Emerson, 1965; Walls, 1980; Kronenberg & Berkhout, 1984; De Turck et al., 1999) as well as *Sinustrombus taurus* (Reeve, 1857), which is restricted to the Marshall islands and the Marianas (Abbott, 1960; Walls, 1980; Kronenberg & Berkhout, 1984; De Turck et al., 1999).

As stated earlier (Kronenberg, 1993) a hybrid specimen would express characters that are in between both supposed parental species, or a mixture of characters of both parental species. That is, characters are expressed in a less conspicuous way, but present, for instance in presence of sculptural elements or colouration of the shell. Based on this assumption, the specimen reported herein is considered a hybrid of *Lambis lambis* (Linnaeus, 1758) × *Sinustrombus latissimus* (Linnaeus, 1758). For characters of these species and the supposed hybrid, see Table 2.

The following species of *Lambis* are reported from the Vietnamese coasts: *Lambis crocata crocata* (Link, 1807); *L. lambis*; *L. millepeda* (Linnaeus, 1758); *L. scorpius scorpius* (Linnaeus, 1758); and *L. truncata sebae* (Kiener, 1843); (Abbott, 1961; Walls, 1980; Kronenberg & Berkhout, 1984; De Turck et al., 1999).

More recently, both *L. crocata pilsbryi* Abbott, 1961 (Thach, 2005: 55, pl. 15 fig. 1; 2007: pl. 82) and *L. s. indomaris* Abbott, 1961 (Thach, 2007: 65, pl. 15, fig. 260) have also been reported from off Vietnam.

As there is a complete absence of plicae on the adcolumnellar side of the outer lip as well as on the columella itself, *L. scorpius scorpius* (Linnaeus, 1758); *L. s. indomaris* Abbott,

1961; and *L. millepeda* (Linnaeus, 1758) (see Abbott, 1961; Walls, 1980; Kronenberg & Berkhout, 1984; De Turck et al., 1999) are rejected as possible parental species. These species also have a vividly coloured aperture, a character they share with *L. crocata crocata* and *L. c. pilsbryi* (see Abbott, 1961; Walls, 1980; Kronenberg & Berkhout, 1984; De Turck et al., 1999; Thach 2005; 2007). For these reasons these species are also rejected as a potential parental species. *Lambis truncata sebae* might be taken into consideration, but the apex of the supposed hybrid discussed herein shows no sign at all of truncation of the spire. Also, the shoulder knobs on the last whorl in *L. t. sebae* are very poorly developed. The size of the shoulder knobs on the last whorl in the supposed hybrid are relatively too well developed in comparison with the shoulder knobs of *L. t. sebae*, when taking into account a possible parental *Thersistrombus* Bandel, 2008 species also.

Sinuistrombus latissimus (Linnaeus, 1758); *S. sinuatus* (Lightfoot, 1786) and *Thersistrombus thersites* (Swainson, 1823) live off the Vietnamese coast (Thach, 2005). *Thersistrombus thersites* has a relatively slender spire, an outer wing that is less expanded lateral in comparison with *S. sinuatus* and *S. latissimus*, and the adapical part of the outer lip stays well below the apex. *Sinuistrombus sinuatus* has a violet to dark purple colour deep within the aperture.

What remains is the possibility of a hybrid of *L. lambis* (Linnaeus, 1758) \times *S. latissimus*. Both these species live off the Vietnamese coast (Thach, 2005) and indeed, this specimen reported herein shows characters that are intermediate between these two species, or characters of one of the parental species, more or less strongly expressed (see also table 2).

The more lobe-like character of the first outer lip projections and the subsequent more open digits in clockwise direction is reminiscent of *Lambis violacea*.

As with all supposed hybrids within Strombidae (see table 1) reported hitherto, the animal of the specimen described herein is unknown. Recently an animal of a supposed hybrid between two species of *Lambis* has become available for study. The results of this examination of both shell and soft parts will be published elsewhere (Simone et al. in prep.). From this specimen a tissue sample for DNA sequencing is also available. Results of this sequencing will also be published elsewhere.

Especially since the last few decades the number of supposed hybrids within the Strombidae, both in supposed combinations as well as in absolute numbers, has increased a lot. There are a few possible explanations for this phenomenon.

First; these hybrids have always been around, but never paid attention to, as large strombs were mostly used as a source of food for people on the Philippines and other countries and islands in the Indo-Pacific. The shells had no value at all, and have always been discarded. Which species taste good and which ones taste bad is of course known. So, the species that taste better, e.g. *Lambis lambis*, are widely collected while other species hardly. With increase of collecting effort on shells for the commercial market, Philippine collectors are more aware of the value of shells for this market and these fishermen sell specimens to local shell dealers. In that respect it is indeed remarkable that most hybrids are reported from Philippine waters (Kronenberg, 2008) and, to a lesser extend, Vietnamese waters (Thach, 2007). An exception seems to be the hybrid *L. millepeda* \times *L. truncata sebae*, which is reported from Tsoi Island, Papua New Guinea (Collins, 1980) and is also known from at least two specimens collected off Pulau Buton, SE Sulawesi, Indonesia (Bunjamin Dharma, pers. comm. 19 August 2008).

Second; as a result of over collecting, both for food and the commercial shell market, the parental species of these large strombs are getting more and more scarce. This has been observed by Mr. Guido T. Poppe (pers. comm. March 2008) for e.g. *L. lambis*. During mating season adults find it harder to find a mate of the same species, and, sometimes successfully interbreed with other species.

Third; these viable hybrids may interbreed with (one of the) parental species, as could be possible in the case of *L. millepeda* × *L. truncata sebae*, or without much success as in those cases where only one or a few hybrids are known. We cannot rule out the possibility that these hybrids out compete (one of the) parental species.

There is, however, insufficient data to support any of these explanations.

Remarks on the splitting of *Tricornis* Jousseaume, 1886

Recently, both Bandel (2007) and Dekkers (2008) split up the genus *Tricornis* in the restricted sense as used by Kronenberg & Vermeij (2002) and Kronenberg & Lee (2007). Four names for genus level taxa have become available. The names by Bandel have been introduced as subgenera of *Strombus*, Dekkers' taxon as a full genus.

1. *Thersistrombus* Bandel, 2007: 146-147. TS *Strombus thersites* Swainson, 1823.

2. *Sinustrombus* Bandel, 2007: 155. TS *Strombus taurus* Reeve, 1857. Another species included by Bandel (2007: 155) is *Strombus oldi* Emerson, 1965. Although not explicitly mentioned in the text, *S. sinuatus* [Lightfoot], 1786 is also allocated by Bandel to this taxon as can be concluded from the caption of his text fig. 21b.

3. *Latissistrombus* Bandel, 2007: 155-156. TS *Strombus latissimus* Linnaeus, 1758. Although not explicitly stated, *Strombus sublatissimus* d'Orbigny, 1852 from the Oligocene of the Western Tethys might belong to this group according to Bandel (2007: 156).

4. *Solidistrombus* Dekkers, 2008: 44. TS *Strombus sinuatus* [Lightfoot], 1786. In the original description erroneously the authors name and year appear between brackets. Other species included (Dekkers, 2008: 46) are *S. latissimus*; *S. taurus*; and *S. thersitus* [sic]. The names of these species appear already as *Solidistrombus* spp. with the author's names and dates between brackets.

So, we have four genus level taxa, with four different type species for five species. These taxa partly overlap one another, and therefore it is important to establish the dates when these papers were published.

In an email sent on April 1st by Bandel to the present author, it was stated: "I finished my Opus on the Strombimorpha ...", without further referring to a date of publication. There is no date of publication printed on the paper by Bandel, but Dr. Olaf Elicki, editor of Freiburger Forschungshefte, informed me (email 24 April 2008) that it was published in December 2007. As no exact date could be specified, the publication of Bandel's paper is 31 December 2007 following ICZN Article 21.3.1.

The cover of "De Kreukel" that carries the paper by Dekkers is dated "maart-april 2008". Mr. Cor Karnekamp had copies of this issue available on April 19th, and when asked he stated that the issue had come from the printers' the previous day, i.e. April 18th.

Therefore, if synonymous, the names introduced by Bandel have priority over *Solidistrombus* Dekkers, 2008.

Species assigned to *Lentigo* Jousseaume, 1886 (TS *Strombus lentiginosus* Linnaeus, 1758); *Euprotomus* Gill, 1870 (TS *Strombus aurisdianae* Linnaeus, 1758); and *Tricornis* sensu Kronenberg & Vermeij (2002) and Kronenberg & Lee (2007) have the rim of the outer lip that runs more or less parallel to the shell axis, when reaching adulthood, bent into adcolumellar direction in various degrees, sometimes barely detectable, and subsequently the outer lip is thickened and the rim of the outer lip more or less extensively glazed. In *Lentigo* the bending is only slight. In *Lentigo lentiginosus* (Linnaeus, 1758) this glazing is rather extensive, but in *L. pipus* (Röding, 1798), the only other recent species of *Lentigo*, this glazing is very narrow (pers.obs.). In all *Euprotomus* spp. the bending is slight and the glazing is extensive. In *Tricornis* the bending is very slight in *T. oldi* and slight in *T. tricornis*.

nis, but in *T. sinuatus*; *T. taurus* and *T. latissimus* the bending is very conspicuous (fig. 5), to a degree where a cavity is formed that is subsequently filled with inner shell material prior to the subsequent glazing of the outer lip.

The difference between a rounded adapical part of the outer lip of the shell as observed in *Tricornis latissimus* and lobes as observed in *T. sinuatus* and digits as in *T. taurus* is nothing but a slight difference in the presence or growth of lobes of the rim of the mantle demonstrated in this hybrid and also in *Lambis violacea* (see above). Therefore I consider the names *Sinustrombus* Bandel, 2007 and *Latissistrombus* Bandel, 2007 to be synonymous. Acting as first reviser (see ICZN Article 24.2) I give precedence to the name *Sinustrombus*. *Solidistrombus* Dekkers, 2008 is a junior synonym.

From a morphological point of view this name could be used to denote a group of species with a derived character of the rim of the outer lip. Therefore I consider *Sinustrombus* a genus within a clade that also encompasses *Tricornis*; *Lambis*; and *Harpago*, and not a subgenus of *Strombus* as indicated by Bandel (2007: 142). The large species reported by Ladd (1972: 58, pl. 17, figs 1, 2) as *Strombus (Tricornis)* sp. A, might also belong to this genus.

Kronenberg & Vermeij (2002) pointed out that projections on the outer lip arose multiple times independently in stromboidean clades. Whether these digits arose independently in *Sinustrombus taurus* in relation to *Lambis* spp. is not very likely. In the consensus tree as presented by Latiolais et al. (2006) *S. sinuatus* and *S. taurus* (both allocated to *Tricornis*) plot out as sister to *Lambis*. Moreover, the case of hybridisation as reported herein shows a close genetic connection between at least one species of *Sinustrombus* and one species of *Lambis*. It seems that within *Sinustrombus* there is a tendency to form extensions on the rim of the outer lip, a tendency that is pushed up further in *Lambis* spp.

The extensive bending of the rim of the outer lip is however not observed in *Thersistrombus thersites*. Bandel (2007: 147) mentioned the resemblance of the spire and form of the outer lip of *T. thersites* with those of *Persististrombus granulatus* (Swainson, 1822). Although at first glance this may seem far-fetched, but going back into the fossil record, there may indeed be a connection with *Persististrombus*. Species allocated to *Persististrombus* are known from the Chattian (late Oligocene) and Aquitanian (early Miocene) of Oman, respectively *P. bernielandau* (Harzhauser, 2007) and *P. gijskronbergi* (Harzhauser, 2007). Another species allocated to *Persististrombus* from the Aquitanian of Tanzania is currently under description (Harzhauser, in press).

Harzhauser et al. (2007) mentioned only *Strombus preoccupatus* Finlay, 1927 as a member of this radiation stating that *S. preoccupatus* was the last surviving species of that radiation. Without critically reviewing the following nominal taxa, as this is beyond the scope of this paper, *Strombus sedanensis* Martin, 1899 from the early Miocene of Java and Pakistan Abbott (1960: 102) and the Langhian and Serravilian, middle Miocene, of Borneo (Raven, 2002: 13); *S. preoccupatus* from the early and late Miocene of Java and Borneo; *S. daviesi* Dey, 1962 from the Miocene Quilon beds of Kerala, SW India; and both *S. quilonensis* Dey, 1962, and *S. cossmanni* Dey, 1962, also from the Miocene Quilon beds of Kerala, SW India; are tentatively considered part of the Indo Pacific radiation of *Persististrombus* by the present author. Whether or not the name *Persististrombus* should be used for these species is not yet resolved.

Strombus preoccupatus was allocated to *Lentigo* by Abbott (1960: 123), mentioning a similarity with *Strombus granulatus*. *Strombus sedanensis* was allocated to *Dolomena* Wenz, 1940, TS *Strombus pulchellus* Reeve, 1851 [*Dolomena* Iredale, 1931 is a nomen nudum, see Kronenberg & Dharma, (2005)], by Abbott (1960: 102) as being a fossil relative of "*Strombus*" *marginatus*.

Subsequently, Abbott (1965) allocated *S. preoccupatus*; *S. daviesi* (as *S. sedanensis daviesi*); *S. quilonensis* (as *S. preoccupatus quilonensis*) and *S. cossmanni* [regarded by Abbott (1965: 402) as a juvenile of *S. p. quilonensis*] to *Dolomena*. The allocation of these species to either *Lentigo* or *Dolomena* by Abbott is rejected here.

The large *Strombus maximus* Martin 1883, allocated to *Tricornis* by Abbott (1960: 56) may also be part of this radiation, but being ancestral to the Recent *Thersistrombus thersites* is not likely in the present author's opinion, judging by the shape of the outer lip in apical view.

Thersistrombus is provisionally accepted as a genus derived from an ancestor within the Indo-Pacific *Persististrombus* radiation, and not a subgenus of *Strombus* as indicated by Bandel (2007: 142). The specimen reported by Ladd (1972: 58, pl. 15 fig. 7) as *Strombus (Tricornis)* aff. *S. thersites* Swainson from the Futuna Limestone, "lower Miocene" of Fiji is too poorly preserved for a proper identification, but is definitely not *Thersistrombus thersites*.

As stated before (Kronenberg & Lee, 2007: 262) the overriding problem of convergence in the Strombidae impedes a morphological analysis of evolutionary relationships. Besides the example already mentioned by Kronenberg & Lee (2007) there is a striking resemblance between *Lobatus goliath* (Schröter, 1805) from Brazil and the Indo-Pacific *Sinuistrombus latissimus*. Also, the non-dilating, unglazed, sharp-rimmed outer lip of *Conomurex* P.Fisher, 1884 and *Margistrombus* Bandel, 2007 (synonym: *Neodilatilabrum* Dekkers, 2008) may very well be due to convergence rather than close phylogenetic relationships.

A re-appraisal combining morphological, anatomical, and molecular data of all species of *Tricornis* (in the broad sense, i.e. including *Sinuistrombus* and *Thersistrombus*) and *Lambis* (in the broad sense, i.e. including *Harpago*) is badly needed.

ACKNOWLEDGEMENTS

First and fore all many thanks are due to Dr Nguyen Ngoc Thach for making the specimen discussed herein available for study. Mr Jean-Pierre Barbier, Cebu, Mactan, Philippines provided important information on his collection of hybrid Strombidae. Mr Barbier; Mr Jeroen Goud, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; Mr Vigilio Liverani, Faenza, Italy; and Mr Joop Wiersma, Kerkrade, The Netherlands shared their opinions on this remarkable specimen. Jeroen Goud also made the photographs. Thanks are also due to Mr Fred Schroeder, Guam for making his specimen of the *Sinuistrombus sinuatus* × *S. taurus* hybrid available for photography and Mr Bob Abela, Guam, for mediation and sending images of this specimen. Thanks are also due to Mr Bunjamin Djarma, Djakarta, Indonesia for sending images of the specimens of *L. millepeda* × *L. truncata sebae* collected off Buton, Indonesia and Mr Sofjan Effendy, also Djakarta, Indonesia, for making the specimens available for photography. Mr Cor Karnekamp, Diemen, The Netherlands presented a copy of an issue of "De Kreukel" containing the Dekkers paper and provided important information on the date of publication. Dr Olaf Elicki, editor of Freiburger Forschungsheftel, provided information on the date of publication of the paper by Klaus Bandel. Dr Geerat J. Vermeij, University of California at Davis, reviewed the manuscript and made useful comments.

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