

Resolving phylogenetic and classical nomenclature: A Revision of *Canarium* Schumacher, 1817 (Mollusca, Neostromboidae, Strombidae)

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ABSTRACT This revision of the genus *Canarium* Schumacher, 1817 after Abbott (1960) advances our understanding of the phylogeny of Strombidae. Morphological characters were used to generate a phylogeny using maximum likelihood and including all of the recognised species. This resulted in the recognition of one tree, and within that tree the existing genera *Canarium* Schumacher, 1817 *Tridentarius* Kronenberg & Vermeij, 2002 and *Terestrombus* Kronenberg & Vermeij, 2002, and two more *Maculastrombus* n. gen. and *Neostrombus* n. gen. were recognisable clades. Furthermore, within the genus *Canarium*, four subgenera, *Canarium* (*Canarium*), *Canarium* (*Conundrum*), *Canarium* (*Elegantum*), and *Canarium* (*Stereostrombus*), were identified and described. We describe and define taxa that are compatible with the requirements of the International Code of Phylogenetic Nomenclature (PhyloCode 2020), and also conform to the requirements of the International Code of Zoological Nomenclature (ICZN 1999). This revision assists in generating a system of nomenclature that reflects the hypothetical relationships, and is at the same time practical in its application. We designate type localities and types for included species that were not yet addressed up until now.

KEY WORDS *Canarium*, *Conundrum*, *Elegantum*, ICZN, *Maculastrombus*, *Neostrombus* PhyloCode, *Stereostrombus*, Taxonomy

INTRODUCTION

The start of this decade has seen a flourish of work on the Stromboidae (Maxwell *et al.* 2020a; Dekkers 2020; Dekkers and Maxwell 2020a; Liverani *et al.* 2021). Consequently, there has been a significant shift in the understanding of the relationships between taxa, and this has commenced to be reflected in the nomenclature (Maxwell *et al.* 2020a; Dekkers and Maxwell 2020a). We use the International Code of Phylogenetic Nomenclature (PhyloCode 2020), and demonstrate how its application can also conform to the requirements of the International Code of Zoological Nomenclature (ICZN 1999).

Abbott (1960) viewed the *Canarium* Schumacher, 1817 as a large subgenus of Indo-Pacific Strombidae incorporating the smaller species of the family that were generally compact shape, with unflaring lips, lirate mouths and strombid operculum not curved. Abbott (1960) presented the fossils for the “*urceus-mutabilis-labiatus* Group” representing a taxonomic demarcation to gather the preceding taxa into a collective group, before presenting the remaining taxa. Many of these remaining taxa have now been removed from *Canarium* into genera such as *Terestrombus* Kronenberg & Vermeij, 2002 and *Tridentarius* Kronenberg & Vermeij, 2002, while others such as the *Canarium elegans* complex remain still

taxonomically nested in the “*urceus-mutabilis-labiatus* Group”.

We present a revision of the *Canarium* as defined by Abbott (1960), and provide a hypothesis for the relationships between species in that taxa which is then reflected in the nomenclature. We erect taxa providing a definition, diagnosis and description (Benton 2000; Maxwell *et al.* 2020a) in compliance with both the ICZN (1999) and PhyloCode (2020), bringing an evolutionary contextualisation of the nomenclature with the *Canarium* clade. Demonstrating that the goals of the PhyloCode, and the ICZN requirements for validity within the nomenclature are not mutually exclusive.

Abbreviations

AMNH	American Museum of Natural History, New York, USA.
ANSP	Academy of Natural Sciences of Philadelphia, Philadelphia, USA
IRNSB	Institut Royal des Sciences Naturelles, Brussels, Belgium.
MHG	Muséum d’Histoire de Genève, Geneva, Switzerland.
MNHN	Muséum National d’Histoire Naturelle, Paris, France
NHMUK	Natural History Museum United Kingdom, London, Great Britain.
QM	Queensland Museum, Brisbane, Australia.
RMNH	Rijksmuseum voor Natuur Historie (now in Naturalis Biodiversity Center), Leiden, The Netherlands.
UZM	Museum of Evolution of Uppsala University, Uppsala, Sweden.
ZMA	Zoölogisch Museum Amsterdam (now in Naturalis Biodiversity Center), Leiden, The Netherlands.

METHODS

A total of 31 taxa were selected based on the classification of Abbott (1960) and the species included in that work or described later but within the subgenus *Canarium* (Table 1) or its derivatives. The (sub)genus *Canarium* of Abbott (1960) is at present regarded as sitting at the rank of genus (MolluscaBase eds. 2020).

Twelve characteristics were chosen for the discrimination of species morphological relationships; the coding is based on the type and examples from the type location (Table 1). Atypical (freak) examples of all species are known and have been omitted for character clarity. Characteristics can be grouped into five categories: 1) shape of shell (Characteristics A-C); 2) form of the labrum (Characteristics D-F); 3) form of columella (Characteristics G-I); 4) inner aperture (Characteristics J); and 5) morphology of the shell (Characteristics K-N).

The MEGA X (Kumar *et al.* 2018) software was used to determine morphologically based clusters of species. The use of software developed for molecular analysis of character states was tested and validated in previous studies with congruence when comparing new outputs with prior studies (Maxwell *et al.* 2020a). Trees were generated using Maximum Likelihood with a neutral evolutionary neutrality. Character states were transcribed and coded (1 = A, 2 = G, 3 = C, 4 = T) to represent states. Maximum Likelihood evolutionary history was inferred based on the Jukes-Cantor Markov 4 -state model (Jukes and Cantor 1969). All trees generated were tested using 50 bootstrap replications, which is reflective of the data matrix size. The principles and criteria for selection of natural clades for formal recognition were based on the theory of Benton (2000) after Maxwell *et al.* (2020a) and applied in Dekkers and Maxwell (2020a), with the

treatment of subspecies and species based on Maxwell and Dekkers (2019). A second data set, with weighting for characters C and D were conducted.

RESULTS

The unweighted character analysis using maximum likelihood analysis produced one tree with log likelihood of -225.20. One species, *Canarium (Conundrum) klineorum* (Abbott, 1960), was problematic in its placement in the characteristic generated tree because of distinctive cross-sectional labrum forms (Characteristics D and E). These distinctive characteristics are reflective of divergent evolutionary trajectories in form, and that a species complex has a fixed morphospace in form represented by these characteristics that binds them (Maxwell *et al.* 2020b). Given the hypothesised defining characteristic in lip rim, *Canarium klineorum* was placed at the base of the subgenus *Canarium (Conundrum)* n. subgen., this hypothesis of the relationships has been used and illustrated (Figure 1). This in practical terms, giving a greater explanatory weight to characteristic E.

Notwithstanding the approach herein, Bandel (2007) recognised that there was a collection of three genera that fell outside the *Canarium* genus, and the results support this hypothesis, and these have previously been recognised at the generic level as *Terestrombus* Kronenberg & Vermeij, 2002, *Tridentarius* Kronenberg & Vermeij, 2002, and *Neostrombus* n. gen. To this we add *Maculastrombus* n. gen. based on the form of the outer lip.

We herein identify four taxa that reflect natural groups with the genus *Canarium* Schumacher, 1817: *Canarium (Canarium)*, *Canarium (Conundrum)* n. subgen., *Canarium (Elegantum)* n. subgen., and *Canarium (Stereostrombus)* n.

subgen.. The internal relationships between these subgenera may shift as more work is carried out, as such we have refrained from erecting formal ranks within the genus *Canarium*.

SYSTEMATICS

Phylum: Mollusca Linnaeus, 1758
 Order: Sorbeoconcha Ponder & Lindberg, 1997
 Superfamily: Stromboidea Rafinesque, 1815
 Epifamily: Neostromboidea Maxwell, Dekkers, Rymer & Congdon, 2019
 Family: Strombidae Rafinesque, 1815

Neostrombini Liverani, Dekkers & Maxwell, new tribe

Type Genus. We designate *Neostrombus* Liverani, Dekkers & Maxwell, new genus (Type: *Strombus fusiformis* Sowerby II, 1842).

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Canarium* Schumacher, 1817, *Maculastrombus* n. gen., *Neostrombus* n. gen., *Tridentarius* Kronenberg and Vermeij, 2002 and *Terestrombus* Kronenberg and Vermeij, 2002 and taxa more closely related to them than other members of Strombidae Rafinesque, 1815.

Diagnosis. Shells are small without a flaring lip, and a basal peg on the lateral teeth of the radula.

Description. Shells small with a narrow aperture that is posteriorly constricted forming a narrow sinus with the body whorl. The radula has a central tooth with five cusps the central being the largest, and lateral teeth with a basal peg.

Etymology. The name is formed from the combination of the genus *Neostrombus*, as “Neo+strombus+” where the prefix “Neo+” is also used to denote a crown clade, and the tribe suffix “+ini” to reflect the taxon’s position within the nomenclature.

Remarks. *Neostrombini* n. tribe differs from other Stromboidean tribes in being small and having non-flaring lip which is thickened toward the margin. The clade shares similarities in radula formulation with members of *Conomurex* Fischer, 1884 and Dolomenini Dekkers and Maxwell 2020a, in having a first lateral tooth with a basal peg.

Canarium Schumacher, 1817

Type Species. *Canarium ustulatum* Schumacher, 1817 (= *Strombus urceus* Linnaeus, 1758).

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Strombus urceus* Linnaeus, 1758 and taxa more closely related to it than to other members of the *Neostrombini* n. tribe.

Diagnosis. Small solid shells with an elliptic-rhomboid form and a variable height of teleoconch, and a cross section of the labrum that is thickened with a fine ridge.

Original Description. “*Testa suboblonga; spira subelongata, acutiuscula. Apertura linearis, postice integerrima, coarctata; rostrum breve subadscendens, subrecurvum; canalis apertus; labium externum acutum, in dorso marginatum, antice lobo semilunari inter sinum sigmoideum et truncaturam obliquam, postice integerrimum, interne substriatum; labium internum callosum, adnatum, columellaque tortilli antice substriatum*” (Schumacher, 1817, p. 219). [Translation: Shell oblong; spire elevated, pointed. Aperture linear, complete in the back and narrowed; siphonal canal short, a bit abaperturally bent; canal open; external lip thickened, with sharp border, anteriorly have a semilunar lobe between the sinus and the oblique cut of the canal, in the back complete, internally slightly striated; internal lip callused, adherent, columella twisted and anteriorly a bit striated]. Note: both the original description and the translation need some interpretation: the

“*apertura postice integerrima*” means probably that the posterior canal is absent; this character is repeated in “*labium externum...postice integerrimum*”.

Canarium (Canarium) Schumacher, 1817

Type Species. *Canarium ustulatum* Schumacher, 1817 (= *Strombus urceus* Linnaeus 1758).

Diagnosis. The labrum cross section is spathulate in form and has a distinctive fine ridge centrally.

Description. A solid shell with an elliptic-rhomboid form and a variable height of teleoconch. The coloured columella is well formed over the length of the aperture, but lirations vary from the entire length to only anteriorly and posteriorly. The sculpture of the spire varies from smooth to highly ornamented.

Synonymy.

Canarium Schumacher, 1817, p. 219 (Type: *Canarium ustulatum* Schumacher, 1817 = *Strombus urceus* Linnaeus, 1758).

Strombidea Swainson, 1840, p. 138 (Type: *Strombus urceus* Linnaeus, 1758).

Conarium Jousseume, 1888, p. 174 (Type: *Strombus mutabilis* Swainson, 1821)

Conorium “Jousseume” Abbott, 1960, p. 63 (Printing error for *Conarium* Jousseume, 1888).

After much debating, the present authors are in agreement to synonymise the genera names *Conarium* Jousseume, 1888, and *Conorium* Abbott, 1960 with the genus *Canarium* Schumacher, 1817. Liverani *et al.* (2021) considered the genus name *Conarium* Jousseume an error for *Canarium*. In the previous entry on the same page, *Gibberulus gibberulus* (Jousseume, 1888, p. 174), Jousseume explicitly states: “Cette espèce ne pouvant être inscrite dans aucune des divisions connues, nous créons pour elle le genre

Gibberulus.” (being not possible to assign this species to any of the known divisions, we create for her the new genus *Gibberulus*). Such a statement is absent in the entry to *Conarium mutabilis*, making it probable that the different vocal is only a typographical refuse. *Conarium* (Abbott 1960) is a misspelling of *Conarium Jousseume* and, therefore, a misspelling of *Canarium* Schumacher, 1817. Abbott (1960) very probably wanted to synonymise the name *Conarium Jousseume* with the genus *Canarium* Schumacher, but on his turn made one more spelling error. We do not consider the reference to *Strombus mutabilis* Sow. (Sow., Th. Conch. Pl. VII, fig. 40, 45-47, 49-52) made by Jousseume as a fixation of type species, or as description, but purely as reference to the original first publication of the species, similar references have been made for all other species cited in Jousseume, 1888.

Included Taxa.

Strombus urceus Linnaeus, 1758, 745, no.

440 (Lectotype: UZM 685; Type Location: Singapore, designated by Maxwell *et al.* 2020c).

Lambis labiata Röding, 1798, p. 63, no. 806 (Holotype: Martini (1777), pl. 78, figs. 804 & 803; Type Locality: Amboina, Indonesia, designated by Abbott (1960), Röding (1798) gave no type locality.)

Strombus incisus Wood, 1828, p. 14, pl. 4, fig. 12 (Lectotype: Wood (1828) p. 14 pl. 4 fig. 12; Type Location: Labuan Bujo, Benonko Beach, Flores, Indonesia, designated by Maxwell *et al.* 2020d).

Strombus anatellus Duclos, 1844, pl. 4, figs. 11 & 12, and pl. 21, figs 8 & 9 (set of 3 syntypes: MNHN IM-2000-32467; Type Location: The Kangean Islands, Indonesia, designated by Maxwell *et al.* 2020d).

Strombus olydius Duclos, 1844, p. 4, pl. 5, fig. 7 (type: the type is presumably in MHG (fide Abbott 1960, p. 69); Type

Locality: Nossi-bé, northwest Madagascar, designated by Abbott 1960).

Strombus (Canarium) urceus orrae Abbott, 1960, p. 66, pl. 20, fig. 28, and pl. 41 fig. 5 (Holotype: ANSP 247756; Type Location: Augustus Island, Western Australia, designated by Abbott 1960).

Canarium esculentum Maxwell, Rymer, Congdon and Dekkers 2020c, p. 339, fig. 4 & 5 (Holotype: AMNH 12927; Type Location: Olango Island, Philippines, designated by Maxwell *et al.* 2020d).

Canarium daveyi Dekkers and Maxwell, 2020b, p. 346, fig. 1 (Holotype: RMNH MOL.112282a; Type Locality: Paulau Auri, Geelvink Bay, Indonesia, designated by Dekkers and Maxwell 2020b).

Canarium geelvinkbaaiense Dekkers and Maxwell, 2020b, p. 349, fig. 2 (Holotype: RMNH MOL.179571a; Type Locality: Manokwari, Western New Guinea, Indonesia, designated by Dekkers and Maxwell 2020b).

Canarium manintveldi Dekkers and Maxwell, 2020b, p. 351, fig. 3 (Holotype: ZMA MOLL.187523a; Type Locality: Malapoa Island, Vanuatu, designated by Dekkers and Maxwell 2020b).

Canarium youngorum Dekkers and Maxwell, 2020b, p. 354, fig. 4 (Holotype: QM MO.85756; Type Locality: Manus Island, Papua New Guinea, designated by Dekkers and Maxwell 2020b).

Canarium (Conundrum) Liverani, Dekkers & Maxwell, new subgenus

Type Species. *Strombus mutabilis* Swainson, 1821.

Diagnosis. A solid shell with a spathulate cross section of the outer lip with a fine ridge located on the inner edge.

Description. The solid shell is elliptic-rhomboid in form with a variable height of spire,

generally low. The cross section of the labrum is spatulate with a fine ridge located on the inner edge. The columella is well formed the length of the aperture and variable in liration from entirely lirate to being lirate posteriorly and anteriorly. The liration of the aperture is variable form distinct to obsolete. The mid teleoconch with distinct sculpture of tubercles which may form axial plications. The ventral body whorl is smooth.

Etymology. From the Latin “conundrum” in the neuter nominative singular, meaning enigma, caused by the long debate about the state of the name *Conarium* Jousseume, 1888.

Included Taxa.

- Strombus mutabilis* Swainson, 1821, pl. 71
(The whereabouts of the Swainson physical type of *mutabilis* is unknown (Abbott 1960, p. 74); Type Locality: Cebu City, Cebu Island, Philippines (restricted by Abbott 1960, originally “East Indies”).
- Strombus ostergaardi* Pilsbry, 1921, p. 320, pl. 12 (Holotype: ANSP 74549; Type Locality: from the dredger dump on the harbour side of Sand Island, Honolulu, Pleistocene, designated by Pilsbry, 1921).
- Canarium microureum* Kira, 1959, p. 37, pl. 15, fig. 5 (Holotype: the type figured by Kira 1959 is probably in the collection of Mr. Tetuaki Kira, Japan (fide Abbott 1960, p. 72); Type Locality: Shirahama, Honshu Island, Japan (restricted by Abbott 1960 from a broad range given by Kira)).
- Strombus (Canarium) mutabilis ochroglottis* Abbott, 1960, p. 74, pl. 20, figs. 9 & 10 (Holotype: ANSP 250187; Type Locality: Mauritius, designated by Abbott 1960).
- Strombus (Canarium) klineorum* Abbott, 1960, p. 70, pl. 20, figs. 20 & 21 (Holotype: ANSP 247621; Type Locality: Powder Bay, Trincomalee, Sri Lanka, designated by Abbott 1960).
- Strombus (Canarium) wilsoni* Abbott, 1967, p. 455, pl. 328, figs. 1 to 3 (Holotype:

ANSP 253088; Type Locality: Zanzibar, designated by Abbott 1967).

Strombus (Canarium) ochroglottis betuleti Kronenberg, 1991, p. 54, fig. 1 (Holotype: Kronenberg Collection no. 911; Type Locality: Trincomalee, Sri Lanka, designated by Kronenberg, 1991).

Remarks. *Canarium (Conundrum)* n. subgen. differs from *Canarium sensu stricto* and other genera included in Neostrombini in the short/large angled spire, the compact short body whorl, and the cross section of the lip border. The species *Canarium wilsoni* (Abbott, 1967) have been emended to *C. wilsonorum* by Kronenberg and Dekker (2000), following article ICZN 32.5.1, on the basis of the fact that Abbott dedicated the species to two different unrelated persons. However, the argued change made by Kronenberg and Dekker is unjustifiable and does not increase stability, but rather generated confusion with Petuch’s *Strombus wilsonorum*, and should therefore be suppressed. Abbott was aware of the use of -orum for names of couples or family relations (*Conus sennottorum* Rehder and Abbott, 1951, etc.), with the two people referred to by Abbott 1967 not having a relationship guiding his construction of *wilsoni*. We therefore return to the correct published epithet by Abbott (1967), reinstate *Strombus wilsonorum* Petuch, 1994, and suppress *Strombus praeraninus* Kronenberg and Dekker, 2000.

Canarium (Elegantum) Liverani, Dekkers & Maxwell, new subgenus

Type Species. *Strombus erythrinus* Dillwyn, 1817.

Diagnosis. Solid shells with a falcate cross section of the outer lip with a fine ridge forming the outer edge.

Description. The solid shell is elliptic-rhomboid with a teleoconch with variable height

of the spire. The cross section of the labrum is falcate, with a fine ridge forming the outer edge. The columella is well formed the length of the aperture and the liration is variable between species. The inside of the labrum is liriate. The sculpture of the shell: shoulder with axially elongated tubercles and fine spiral cords; last whorl ventral side may have axially elongate tubercles, or axial plicae, dorsal side with axially elongate tubercles.

Etymology. Derived from the Latin *elegans*, meaning elegant, refined, of fine manners, in the neuter singular nominative, in recognition of the elegant shape of the shells within the genus.

Synonymy.

Strombidea Jousseume, 1888, p. 174 (Type: *Strombus erythrinus* Chemnitz, 1795 = *Strombus erythrinus* Dillwyn, 1817) (preoccupied).

Included Taxa.

Strombus erythrinus Dillwyn, 1817, p. 673 (Lectotype: We designate Chemnitz (1795 p. 195, fig 1874 and 1875); Type Locality: Red Sea (designed by Abbott 1960)).

Strombus elegans Sowerby II, 1842, p. 30, pl. 7, figs. 43 & 48 (Lectotypes: 2 in the NHMUK; Type Locality: The type locality for *Strombus elegans* is not given with the original description, nor does Abbott (1960) give one. Abbott mentions a lectotype (“cotype”) from New Caledonia. We therefore designate New Caledonia as type locality. The species is known from South Western Pacific).

Strombus radians Duclos in Chenu, 1844, p. 5, pl. 4, figs. 15 & 16 (Lectotype: Duclos in Chenu, 1844, p. 5, pl. 4, figs. 15 & 16; Type Locality: Japan, designated by Abbott 1960).

Strombus rugosus Sowerby I, 1825, p. 20, no. 1791 (Unknown location of type material (Abbott 1960), but maybe NHMUK (Abbott 1960); The type locality of *Strombus rugosus* is East Indies and is

obviously erroneous. It is a very localised species with records from Fiji, Ellice, Samoa and Tonga (Abbott 1960). We herewith designate as type locality: Tonga, without further refining).

Remarks. *Canarium (Elegantum)* n. subgen. differs from *Canarium sensu stricto* and other genera included in Neostrombini in the strongly sculptured spire, the slender and tuberculated/plicated body whorl, and the cross section of the lip border.

The use of *S. elegans* is often neglected and erroneously replaced by *S. erythrinus* which is an African species. *Canarium radians* is sold in many colour forms from the Philippines, almost always erroneously named *C. erythrinum*, the endemic Red Sea species. *Strombus rugosus* seems to be intermediate between *S. elegans* and the rougher and smaller *S. scalariformis* and *S. hellii* and can be a link in the evolution of these species, from the smoother *S. erythrinus* from the Red Sea to the smaller and coarser species in the eastern range of the genus.

Canarium (Stereostrombus) Liverani, Dekkers & Maxwell, new subgenus

Type Species. *Strombus scalariformis* Duclos, 1833.

Diagnosis. The shell is small and solid, with a labrum cross section that is acuminate and a fine ridge that is extended forming the edge, the columella is coloured and liriate.

Description. Small shells, last two whorls may rapidly increase in diameter giving a fat shape to the shell. The surface of the shell is entirely sculptured spirally by thin cords, and axially by elongated ribs, with stronger tubercles on dorsum of last whorl. The lip is thin formed with a labrum with a cross section that is acuminate and a fine ridge that is extended forming the edge. The inside of the labrum is

lirated, the stromboid notch shallow, adapical part of lip with one or two lobes, of which the one close to the strombid notch is the biggest and often protruding. The columellar callus thick, coloured, marginated and lirated.

Etymology. The name is a combination of the Ancient Greek adjective *στερεός* meaning ‘solid’ as in hard or firm in the masculine singular nominative (as prefix), and the genus *Strombus*.

Synonymy.

Strombus (Hawaiiistrombus) Bandel 2007, p. 151 (Type: *Strombus hellii* Kiener, 1843 = *Strombus hellii* Kiener, 1843) (*nomen nudem*).

Included Taxa.

Strombus hellii Kiener, 1843, p. 59, pl. 13, fig. 2 (Lectotype is NHMUK 1961180; Type Locality: The original type locality of *Strombus hellii* as Mer des Indies, Les cotes de I’île Zanzibar (Kiener 1843, p. 59). This is obviously incorrect as it is endemic to the Hawaiian Island Chain. We herewith designate off Oahu Island, Hawaii as type locality).

Strombus scalariformis Duclos, 1833, pl. 28 (Syntype: MNHN-IM-2000-32462; Type Locality: The original type locality of *Strombus scalariformis* is: *Mers de la Chine*. This was a commonly used origin entry in many descriptions of species in the 19th century and as such of little value. We here designate Reunion island as a more restricted type locality).

Remarks. *Canarium (Stereostrombus)* n. subgen. differs from *Canarium sensu stricto* and other genera included in Neostrombini by the sculptured spire and body whorl, the uniformly and strongly coloured columella and the cross section of the lip border.

The morphological results indicate that *Strombus hellii* and *Strombus scalariformis* may share a common ancestor, but information on this subject is lacking.

Maculastrombus Liverani, Dekkers
& Maxwell, new genus

Type Species. *Strombus maculatus* Sowerby II, 1842.

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Strombus maculatus* Sowerby II, 1842 and taxa more closely related to it than to other members of the *Neostrombini* n. tribe.

Diagnosis. Shells with a cuneate outer lip and smooth body whorl, the later teleoconch with distinctive tubercles.

Description. The solid shell is elliptic-rhomboid in form and has a teleoconch that is ~ 1/5 the height of shell. The cross section of the labrum is cuneate and there is no labial ridge. The columella is well formed and runs the length of the aperture, with the columella having lirations both posteriorly and anteriorly. The inside of the labrum is lirated. The later teleoconch is tuberculate; a subsutural cord is present. The mid body whorl is smooth with small to obsolete shoulder nodules. The anterior part of the body whorl bears about 12-15 quadrate flattish spiral lines.

Etymology. The name is a combination of the Latin adjective “maculatus” in singular masculine nominative, meaning patterned with spots or blotches, and the genus *Strombus*.

Included Taxa.

Strombus floridus var. *depauperata*
Dautzenberg & Bouge, 1933, p. 296
(Syntypes: IRNSB IG. 10591; Type
Locality: Makatea, Tuamotus, selected by
Abbott 1960).

Strombus maculatus Sowerby II, 1842, p. 30,
pl. 7, fig. 53 (Syntypes: NHMUK
1969340; Type Locality: Kawaihoa,

Hawaii, originally the Sandwich Islands, but restricted by Abbott 1960).

Canarium rapanuensis Liverani, Wieneke & Kronenberg, 2021, p. 63, pl. 1, figs. 7-10 (Holotype: RMNH. Mol. 178344; Type Locality: La Perousse Bay, Rapa Nui, Chile selected by Liverani *et al.* 2021).

Remarks. *Maculastrombus* n. gen. differs from *Canarium* sensu stricto and other genera included in Neostrombini by the compact spire and body whorl with almost no sculpture, and the cross section of the lip border.

Neostrombus Liverani, Dekkers & Maxwell, new genus

Type Species. *Strombus fusiformis* Sowerby II, 1842.

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Strombus fusiformis* Sowerby II, 1842 and taxa more closely related to it than to other members of the *Neostrombini* n. tribe.

Diagnosis. The shell is fusiform with a columella that is diminished posteriorly, with a cuneate cross section of the labrum and lacking a fine ridge at the edge.

Description. Shell solid, relative heavy, fusiform. The type species is from 26 to 45 mm. The height of the teleoconch is ~ 1/4 height of shell. Spire with small former varices. Post nuclear whorls with a sutural cord. The sculpture of the mid body whorl is smooth, but may have obsolete shoulder nodules. The body whorl develops spiral sculpture towards the labrum. Base of the shell with small spiral cords. The labrum in cross section is cuneate without a fine ridge at the edge and has many lirae. Labial ridge present. The columella is liriate, sometimes totally and sometimes the mid-section is smooth. Strombid notch poorly developed. Anterior canal broad and depressed. The inside of the labrum of the shell is liriate.

Etymology. The name is a combination of the Ancient Greek adjective, *vέος* meaning ‘fresh, youthful or new’ in the masculine singular nominative (as prefix), and the genus *Strombus*.

Synonymy.

Fusicanarium Romagna Manoja 1980, p. 13 (Type: *Strombus fusiformis* Sowerby II, 1842) (*nomen nudem*).

Strombus (Fusistrombus) Bandel 2007, p. 151 (Type: *Strombus fusiformis* Sowerby II, 1842) (*nomen nudem*).

Included Taxa.

Strombus fusiformis Sowerby II, 1842, p. 31, pl. 9, figs. 91 & 92 (Holotype: NHMUK n. 1969327; Type Locality: Chumbi Island, Zanzibar, designated by Abbott 1960).

Remarks. *Neostrombus* n. gen. differs from *Canarium* and other members of the Neostrombini in having a columella that is not uniform in form the length of the aperture. The spire of *Neostrombus* n. gen. is high and smooth, the body whorl is slender and smooth, and the cuneate cross section of the lip distinguishes this species.

Neostrombus n. gen is erected to replace two older names, both of which have failed to comply with article 13 of the ICZN (1999), namely *Fusicanarium* Romagna Manoja, 1980 and *Strombus (Fusistrombus)* Bandel, 2007.

Terestrombus Kronenberg and Vermeij, 2002

Type Species. *Lambis fragilis* Röding, 1798.

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Lambis fragilis* Röding, 1798 and taxa more closely related to it than to other members of the *Neostrombini* n. tribe.

Original Diagnosis. “Small, thin-shelled, spirally and axially almost smooth strombids with rounded, basally unconstricted whorls, thin,

determinate, unglazed outer lip, indistinct stromboid notch, and thin columellar callus” (Kronenberg and Vermeij 2002, p. 49).

Original Description. “Shell small for family (maximum height about 49 mm), fusiform, basally unconstricted on left side opposite outer lip, very weakly constricted at outer lip of adult. Protoconch of about 2.5 smooth whorls. First one to two teleoconch whorls with about eight fine spiral incised lines, other whorls of spire smooth, rounded, little inflated, with or without weak rounded varices. Last whorl smooth except for fine spiral grooves on base. Terminal adult varix present but low, defined by weak axial ridge behind sharp, unglazed edge of lip. Inner (adaxial) surface of outer lip with or without very fine, short spiral striae. Columellar callus thin, narrow, smooth. Stromboid notch on adult outer lip shallow, poorly defined; projection between stromboid notch and anterior canal narrow, pointed. Adapical canal present or absent. Operculum stromboid, elongate, arched, serrated on convex edge” (Kronenberg and Vermeij 2002, p. 50).

Supplementary Description. The teleoconch is approximately 1/5 of the axial height of shell. The shells are thin and fragile. The cross-section of the labrum is falcate and there are no teeth or formed fine ridge on the edge. The columella is weakly formed. The liration of the inner aperture is typically diminished. The shell is smooth and lacking in distinctive sculpture.

Synonymy.

Terestrombus Kronenberg and Vermeij, 2002, p. 49 (Type: *Lambis fragilis* Röding, 1798)

Included Taxa.

Lambis fragilis Röding, 1798, p. 62, no. 792 (Lectotype: Chemnitz 1788, plate 157, fig. 1503; Type Locality: Zamboanga, Mindanao, selected by Abbott 1960).

Strombus terebellatus Sowerby, 1842, p. 31, no. 30, pl. 9, figs. 84 & 85 (Syntypes: NHMUK n. 1969338; Type Locality: Viti

Levu Island, Fiji, selected by Abbott 1960).

Strombus (Canarium) terebellatus afrobellatus Abbott 1960, p. 88, pl. 61 fig. 2 (Holotype: ANSP no 214295; Type Locality: Pange Island, Zanzibar, designated by Abbott 1960).

Remarks. This is a genus of thin walled shells that lacks any major sculpture. The base of the shell is relatively open and this may give the shell a superficial look of some members of the allied Seraphsidae.

Tridentarius Kronenberg and Vermeij, 2002

Type Species. *Strombus dentatus* Linnaeus, 1758.

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Strombus dentatus* Linnaeus, 1758 and taxa more closely related to it than to other members of the *Neostrombini* n. tribe.

Original Diagnosis. “Small, high-spired strombids with strongly reduced spiral sculpture, determinate outer lip with glazed adult edge and three sharp basal projections. An indistinct stromboid notch is separating the two abapical most projections. A thick, narrow columellar callus is present, and a long adapical apertural channel” (Kronenberg and Vermeij 2002, p. 51).

Original Description. “Shell small for family (maximum height 56.5 mm), fusiform, basally very weakly or not constricted. Protoconch of about 2.5 smooth whorls. First one to two teleoconch whorls with eight very fine incised spiral lines and fine growth lines. First three to four teleoconch whorls with varices. Later spire whorls with gradually appearing axial ribs, most strongly expressed at periphery, abapically fading out above midpoint of whorl. Determinate adult outer lip little expanded, with glazed edge, adapically extending as narrow apertural channel with the adapical extension of

the thickened, narrow columellar callus. Edge of adult outer lip dentate, the abapical two teeth axially broad and rounded, lobe-like, the abapical three teeth sharp, triangular, spinelike, directed ventrally and abapically. Stromboid notch shallow but distinct, situated between the two abapical-most teeth. Abapical end of inner lip pointed, extending beyond abapical most tooth on outer lip. Columella abapically and adapically with a few indistinct thin plicae. Outer lip very little expanded abaxially, finely spirally striate on inner (adaxial) surface. Aperture narrow, widening abapically. Operculum stromboid, elongate, arched, serrated on convex edge” (Kronenberg and Vermeij 2002, p. 51).

Supplementary Description. The teleoconch is approximately 1/5 of the axial height of shell. The shells are solid. The cross-section of the labrum is falcate and distinctive teeth anteriorly. The columella is well formed the length of the aperture and lirate at both ends. The liration of the inner aperture is well formed. The shell is smooth and lacking in distinctive sculpture.

Synonymy.

Tridentarius Kronenberg and Vermeij, 2002, p. 49 (Type: *Strombus dentatus* Linnaeus, 1758).

Included Taxa.

Strombus dentatus Linnaeus, 1758, p. 745, no. 0 (Lectotype: We designate Chemnitz 1788, pl. 157, no. 1501 and 1502 as the types; We designate Olango Island as the type locality).

Remarks. Linnaeus described the species we now know as *Tridentarius dentatus* in the 10th edition of the *Systema Naturae* on page 745 as no “0” between species 440 (*urceus*) and 441 (*ater* = *Faunus ater* (Linnaeus, 1758), not a Strombidae species). It looks like he added it at a later moment before printing, not altering the numbering he already had used throughout the work. He did not supply a reference for this species which is rather unusual for Linnaeus,

but his description is clear enough. Dodge 1946 who addressed the identity problem of this species was very clear about the unambiguous nature of the species, just as later authors after him. The original description of *Strombus dentatus* reads: *S. testa labro attenuato brevi dentato, ventre spiraque plicatis*. Translated (Dodge 1946): Shell with a “thinned-out” short and toothed lip, body-whorl and spire plicate. Dodge, however, does not mention a type for this Linnean species. Abbott 1960 also refrains of referring to a type. Kronenberg & Vermeij 2002 also remain in silence about a type for this species. According to Dodge 1956 no Linnean type was found, nor was a type locality given.

DISCUSSION

While Abbott 1960 recognised that there are several morphological groups that were distinctly distinguishable within the *Canarium*, his use of the subgeneric rank gave him limited taxonomic ability to formally recognise these. The elevation of *Canarium* to genus has allowed the space within the formal ICZN (1999) for these to be recognised. However, there was much discussion between the authors on whether to define a clade to contain both the *Canarium* (*Stereostrombus*) n. subgen. and the *Canarium* (*Elegantum*) n. subgen.. The decision to not name the clade was based on that there were no officially recognised ranks left. Some authors did not want to inflate the higher taxonomy to fit the nomenclature, even though it was argued, and rejected, that the ICZN (1999) does allow for more informal ranks.

Canarium (*Conundrum*) *klineorum* shares similarities to both the *Canarium* and *Conundrum* subgenera and may be an ancestral form between them. *Canarium klineorum* is a highly geographically restricted, and morphologically stable species, which may indicate a shallow genetic pool of diversity that

has significant impact on the potential for divergence.

CONCLUSION

This revision provides another step in the understanding of the internal relationships within the Stromboidea. The clades identified herein form natural morphological groups that reflect a particular morphological evolutionary pathway unique to each of them, generating a system of nomenclature that reflects the hypothetical relationships, and is at the same time practical in its application, achieved with the use of both a definition and diagnosis. The definition expresses a statement that reflects the understanding of the sister taxa relationships. In contrast, the diagnosis enables the physical recognition of the taxon from other taxa.

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<i>afrobellatus</i>	3	1	1	3	1	1	3	4	1	1	1	1	1	1
<i>anatellum</i>	3	1	2	1	2	1	1	1	3	3	2	1	3	3
<i>betuleti</i>	3	1	2	1	3	1	1	2	3	3	1	1	2	2
<i>daveyi</i>	3	2	2	1	2	1	1	1	3	3	2	1	3	3
<i>dentatus</i>	3	1	2	3	1	2	1	1	3	3	2	1	2	2
<i>depauperatus</i>	3	1	2	3	1	1	1	1	3	1	1	1	2	2
<i>elegans</i>	3	3	2	3	4	1	1	2	4	3	2	2	3	3
<i>erythrinum</i>	3	2	2	3	4	1	1	2	4	3	2	2	3	3
<i>esculentum</i>	3	2	2	1	2	1	1	3	3	3	2	1	1	1
<i>fragilis</i>	3	1	1	3	1	1	3	1	1	3	1	1	1	1
<i>fusiformis</i>	1	2	2	2	1	1	2	1	4	2	1	1	1	1
<i>geelvinkbaaiense</i>	3	2	2	3	2	1	1	1	3	3	2	1	3	3
<i>hellii</i>	2	2	2	4	4	1	1	1	2	2	2	2	3	3
<i>incisum</i>	3	1	2	1	2	1	1	1	3	3	1	1	3	3
<i>klineorum</i>	3	2	2	1	3	1	1	2	3	3	3	1	3	3
<i>labiatum</i>	3	2	2	1	2	1	1	1	2	3	2	3	3	3
<i>maculatus</i>	3	1	2	3	1	1	1	1	3	1	1	1	2	2
<i>manintveldi</i>	3	1	2	1	2	1	1	1	3	3	2	1	3	3
<i>microurceus</i>	3	1	2	1	3	1	1	2	2	2	1	1	2	2
<i>mutabile</i>	3	1	2	1	3	1	1	1	2	2	1	1	2	2
<i>ochroglottis</i>	3	2	2	1	3	1	1	2	3	3	2	1	2	2
<i>olydium</i>	3	2	2	1	2	1	1	1	2	3	2	3	3	3
<i>orrae</i>	3	2	2	1	2	1	1	1	3	3	2	3	3	3
<i>ostergaardi</i>	3	1	2	1	3	1	1	2	3	2	1	1	2	1
<i>radians</i>	3	2	3	3	4	1	2	3	2	3	2	2	3	3
<i>rapanuensis</i>	3	1	2	3	1	1	1	1	3	1	1	1	2	2
<i>rugosum</i>	3	2	2	3	4	1	1	1	4	1	2	2	3	3
<i>scalariformis</i>	3	2	2	4	4	1	1	1	2	2	2	2	3	3
<i>terebellatus</i>	3	1	1	3	1	1	3	4	1	2	1	1	1	1
<i>urceus</i>	3	2	2	1	2	1	1	3	3	3	3	1	3	3
<i>wilsoni</i>	3	1	2	1	3	1	1	1	3	3	2	1	2	2
<i>youngorum</i>	3	2	2	3	2	1	1	1	3	3	2	1	3	3

Table 1. Characteristics and coding used to determine species relationships. Form of shell (A): fusiform (1); orbicular (2); elliptic-rhomboid (3). Teleoconch height (ventral) (B): ~ 1/5 height of shell (1); ~ 1/4 height of shell (2); ~ 1/3 height of shell (3). Shell thickness (C): fragile (1); solid (2). Cross section of the labrum (D): spatulate (1); cunicate (2); falcate (3); acuminate (4). Cross section of labrum with fine rim ridge (E): absent (1); located centrally (2); located on the inner edge (3); forming outer edge of labrum (4). Labrum with teeth (F): absent (1); present (2). Columellar callus (G): well-formed the length of aperture (1); diminished posteriorly (2); diminished (3). Columella colouration (H): single colour (1); axially bicoloured (2); variability flushed with colour (3); diminished columella (4). Columella liration (I): absent (1); completely lirated (2); anteriorly and posteriorly lirated only (3); specimen dependant (4). Aperture colouration (J): white (1); colouration only where lirated (2); coloured (3). Ventral body whorl shoulder sculpture (K): smooth (1); nodules which may form shoulder plications, these may be diminished (2); strongly knobbed (3). Central ventral body whorl (L): smooth (1); axially ribbed (2); variable (3). Mid-teleoconch sculpture (M): smooth (1); tuberculated, which may be axially compressed and elongated (2); axially plicated (3). Sculpture of penultimate whorl (N): smooth (1); tuberculated, which may be axially compressed and elongated (2); axially plicated (3).

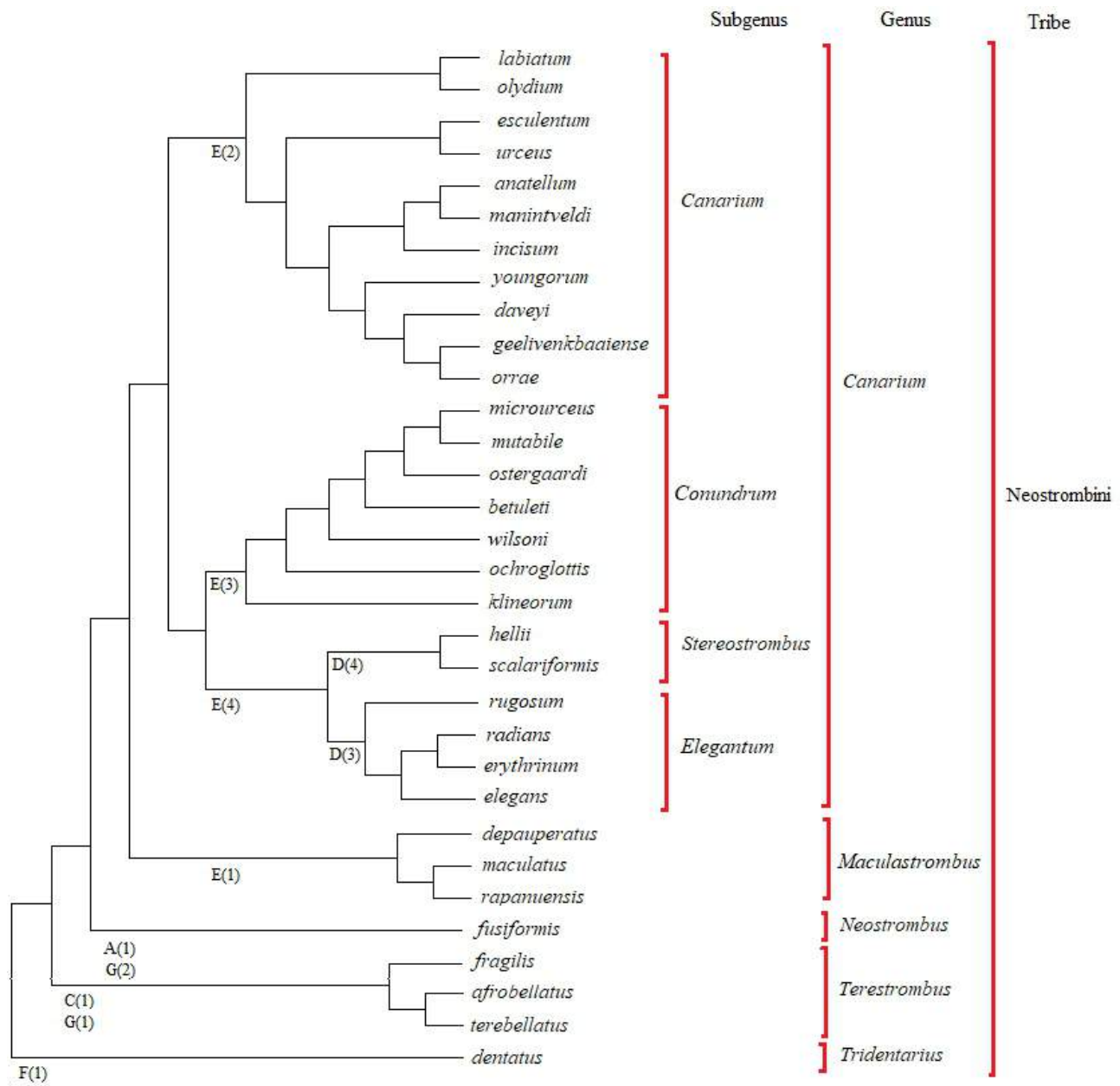


Figure 1. Neostrombini n. tribe showing the clusters of species and proposed names for those clusterings, with important defining character states inserted.



Figure 2. Apertures of members of *Canarium* (genus) grouped by sub-clade membership.



Figure 3. Apertures of members of *Neostrombini* grouped by clade membership excluding *Canarium*.

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