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A classical taxonomic revision of Seraphsidae Gray, 1853 (Gastropoda) using a pluralist approach to species assessment

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Abstract

The use of classical taxonomy, with its reliance on the physically observable, is currently waning in the face of increased reliance on molecular phylogenetics. This thesis demonstrates that a pluralistic approach to classical taxonomic practice can lead to increased internal cladistic resolution within a clade, including the recognition of new taxa at all nomenclatural levels. In particular, this thesis has three aims to bring greater resolution to the clade Stromboidea Rafinesque, 1815 (Gastropoda Linné, 1758): 1) to divide the Stromboidea into two distinctive evolutionary crown clades using morphological evidence, thereby reinstating the historical understanding of the internal cladistic relationships that have been lost as a consequence of taxonomic inflation; 2) to complete an α-taxonomic revision of Seraphsidae Gray, 1853 (Stromboidea) based on a pluralist approach to species conception; and 3) to resolve the infrafamilial relationships within Seraphsidae using morphological cladistics. This thesis examined all species hypotheses and their synonymies, and revised these in a pluralist light against the rules that govern precedence and availability. From this information, an annotated synonymy was generated for each taxon, the precedence of names determined, and revised descriptions formulated. Character sets that reflect the synapomorphies within the major subclades of Seraphsidae were coded and a cladogram generated using maximum likelihood within the *tnt* program with default settings. Four forms of material and evidence were used in this systematic review: 1) the type material for each taxon; 2) physical material; 3) published images; and 4) literary references for specimen localities without illustration. The current morphologically-based classification of Seraphsidae was found to be sound in terms of current species delimitations. Regardless of this, the use of a pluralist approach improved understanding of the internal cladistic relationships within Seraphsidae, which led to higher resolution of the internal cladistic arrangements and taxonomic delimitation. Furthermore, this increased resolution is now reflected in the higher evolutionary contextualisation of the family nomenclature. This thesis included *Mauryna* de Gregorio, 1880 within Seraphsidae on the grounds that it provides a basal link to the Seraphsidae sister taxa *Semiterebellum* Cossmann, 1889 and *Terebellopsis* Leymerie, 1846, both contained within Rostellariidae Gabb, 1868, and all three clades may in time be brought together under one family. It was not possible within the context of this thesis to test the results of the pluralist α-taxonomic findings against phylogenies generated with molecular data. This was due to the high number of extinct taxa within the Seraphsidae. Therefore, it is imperative that further revisions be undertaken with groups of predominantly extant taxa to test the pluralist classical taxonomic methodologies against molecular data, and thereby seek to reverse the trend in the literature whereby classical taxonomy is deemed fundamentally redundant in the face of advances in analysis of molecular data.

Declaration and Statement of Contribution of Others

I, Stephen John Maxwell, declare that the Master by Research thesis entitled *A Classical Taxonomic Revision of Seraphsidae Gray, 1853 (Gastropoda) Using a Pluralist Approach to Species Assessment* is no more than 60,000 words in length including quotes but exclusive of tables, figures, bibliography, references. This thesis contains no material that has been submitted previously, in whole or in part, for the award of any other academic degree or diploma. Except where otherwise indicated, this thesis is my own work.

Every reasonable effort has been made to gain permission and acknowledge the owners of copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.

All papers derived from the thesis are indicated within the text where appropriate. In relation to extant *Terebellum* Röding, 1798 (s.l.), the author acknowledges the contribution given by Aart M. Dekkers and Virgilio Liverani in terms of species identification and co-authorship of related publications.

Stephen John Maxwell 1st December, 2018

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I am thankful to Mark Florence from the United States National Museum, Paleontology Department for his assistance in the designation of type material. I would like to gratefully acknowledge those who gave permission for images to be used, in particular Guido Poppe and Sheila Tagaro from www.conchology.be. To those who supplied additional information on species from Queensland I am most grateful, particularly those who generously gave specimens with detailed data: Uwe "Tassey" Weinreich from Cairns and Jack Worsfold from Townsville. A special mention is given to Trevor and Marguerite Young from Proserpine who have encouraged my studies and have been invaluable to the proof reading of this thesis and publications derived from it.

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Chapter 1.0 Introduction

One of the major problems when undertaking a revision of a largely extinct group of organisms is the realisation that only an estimated 10% of all biota that have become extinct are preserved in the geological strata (Forey *et al*. 2004). This means that, unlike neonatologists, palaeontologists are faced with a fixed, but incomplete, set of data sources that are subject to ongoing revision and subjective interpretation. This subjectivity is a natural consequence of the entry of new authors that use differing species and generic conceptions, and differing taxonomic indicators, often leading to significant discontinuity in revisions (Kunz 2002; Forey *et al*. 2004; Frankham *et al*. 2012). Furthermore, new technological advancements, such as UV-colour detection in fossil shells, have led to the expansion of what were once considered stable cladistic entities (Caze *et al*. 2010). Technological advances, and the use of mixed evidence for diversity, means that a single idea or concept of what a species is, may no longer provide sufficient basis to enable a full recognition of taxonomic diversity.

A pluralistic approach to species recognition is grounded on the premise that, in palaeontology, taxonomic entities are not objectively equivalent and therefore, different forms of evidence are needed to define these taxa due to the complexity associated with morphospace boundary demarcation (Forey *et al*. 2004). Collinson (1986) argued that it is only by explicitly defining the characteristics and context of taxa that their phylogenetic relevance can be identified. This can be achieved by being explicit both in the species concept that is applied and by giving each taxon a position in both space and time. Pluralism allows for the use of a variety of species conceptionalities, which enables the explicit demarcation of taxa without the need to apply a particular species definition that would otherwise limit the taxonomist's ability to define new taxa (de Meeûs *et al*. 2003). This facilitates a more flexible approach to taxonomic understanding of diversity and leads to increased stability in cladistic arrangements going forward.

The classification of the Seraphsidae Gray, 1853 has historically been phenetically conceptional, centred on the morphology of the shells. This has been problematic due to the lack of significantly different structural features and the poor quality of much of the fossil record (Jung 1974; Caze *et al.* 2010). Notwithstanding, small structural differences remain the primary mode of distinguishing between taxa (Rolando 2001; Poppe and Tagaro 2016). One of the failings of this phenetic approach has been the overlooking of spatiotemporally dispersed taxa and the lumping of them with similar morphologically structured organisms. This has led to a potential underestimation of the actual number of potential taxa within the complex (Jung 1974).

Until recently, the Seraphsidae complex was thought to have only one extant member, and the fossil record was considered to be relatively stable (Jung and Abbott 1967). The last ten years has seen resurgence in the study of seraphsid gastropods (Caze *et al.* 2010; Rolando 2001). This rejuvenated interest has led to the reassessment of the living species and has resulted in differentiation of the previously monospecific complex (Liverani 2014; Poppe and Tagaro 2016; Maxwell *et al*. 2018; Dekkers *et al*. 2019). Furthermore, over the past decade, there have been several fossil taxa defined that have challenged the long held orthodox understanding of what was previously included within many taxa (*Paraseraphs* Jung, 1974; Caze *et al*. 2010). These new additions to the known taxa suggest that a complete revision of the complex is required to bring some understanding of the current taxonomic developments, and to place these new taxa within a context of revised intrafamily relationships.

1.1 Aims

This thesis presents a revision and synthesis of both extant and extinct Seraphsidae. The revision is grounded within a pluralist framework based on first principles: type recognition and the redefinition and redescribing of taxa using spatiotemporal positioning as well as morphological structure. The use of this approach, for the first time, enables all available information to be combined and synthesized to provide the most comprehensive understanding of the current systematic arrangements of taxa within the family. Brief overviews of the evolutionary pressures that have influenced the morphological evolution of each subclade are presented, with the aim of bringing causal understanding and an evolutionary context to the higher systematics within the family. Furthermore, where evidenced, new species are described using additional information, such as spatiotemporal positioning, in conjunction with morphological analysis. Historically, the methodological approach to species determination has dominated species classification (Jung 1974). In this thesis, the approach to species demarcation is pluralist, enabling the discernment and description of new material and taxa, which has not been possible with previous revisions that were bound under restrictions of species conceptionality, such as the phenetic concept, with its sole reliance on morphological characteristics.

This thesis has three aims. The first aim is to divide the superfamily Stromboidea Rafinesque, 1815 by morphological evidence into two distinctive evolutionary crown clades. Crown clades are clades that are defined based on living taxa. The crown clade in focus contains the families Seraphsidae, Strombidae Rafinesque, 1815, Rostellariidae Gabb, 1868 and Rimellidae Stewart, 1927. The second aim is to complete a classical α-taxonomic revision from first principles, which involves the use of original literature and type specimens of the family Seraphsidae (Stromboidea). This thesis tests the current phenetic species hypotheses against a pluralist approach to species conception. A pluralist approach includes all available evidence including morphological, spatiotemporal and anatomical/physiological. This approach seeks to discern the distinctiveness of organisms in ways that help explain evolution and radiation, and to present explanatory justifications for erecting each species within the complex. Finally, this thesis aims to resolve the infrageneric relationships within Seraphsidae using morphological cladistics.

1.2 Methods and Materials

Within this thesis I applied the pluralist approach to α-taxonomic revisions of a group of predominantly fossil gastropods. This thesis is grounded upon type material that was used in conjuction with published taxonomic descriptions. However, there was a strong need to rely on lectotypes to give meaning to the intention of the original authors, as physical type material was often either lost or destroyed (*cf.* de Gregorio 1880). Furthermore, I examined the taxonomy of all described taxa and their synonymic lists, and sought to explain or correct the discrepancy between the over synonymisation of some taxa (Jung 1974) and the incorrect recognition of taxa based on phenotypic forms of variable species (de Gregorio 1880). I also tested current species hypotheses against articles contained within the International Code of Zoological Nomenclature (ICZN 1999) on precedence and other rules concerning known alternative names.

The Revsion

The first stage of the revision involved the compilation of a list of all described taxa. This commenced with the taxa contained within the last major revision by Jung (1974). All synonyms were added to the list of potential valid taxa as no assessment of taxonomic validity was undertaken at this stage. An annotated taxonomy was then described, which included a review of pre-binominal lectotypes where necessary. The original descriptions were then examined, original author intent discerned, and the internal systematics of each work reviewed to uncover taxa that may have been overlooked by Jung (1974). Taxa that were previously not identified were then included within the annotated taxonomy, and the original works examined, again to discern author intent and to identify taxa that may have been further overlooked. Where subspecies or forms were described, and these were able to be matched to a cline, these were presented independently. Databases, such as the *Biodiversity Heritage Library* and *Summon 2.0*, were mined for works that contained references to material that were used in association with all taxa on the list. Furthermore, physical searches of historic texts were made to uncover taxa that may have been lost in time or not included in databases.

The second part of the taxonomic revision focused on the validity of each described entity, including the reassessment of current synonyms assigned to taxa within Seraphsidae chronologically. Validity was based on a pluralist approach, and was tested with evidence from current systematic arguments within the literature and all available evidence, such as infraspecific morphological variation, distribution, and temporal positioning. From this information, the precedence of names was determined, revised descriptions formulated, a list of taxonomic entities generated and an annotated synonymy was created for each identified taxon. The list of valid taxa and their synonymy was restricted to taxa described after 1758 following ICZN (1999) Article 3: *Starting point. The date 1 January 1758 is arbitrarily fixed in this Code as the date of the starting* *point of zoological nomenclature*. Working with the list of known taxonomic entities, the location of type material and its morphology were compared with all available evidence to establish identification, and to determine the known distribution of each currently defined taxonomic entity. This was then used to formulate a basis for species recognition allowing for the determination and identification of outliers that did not conform to a defined enitiy in terms of morphology or spatiotemporal positioning.

The literature in which the species were referred to and not illustrated or not supported by an external literary source that contained an illustration were only considered if the description enabled a clear resolution of author intent. Abbott (1960) noted that it was generally impossible to gauge author intent in early taxonomic works, such as Linné (1758), without an illustration due to the complexity of the modern taxonomy and the resultant misidentification through reclassification. These issues are noted under each taxon where appropriate.

Material Examined

Four forms of material and evidence were used in this review. These were then ranked in priority for the validation of taxa based on the accuracy of identification and certainty of locality data. The first priority was given to the type material for each taxon. The second priority was given to physical and photographic observations made from the privately owned systematic collections of self-collected material such as those of Valda Cantamessa and Uwe Weinreich. Third priority was given to published images in journals and online databases such as those owned by Conchology Inc. Finally, least priority was given to literary references for specimen localities without illustration; this is taxonomically problematic as the locality references generally lack supportive material. In addition, there is a high possibility of taxonomic confusion between species within the literature, exemplified by the long historical relegation of *Terebellum delicatum* Kuroda and Kawamoto in Kawamoto and Tanabe, 1956 as a form or synonym of *Terebellum terebellum* (Linné, 1758)(Jung and Abbott 1967; Jung 1974) or the use of *Seraphs sopitus* (Brander, 1766) as a repository for difficult taxa (Jung 1974). Complete lists of material considered in the thesis and their spatiotemporal distributions, are contained under the distribution of each taxon.

Cladistic methods

Character sets that reflect the synapomorphies within the major subclades of Seraphsidae were codified (Table 1). This coding was used to generate cladograms using maximum likelihood within the *tnt* program with default settings (Goloboff *et al*. 2008). Six characters were chosen and coded for:

1) The nature of the shell coiling: 0 – involute; 1 – evolute.
2) The absence or presence of the posterior canal: 0 – absent; 1 – present.

3) The nature of the ridge of the labrum: 0 – prosocyrt; 1 – opisthocyrt and prosocyrt in part; 2 – opisthocyrt.
4) The shape of the labrum: 0 – straight; 1 – undulating.
5) The form of the suture: 0 – not channelled; 1 – channelled.
6) The relative position of the axial maximum diameter: 0 – near mid-height; 1 – toward the base; 2 – toward the apex.

Table 1: Character states for the genera contained within Seraphsidae Gray, 1853.

Taxon	Character State					
	1	2	3	4	5	6
Seraphs	0	0	1	1	0	0
Miniseraphs	0	0	1	1	0	2
Diameza	0	0	1	1	0	2
Paraseraphs	1	1	0	0	0	1
Pseudoterebellum	1	0	0	0	1	2
Terebellum	1	0	0	0	1	1
Mauryna	1	1	2	1	0	0

There was only one cladogram produced, and this can be attributed to the limited number of characters and taxa (Figure 1). This tree formed the basis upon which the internal resolution within the clade was based.

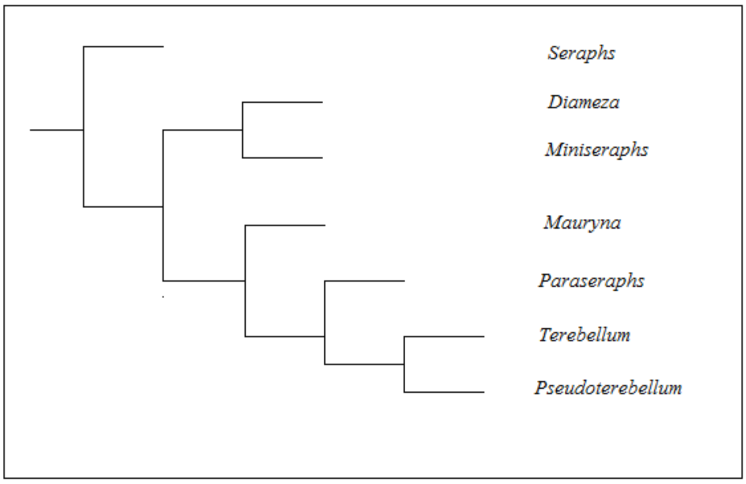


Figure 1: The single *tnt* generated maximum likelihood cladogram showing internal cladistic relationships within Seraphsidae Gray, 1853.

Chapter 2.0 Defining the Strombids

Early studies classified the internal cladistic structure of Mollusca Linné, 1758 in terms of gross anatomy, with the radula being the dominating feature in some classifications (Troschel 1856-1863; Mörch 1866; Cooke 1885, 1927; Thiele 1931), while other classifications were based on the structure and positioning of the mantle cavity and the buccal mass, or movement of the sole of the foot (MacDonald 1857; Cooke 1885, 1927).

The historically recognised recent members of the Strombidae (s.l.) included the now separated Rostellariidae, Seraphsidae, all of which share a universal similarity in the positioning of the eye on the end of the peduncles, and a diminished cephalic tentacle that arises mid to end on the peduncle. This contrasts with other members of the Stromboidea, the out-groups Strutholariidae Gabb, 1868 and Aporrhaidae, Gray 1850, where the eye is located at the base of the cephalic tentacle, which is not reduced (Figure 2).

This study argues for the division of the crown clade Stromboidea based on shared morphological synapomorphies between differing families within this clade which indicate a level of divergent and independent evolutionary life histories. This separation is needed to assist in resolving the higher order internal systematics of the Stromboidea to enable a more focused approach to understanding internal relationships and ancestral morphological states and patterns. There is a requirement for a name-bearing reference point that brings together the historically recognised members of the Strombidae that have now been divided into three separate families, and to distinguish those families from the other Stromboidea taxa, to achieve basal resolution of the crown clade through a clear definition and diagnosis enabling the separation from sister taxa, thus enabling an evolutionary meaning to be brought to the nomenclature of the clade.

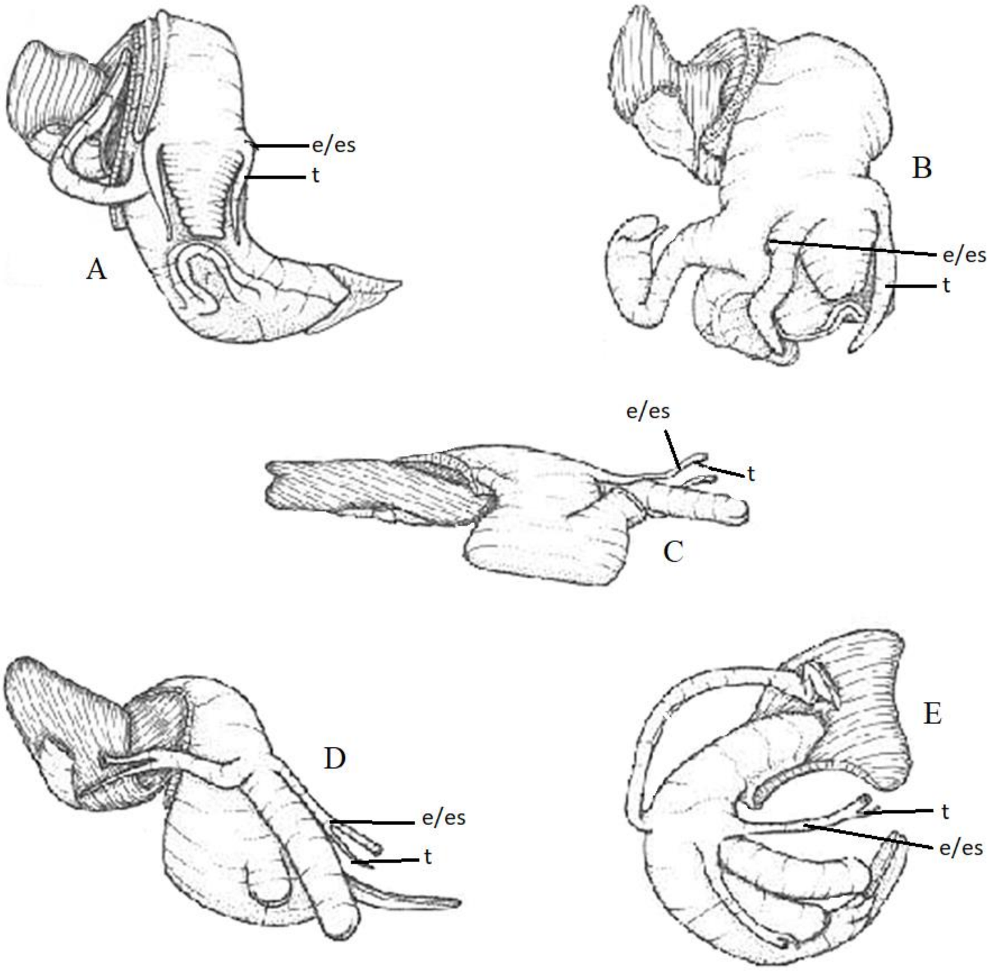


Figure 2: The anatomy of representatives of the five families with Stromboidea Rafinesque, 1815 indicating the eye (e) eye stalk (es) and the tentacle (t) : A – Strutholariidae Gabb, 1868 – *Tylospira scutulata* (Gmelin, 1791)(Simone 2005, fig. 254); B – Aporrhaidae Gray, 1850 – *Aporrhais occidentalis* (Beck, 1836)(Simone 2005, fig. 297); C – Seraphsidae Gray, 1853 – *Terebellum terebellum* (Linné, 1758)(Simone 2005, fig. 231); D – Rostellariidae Gabb, 1868 – *Tibia insulaechorab* (Röding, 1798)(Simone 2005, fig. 249); E – Strombidae Rafinesque, 1815 – *Strombus gallu*s Linné 1758 (Simone 2005, fig. 164).

2.1 Systematic Part

MOLLUSCA Linné, 1758
CAENOGASTROPODA Cuvier, 1797
SORBEOCONCHA Ponder and Lindberg, 1997
STROMBOIDEA Rafinesque, 1815

NEOSTROMBOIDAE

Maxwell, Dekkers, Rymer and Congdon, 2019

(SORBEOCONCHA STROMBOIDEA)

Type. The type genus is *Strombus* Linné, 1758

1853 Strombidae Gray, 11(62), p. 13. Notes: Invalid – preoccupied Strombidae Rafinesque 1815.
= Strombidae Adams and Adams, 1858, p. 257. Zittel 1885, p. 257.
= Strombidae d'Orbingy – Fisher 1873, 9, p. 375. Zittel 1885, p. 257.

Definition. The clade is nested within Stromboidea Rafinesque, 1815, with the characteristics outlined in the diagnosis, and contains taxa more closely related to *Strombus pugilis* Linné, 1758 (Strombidae Rafinesque, 1815) *Terebellum terebellum* (Linné, 1758)(Seraphsidae Gray, 1853) and *Tibia fusus* (Linné, 1758)(Rostellariidae Gabb, 1868) than Strutholariidae Gabb, 1868 and Aporrhaidae Gray, 1850 (Maxwell *et al*. 2019).

Diagnosis. The animal possesses eyes on the end of the peduncles. The cephalic tentacle is also located on the peduncle towards the distal end. The radula has a central rachadian tooth with three lateral teeth either side. The foot is laterally compressed, with a defined propodium and a metapodium. The shell form changes upon maturation with the development of an outer lip structure (Maxwell *et al*. 2019).

2.2 Discussion

The Neostromboidae falls within the clade Stromboidea, which belongs to the highly variable invertebrate Gastropoda (Mollusca). The ancestral resolution of Neostromboidae is extremely unstable, with many conflicting views on the exact ancestors that provide a division between Neostromboidae and the two immediate outgroups Strutholariidae and Aporrhaidae (Gabb 1869; Roy 1994; Kiel and Bandel 2002; Bandel 2007). It is postulated herein that *Phyllocheilus* Gabb, 1868 and *Pterodonta* d'Orbigny, 1843 form the immediate ancestral link with the Aporrhaidae and Strutholariidae out-groups based on gross morphology and the similarities with known stromboidal ancestors with Rimellidae Stewart, 1927 and Rostellariidae.

The Cretaceous clade Pugnellidae Kiel and Bandel, 1999, which is considered a precursor of Strombidae (Wenz 1938; Sohl 1960), is somewhat fluid in its content. However, recent revisions have clarified the taxonomic position of Pugnellidae, which is now considered to be a descendant of the Aporrhaidae (Kiel and Bandel 1999). This position is based on the structure of the protoconch, the low height of the teleoconch, the lack of ornamentation typical of Strombidae, the presence of a posterior rostrum with groove and importantly, the extension of the callus from the inner lip, which covers a greater portion of the teleoconch (Popenoe 1983; Kiel and Bandel 1999).

Morphologically, recent members of the Strutholariidae and Aporrhaidae differ from Neostromboidae in having a broader rather than flattened foot, as well as eyes on the base of the tentacles, rather than on peduncles as with the Neostromboidae (Gardner 1875). These recent members also differ for the most part in the feeding process, whereby the animal lies buried and extends its proboscis, 'grasping' at potential food items, or are filter feeders (Purchon 1977; Savazzi 1988b, 1991). However, the buried rasping feeding habit is not a significant distinguishing characteristic separating Strutholariidae and Aporrhaidae from the Seraphsidae (Jung and Abbott 1967). Given the general instability of the aporrhid group, it is not in the scope of this study to argue inclusiveness or provide a definition for that complex.

The Neostromboidae incorporates those taxa that developed a basal sinus on the shell outer lip in conjunction with eyes on peduncles. This co-evolution of a shell structure and morphological trait allowed the eyestalk to protrude whilst the animal remained aperture down on the substrate, protecting the soft parts from exposure. Furthermore, the movement of the cephalic tentacle towards the distal end of the eyestalk, thus protruding out from the basal sinus, enables the animal to achieve sensory awareness without any of the soft parts being exposed.

Chapter 3.0 Systematics of Seraphsidae

This review of Seraphsidae found the name to be valid with two synonyms and their derivations. The name Seraphina and its derivations reflect a crown clade within the family Strombidae that excluded fossil genera and, by definition, contained the *Terebellum* Röding, 1798 only. The name *Terebellinae* Adams and Adams, 1858 and its derivations were determined to be invalid on grounds of preoccupation.

Initial results indicated a considerable time gap in the geological record for the historically recognised members of the *Terebellum* (Figure 3). These two spatially divided sets within *Terebellum* also showed a structural difference in shell morphology based on maximal widths. The earlier set of taxa is herein removed from *Terebellum* and defined as *Pseudoterebellum* new genus.

The cladograms constructed from morphological data suggest that there are two distinct clades within the Seraphsidae (Figure 4). These two clades can be defined in terms of shell coiling: the involute *Seraphsinae* new subfamily and the evolute *Neoterebellinae* new subfamily. The Seraphsidae after Jung (1974) consists of three genera: *Terebellum*, *Paraseraphs* Jung, 1974 and *Seraphs* Montfort, 1810, which contained the subgenera *Diameza* Deshayes, 1865 and *Miniseraphs* Jung, 1974. The members of *Mauryna* de Gregorio, 1880 are herein included into Seraphsidae based on the morphological similarity to the *Seraphs* and *Paraseraphs*, and therefore are not seen as members of the Rostellariidae (Jung 1974).

The monotypic genus *Terebellominus* Pacaud, 2008 containing *Terebellominus quaggiottoi* Pacaud, 2008 is herein considered more closely related to *Terebellopsis* Leymerie, 1846 based on the morphology of the aperture. *Terebellominus* Pacaud, 2008 is therefore not included in Seraphsidae and is redirected to Rostellariidae.

In this study, the *Miniseraphs* and *Diameza* are considered of equal rank following Jung (1974), but unlike Jung (1974) these two clades are not considered subgenera contained with *Seraphs*. Recent studies have also placed *Miniseraphs* Jung, 1974 as a subgenus of *Diameza* (Caze *et al.* 2010). However, while they share similar morphology and spatiotemporal positioning each possess distinct morphology which indicates evolutionary divergence.

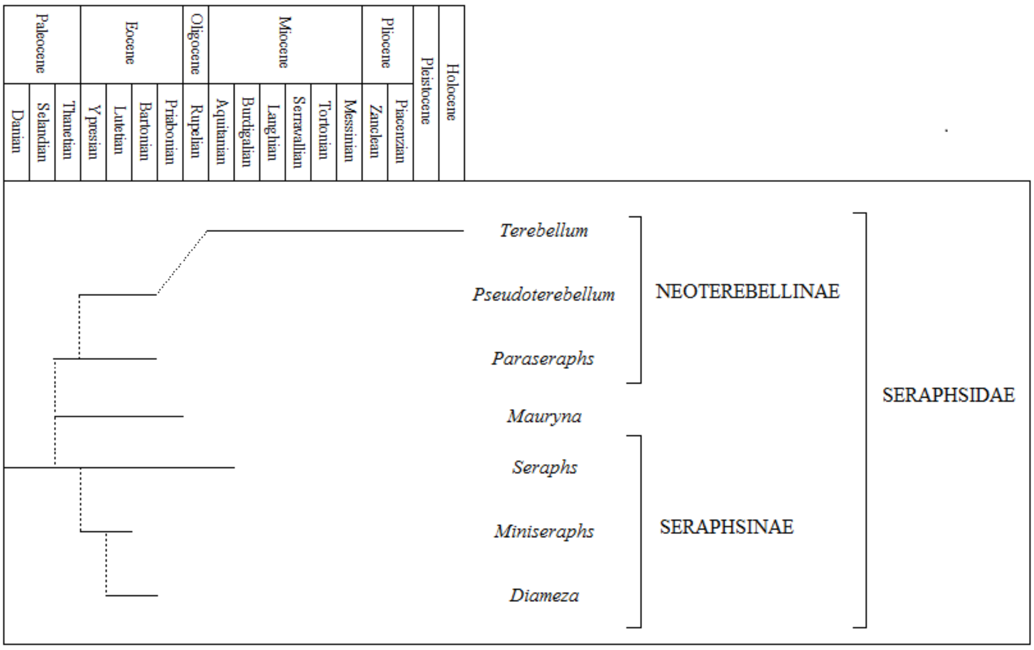


Figure 3: The clade Seraphsidae Gray, 1853 temporal distribution: solid lines indicate presence; dotted lines indicate a geological gap and hypothetical internal relationship.

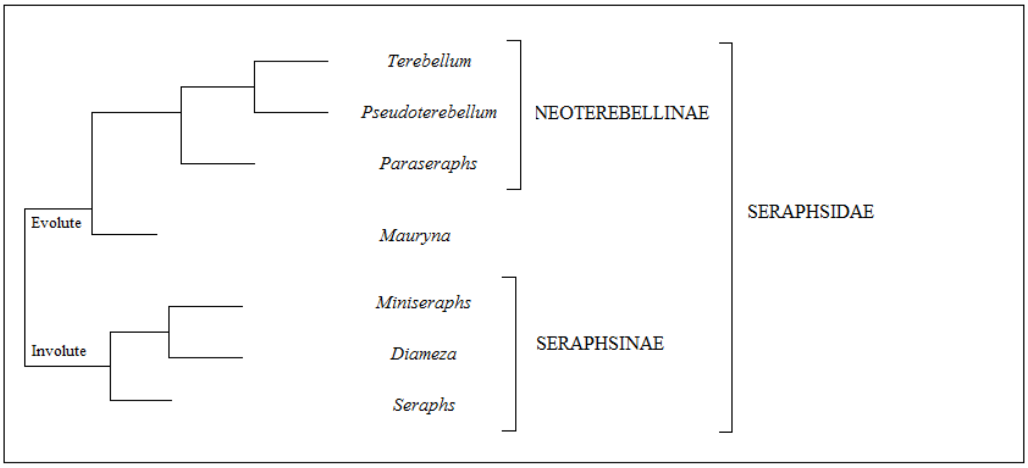


Figure 4: The clade Seraphsidae Gray, 1853 derived from character analysis.

3.1 Systematic Part

Seraphsidae Gray, 1853

1853 Seraphina Gray, p. 131. Maxwell *et al.* 2018b, p. 62. Type: *Seraphys* Gray, 1847 (= *Seraphs* Montfort, 1810). Notes: excluded– ICZN (1999) article 35.5 (Maxwell *et al.* 2018b). = *Seraphyinae* Gill, 1870 ex Gill 1871, p. 9. Maxwell *et al.* 2018b, p. 62. Type: *Terebellum terebellum* Linné, 1758. Notes: synonymised – Emendation of original name *Seraphina* Gray, 1853. = Seraphidae Gray – Bouchet & Rocroi 2005, p. 253. Bandel 2007, p. 136. Maxwell *et al.* 2018b, p. 62. Type: *Seraphs* Montfort, 1810. Notes: synonymised – Emendation of original name *Seraphina* Gray, 1853. = Seraphsidae Gray – Bouchet e*t al.* 2017. Maxwell *et al.* 2018b, p. 63. Type: Bruguière, 1798 (*Terebellum* Klein, 1753 = *Terebellum* Röding, 1798). Notes: synonymised – Emendation of original name *Seraphina* Gray, 1853.

1858 Terebellinae H. Adams & A. Adams, p. 262. de Gregorio 1880, p. 19. Maxwell *et al.* 2018b, p. 63. Type: *Terebellum subulatum* Chemnitz (= *Terebellum terebellum* (Linné, 1758)). Notes: excluded – Preoccupied – Terebellinae Johnston, 1846 (Polychaeta Grube, 1850). = Terebellidae Sacco, 1893, p. 21. Maxwell *et al.* 2018b, p. 63. Type: *Terebellum terebellum* (Linné, 1758). Notes: excluded – Preoccupied – Terebellinae Johnston, 1846 (Polychaeta Grube, 1850).

1974 Seraphsidae Jung, p. 12. Caze *et al.* 2010, p. 426. Maxwell *et al.* 2018b, p. 63. Type genus: *Seraphs* Montfort, 1810. Notes: accepted – Name derived directly from type genus (Jung, 1974). This family was defined as containing two distinct groups: the involute *Seraphs* Montfort, 1810 and the evolute *Terebellum* Röding, 1798 and *Paraseraphs* Jung, 1974 (Jung 1974).

Type genus. *Seraphs* Montfort, 1810 p. 375 (Jung 1974, p. 14).

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Terebellum terebellum* (Linné, 1758) and taxa more closely related to it than to Rostellariidae Gabb, 1868, Hippochrenidae Bandel, 2007 and Strombidae Rafinesque, 1815.

Diagnosis. The shell is typically long and narrow, with the last whorl extending over much of the earlier whorls. The stromboidal notch is poorly developed or absent.

Seraphsinae new subfamily
(Seraphsidae)

Type genus. *Seraphs* Montfort, 1810, p. 375.

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Seraphs sopitus* (Brander, 1766) and all taxa more closely related to it than defining members of *Mauryna* de Gregorio, 1880, *Paraseraphs* Jung, 1974 and *Terebellum* Röding, 1798.

Diagnosis. The shell is long and narrow, with the last whorl extending over much of the earlier whorls. The stromboidal notch is not well-developed. The involute shell is without a posterior canal. The columella is smooth.

Discussion. This clade unites the involute members of Seraphsidae that have historically been accepted as related (Jung 1974). Jung (1974) placed *Diameza* and *Miniseraphs* as subgenera of *Seraphs*. Recently Caze *et al.* (2010) elevated *Diameza* to include both subgenera *Diameza* and *Miniseraphs* and excluded *Seraphs*. Given *Diameza* and *Miniseraphs* form a monophyletic clade, such a move is herein deemed systematically problematic until its ancestral lineages are better understood.

Seraphs Montfort, 1810

(Seraphsinae)

Plates 1 – 3

1810 *Seraphs* Montfort, p. 375. Sowerby 1820–1825, pl. 263. Sowerby 1842, p. 255. Sowerby 1846, p. 255. H. Adams & A. Adams 1858, p. 263. Chenu 1859, p. 264. Tryon 1885, p. 103. Zittel 1885, p. 259. Cossmann 1889, p. 92. Jung 1974, p. 14. Bandel 2007, p. 137. Caze *et al*. 2010, p. 426. Notes: accepted. = *Seraphys* Montfort – Gray 1847, p. 132. Sowerby 1852, p. 273. Notes: synonymised – Emendation of original name *Seraphs* Montfort, 1810. This included *Terebellum* Röding, 1798. Type: *Seraphs convolutum* (Lamarck, 1803) (= *Seraphs volutatus* (Brander, 1766)). = *Seraphys* Gray, 1853, p. 133. Jung 1974, p. 14. Adams & Adams 1858, p. 263. Type: *Terebellum convolutum* Lamarck, 1803 (= *Seraphs volutatus* Brander, 1766). Notes: synonymised – Emendation of original name *Seraphs* Montfort, 1810. = *Seraps* Férussac – Jung 1974, 8, p. 14. Adams & Adams 1858, p. 263. Notes: synonymised – Emendation of original name *Seraphs* Montfort, 1810. = *Seraphe* Blainville – Jung 1974, 8, p. 14. Notes: synonymised – Emendation of original name *Seraphs* Montfort, 1810. = *Serapis* Link – Jung 1974, p. 14. Notes: synonymised – Emendation of original name *Seraphs* Montfort, 1810.

Type. *Terebellum convolutum* Lamarck, 1803 (*Bulla sopitus* Brander, 1766 = *Seraphs volutatus* (Brander, 1766)).

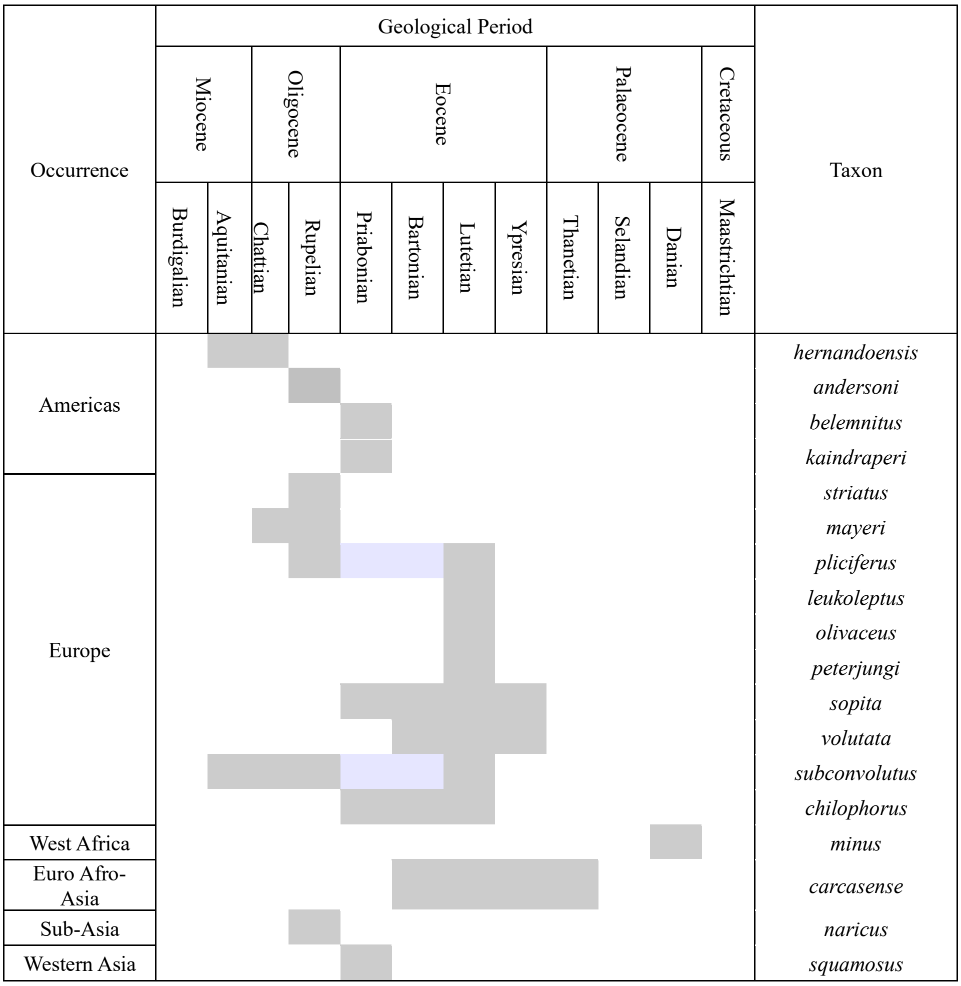
Definition. This genus has the characteristics outlined in the diagnosis, and contains *Seraphs sopitus* (Brander, 1766) and all taxa more closely related to it than to the defining members of *Miniseraphs* Jung, 1974, *Diameza* Deshayes, 1865, *Paraseraphs* Jung, 1974 and *Terebellum* Röding, 1798.

Diagnosis. The shell is involute without a posterior canal. The labrum of the shell is undulating. The aperture is narrow. The suture does not have a channel. The region of maximum width occurs at approximately mid-height.

Discussion. The geological range of *Seraphs* is considered to be the early Palaeocene (Danian) to the early Miocene (Aquitanian) (Figure 5). *Seraphs* arose in western Africa and then diversified, most significantly in Europe and western and central Asia. The complex soon dispersed away from the centre of early diversification, and arrived in the Indonesian archipelago and in North America by the Priabonian. The genus reached its greatest geographic range during the Oligocene (Jung 1974).

The problem of the quality of the fossil record is a significant taxonomic hindrance to the resolution of the *Seraphs* clade. The Egyptian *Terebellum dautzenbergi* Cuvillier, 1933 is based on material from the Lutetian of Gebel Mokattam, near Cairo (Jung 1974). This taxon is represented by a single internal cast that Jung (1974) likened to *Seraphs olivaceus* (Cossmann, 1889) and concluded that it may be that species. I herein incorporated *Terebellum dautzenbergi* within the synonymy of *Seraphs olivaceus*, but this species remains somewhat unresolved, requiring additional material to allow greater taxonomic resolution.

The taxon *Terebellum brongniartianum* d'Orbigny, 1850 is based upon material from the Middle Eocene of Roncá, northern Italy (Jung 1974). The type material has not been located, nor the types illustrated (Jung 1974). In the original description, d'Orbigny (1850) aligned the material to *Seraphs* and offered a comparison to *Seraphs sopitus*, and is herein provisionally incorporated within the synonymy of that taxon (Jung 1974; Pacaud 2008). Another significant problem faced with the review of the *Seraphs* is the use of some taxa, such as *Seraphs sopitus*, as repositories for confusing, or poor quality material: Jung (1974) synonymised *Seraphs caracasense* (Leymerie, 1846) and *Seraphs volutatus* under *Seraphs sopitus*, but all are herein accepted as full species (Caze *et al*. 2010).The taxon *Seraphs thompsoni* Dickerson, 1914 has been determined by previous workers, having examined the type materials, not belonging to Seraphsidae (Vokes 1939; Jung 1974).



Occurrence	Geological Period												Taxon
	Miocene		Oligocene		Eocene				Palaeocene			Cretaceous	
	Burdigalian	Aquitanian	Chattian	Rupelian	Priabonian	Bartonian	Lutetian	Ypresian	Thanetian	Selandian	Danian	Maastrichtian	
Americas		▨	▨										*hernandoensis*
				▨									*andersoni*
					▨								*belemnitus*
					▨								*kaindraperi*
Europe				▨									*striatus*
			▨	▨									*mayeri*
				▨	░	░	▨						*pliciferus*
							▨						*leukoleptus*
							▨						*olivaceus*
							▨						*peterjungi*
					▨	▨	▨	▨					*sopita*
						▨	▨	▨					*volutata*
		▨	▨	▨	░	░	▨						*subconvolutus*
					▨	▨	▨						*chilophorus*
West Africa											▨		*minus*
Euro Afro-Asia						▨	▨	▨	▨				*carcasense*
Sub-Asia				▨									*naricus*
Western Asia					▨								*squamosus*

Figure 5: The spatiotemporal distribution of *Seraphs* Montfort, 1810, darker shading indicates presence, whereas the lighter areas indicate a gap in the record between geological periods.

Seraphs andersoni (Dickerson, 1917)

Plate 1A

1917 *Terebellum andersoni* Dickerson, p.180, pl. 31, figs. 9a and b. Jung 1974, p. 29. Effinger 1938, p. 363. = *Seraphs* (*Seraphs*) *andersoni* Dickerson – Jung 1974, p. 29, pl. 9, figs. 5 & 6. Effinger 1938, p. 380.

Terebellum fusiforme Lamarck – de Gregorio 1890, p. 116, pl. 10, figs. 9 & 10.

Type Material. Holotype –CAS no. 434. The type measures 38 mm in length, with a width of 11 mm.

Type Locality. Cowlitz River, Vader, Lewis County, Washington [Rupelian].

Diagnosis. The shell is moderately stout and convolute. The apex is pointed, and there is no evidence of sutures between the volutions. The whorls have protocyrt growth lines. The aperture has a thin labrum and a columella that is basally recurved.

Distribution. OLIGOCENE – Rupelian – *USA,* east bank of the Cowlitz River, near Vader, Lewis County, Washington (Jung 1974); Santa Barbara County, California (Effinger 1938); Griens Ranch Fauna of Western Washington (Effinger 1938).

Seraphs belemnitus (Palmer in Richards & Palmer, 1953)

Plate 2B

1953 *Terebellum* (*Seraphs*) *belemnitum* Palmer in Richards & Palmer, p. 25, pl. 3 figs. 9 & 12. Jung 1974, p. 25. Woodring 1959, p. 192, pl. 25, fig. 6. = *Seraphs* (*Seraphs*) *belemnitus* Palmer – Jung 1974, p. 25, pl. 6, figs. 11 – 16.

Type Material. Holotype – FGS No. I-7642. The type measures 49 mm in length, with a width of 15 mm.

Type Locality. 4.7 km south of the town of Gulf Hammock, Road metal pit [Priabonian].

Diagnosis. The shell is convolute and slender. The whorls have rectilinear growth lines. The aperture has a rectilinear labrum margined at the peristome. The labial callus is well developed.

Distribution. EOCENE – Priabonian – *USA,* Gulf Hammock, Florida (Jung 1974). Panama Canal Zone, Gatuncillo Formation (Woodring 1959).

Seraphs carcasense Leymerie, 1846

Plate 3C

1846 *Terebellum carcasense* Leymerie, p. 33, pl. XVI, no. 9. = *Terebellum* (*Terebellum*) *carcassense* Leymerie – Jung 1974, p. 17. = *Terebellum carcassonense* Leymerie – Jung 1974, p. 17. Eames 1952, p. 73. = *Terebellum carcasensis* Leymerie – Eames 1952, p. 73. = *Terebellum carcassense* Leymerie – de Gregorio 1896, p. 36. Eames 1952, p. 73. Jung 1974, p. 17, pl. 4, figs. 10 & 11.

Terebellum oliviforme Mayer – de Gregorio 1880, p. 25. Jung 1974, p. 17, pl. 4, fig. 5.

Seraphs (*Seraphs*) sp. Jung, 1974, pl. 5, figs. 1 & 2.

Type Material. Lectotype – Leymerie 1846, p. 33, pl. XVI, no. 9. The type measures 58 mm in length, with a width of 20 mm (Leymerie 1846).

Type Locality. Montagne Noire, Carcassonne, France [Eocene].

Diagnosis. The shell is smooth and ovate. The spire is moderately high and blunted. The columella is straight, and the aperture is narrow.

Distribution. EOCENE – *Pakistan* Bhagothoro Hill, Sind, Laki Beds (Jung 1974); Zinda Pir (Jung 1974). *Republic of Georgia* Akhaltsikhe (Jung 1974). *Iran* Transcaspia or northern Persia (Eames 1952). *Spain* (Eames 1952). *Switzerland* (Eames 1952). *Italy* (Eames 1952). *France* (Eames 1952). Bartonian/Lutetian – *Armenia* (Eames 1952). Bartonian – *Italy* (Eames 1952). Lutetian – *France* (Eames 1952). *Italy* The Bavarian Alps and Bahrein Island (Eames 1952). Ypresian – *France* (Eames 1952). PALEOCENE – Thanetian – *France* Carcassonne (Jung 1974).

Seraphs chilophorus (Cossmann, 1889)

Plate 1D

1889 *Terebellum* (*Seraphs*) *chilophorum* Cossmann, p. 94, pl. 3, figs. 5 & 6. Jung 1974, p. 22. Caze *et al*. 2010, p. 440.

= *Seraphs* (*Seraphs*) *chilophorus* Cossmann – Jung 1974, p. 22, pl. 5, figs. 12–21, tfs. 15 & 16. = *Seraphs chilophorus* Cossmann – Caze *et al*. 2010, p. 440, figs. 15A–I.

Seraphs volutatus Quaggioto & Mellini 2008, p. 48, pl. V, fig. 29.

Type Material. Neotype – MNHN A25009 (Caze *et al*. 2010). The Cossmann (1889) type measures 29 mm in length, with a width of 8 mm.

Type Locality. Chaussy, France [Luteian].

Diagnosis. The shell is moderately slender. The body whorl has a narrow, obsolete and longitudinal sulcus. The teleoconch has longitudinal sulci that are posteriorly reflected becoming axial, and terminating at the peristome. The aperture is smooth, and the labium has a salient narrow columella that is well developed and separated from the shell surface. The labrum basally runs parallel to the columella but gradually becomes confluent forming a posterior sinus, is marginated at the peristome, and sinuous adapically. The posterior sinus is decumbent becoming apically first sinistrally deflected, then reflected and recurved over the apex where it terminates dorsally. The columella is anteriorly recurved and extends further than the labrum.

Distribution. EOCENE – Bartonian/Lutetian – *France* Les Boves, Paris Basin (Jung 1974). Bartonian – *France* Caumont, Seine-et-Marne (Caze *et al*. 2010). *Italy* Fontana del Cavaliere (Eames 1952); Monte Postale, Ciuppio, Valsugana and Croce Grand; San Giovanni, Ilarione (Eames 1952; de Gregorio 1880); Sorne (Eames 1952). Lutetian – *France* Chaussy, Val d'Oise (Jung 1974; Caze *et al*. 2010); Saint-Lubin-de-la-Haye, Eure-et-Loir (Caze *et al*. 2010); Fontenay-en-Vexin, Eure (Caze *et al*. 2010); Vandancort, Oise (Caze *et al*. 2010); Parnes, Oise (Jung 1974; Caze *et al*. 2010); Fercourt, Oise (Caze *et al*. 2010); Châteaurouge, Oise (Caze *et al*. 2010); Saint-Félix, Oise (Caze *et al*. 2010); Tiverval, Yvelines (Caze *et al*. 2010); Grignon, Yvelines (Jung 1974; Caze *et al*. 2010); Saulx-Marchais, Yvelines (Jung 1974; Caze *et al*. 2010). Priabonian – *Italy* Cimome (Eames 1952).

Seraphs hernandoensis (Mansfield, 1937)

Plate 1E

1937 *Terebellum henandoensis* Mansfield, p. 146, pl. 5, figs. 2 & 3. Jung 1974, p. 29. = *Seraphs* (?) *hernandoensis* Mansfield – Jung 1974, p. 29, pl. 9, figs. 7 to 9. = *Orthaulax pugnax hernandoensis* Mansfield – Shimer & Shrock 1944, p. 499. Vokes & Vokes 1968, p. 78. Petuch 1988, p. 49. = *Orthaulax hernandoensis* Mansfield – Vokes & Vokes 1968, p. 78. Vokes 1979, p. 112.

Terebellum fusiforme Lamarck – de Gregorio 1890, p. 116, pl. 10, figs. 7 & 8.

Type Material. Holotype – USNM 495948. The type measures 31.4 mm in length, with a width of 9.5 mm.

Type Locality. Brooksville, Hernando County, Florida [Rupelian].

Diagnosis. The shell is moderately slender. The labrum is not thickened. The growth lines are slightly prosocyrt. The columella is bent backward basally.

Distribution. MIOCENE – *USA* Tampa, Florida (Shimer & Shrock 1944). OLIGOCENE – *USA* Brooksville, Hernando County, Florida (Jung 1974); Alabama (Vokes & Vokes 1968); Georgia (Vokes & Vokes 1968).

Seraphs kaindraperi new species

Plate 1F

1974 *Seraphs* (*Seraphs*) cf. *sopitus* Solander – Jung 1974, p. 21, pl. 5, figs. 3 & 4.

Type Material. Holotype – USNM 135098. The type measures 56.9 mm in length.

Type Locality. Near Port Antonio, Portland Parish, Jamaica [Priabonian].

Diagnosis. The shell is convolute and moderately inflated and similar to *Seraphs sopitus* Brander, 1766. The teleoconch is blunt with a blunt apex. The volutions of the shell are smooth. The aperture is elongated and narrow. The labrum is not marginated and the peristome is sharp.

Distribution. EOCENE – Priabonian – *Jamaica* Port Antonio (Jung 1974).

Seraphs leukoleptus Jung, 1974

Plate 1G

1880 *Terebellum* (*Seraphs*) *fusiformopse* de Gregorio, p. 22, pl. 1, fig. 17 (in part). Cossmann 1889, p. 93, pl. 3, figs. 3, 4. Caze *et al*. 2010, p. 438.

1974 *Seraphs* (*Seraphs*) *leukoleptus* Jung, p. 23, pl. 6, figs. 1 to 3, tf. 17. = *Seraphs leukoleptus* Jung – Pacaud 2008, p. 727. Caze *et al*. 2010, p. 438, figs. 11F, H & I, and 13A– to H.

1880 *Terebellum* (*Seraphs*) *fusiformopse* de Gregorio, p. 22, pl. 1, fig. 17. Cossmann 1889, p. 93, pl. 3, figs. 3 & 4. Caze *et al*. 2010, p. 438.

Type Material. Neotype – MNHN no. A28781 (Caze *et al*. 2010). The Jung (1974) type measures 27.6 mm in length, with a width of 6.2 mm.

Type Locality. Chaussy, France [Lutetian].

Diagnosis. The shell is convolute, slender, becoming broader towards the base with the widest part just above the base. The surface of the shell is smooth with a few faint basal spiral sulci. The columella is slightly bent backward near the base. The labial callus is conspicuous, reaching the apex, and is separated from the surface of the shell. The labrum is straight in profile and slightly opisthocline. The base of the labrum is only slightly above the base of the columella.

Distribution. EOCENE – Lutetian – *France* Chaussy (Jung 1974; Caze *et al*. 2010).

Seraphs mayeri Jung, 1974

Plate 2A

1974 *Seraphs* (*Seraphs*) *mayeri* Jung, p. 27, pl. 8, figs. 13 to 21, tf. 18.

2008 *Seraphs sopitus* Quaggioto & Mellini, p. 48, pl. V, fig. 28.

Type Material. Holotype – NMB 16578. The type measures 21.4 mm in length, with a width of 7.3 mm.

Type Locality. Monte Grumi, Castelgomberto, Italy [Oligocene].

Diagnosis. The shell is moderately slender with a moderately acute apex. The labium is thin and continues above the adapical end of the aperture to the apex. The labrum is thin but thickens forming a posterior canal. The columella is basally slightly bent backward.

Distribution. OLIGOCENE – *Italy* Monte Grumi, near Castelgomberto (Jung 1974); Santa Trinità, near Montecchio Maggiore (Jung 1974).

Seraphs minus (Vincent, 1913)

Plate 2B

1913 *Terebellum* (*Seraphs*) *minus* Vincent, p. 19, pl. 1, figs. 23 & 24. Jung 1974, p. 25. = *Seraphs* (*Seraphs*) *minus* Vincent – Jung 1974, p. 25, pl. 6, figs. 9 & 10.

Type Material. Lectotype – Vincent 1913, pl. 1, figs. 23 & 24. The type measures 8 mm in length (Vincent 2013).

Type Locality. Landra, Cabinda, Angola [Danian].

Diagnosis. Jung (1974: 21) noted that the *Seraphs minus* Vincent, 1913 type material could not be located, and he recommended that the taxon should be considered *novem dubium* as the morphology is, at present, best described as unclear, the type material being a small juvenile specimen. However, given the restricted geographic range, and as the only representative of *Seraphs* Montfort, 1810 from this region in Africa, it is herein considered taxonomically significant and worthy of recognition.

Distribution. ?PALEOCENE – Danian – *Angola* Cabinda (Jung 1974).

Seraphs naricus (Vredenberg, 1925)

Plate 2C

1925 *Terebellum* (*Seraphs*) *naricum* Vredenberg, p. 323, pl. 13, figs. 4A to C. Jung 1974, p. 28. = *Seraphs* (*Seraphs*) *naricus* Vredenberg – Jung 1974, p. 28, pl. 6, figs. 20 to 22. = *Seraphs naricus* Vredenberg – Harzhauser 2009, p. 138.

Type Material. Holotype – GIS no. 12614. The type measures 38.6 mm in length, with a width of 10.8 mm.

Type Locality. Bhagothoro Hill, Sind, Pakistan [Rupelian].

Diagnosis. The shell is slender and cylindrical with a moderately pointed apex. The aperture is long and narrow. The labrum is thin and prosocyrt near the adapical end of the aperture, becoming opisthocline on the teleoconch.

Distribution. OLIGOCENE – Rupelian – *Pakistan* Bhagothoro Hill, Sind (Jung 1974).

Seraphs olivaceus (Cossmann, 1889)

Plate 2D

1889 *Terebellum* (*Seraphs*) *olivaceum* Cossmann, p. 93, pl. 3, figs. 1 & 2. Jung 1974, p. 21. Caze *et al*. 2010, p. 430. = *Seraphs* (*Seraphs*) *olivaceus* Cossmann – Jung 1974, p. 21, pl. 5, figs. 5 to 11, tf. 15. = *Terebellum* (*Seraphs*) *olivaceus* Cossmann – Caze *et al*. 2010, p. 430. = *Seraphs olivaceus* Cossmann – Caze *et al*. 2010, p. 430, figs. 6H to J & 10.

1933 *Terebellum dautzenbergi* Cuvillier, p. 46, pl. 6, figs. 3 & 4. Jung 1974, p. 45.

Terebellum (*Seraphs*) *fusiforme* Lamarck – Tessier 1952, p. 374, pl. XXXII, figs. 16 to 18. Jung 1974, p. 21, pl. 5, figs. 10 & 11.

Type Material. Neotype – MNHN A28885 (Caze *et al*. 2010). The Cossmann (1889) type measures 32 mm in length, with a width of 9 mm.

Type Locality. Chaussy, France [Lutetian].

Diagnosis. The shell is moderately slender with straight sides with the widest part being just below the adapical end of the aperture. The apex is acute. The surface of the shell is smooth with faint sinuous growth lines. The labial callus is not well-developed and is inconspicuous. The labrum is not thickened, and has a sinuous profile. The columella is bent backward near the base. The base of the labrum does not extend as far as the end of the columella.

Distribution. EOCENE – Lutetian – *France* Chaussy, Val d'Oise (Jung 1974; Caze *et al*. 2010); Fercourt, Oise, Mouchy-le-Châtel, Oise (Caze *et al*. 2010); Parnes, Oise (Jung 1974; Caze *et al*. 2010); Fontenay-en-Vexin, Eure (Caze *et al*. 2010); Chaussy Vaudancourt (Jung 1974); Parnes (Jung 1974); Sondage de Tivsouane (Tessier 1952) Beronkhout (Tessier 1952) Thiès-Saint–Louis (Tessier 1952) Teugge (Tessier 1952). *Italy* Piana, west of Schio (Jung 1974). *Egypt* Gebalmakattam (Cuvillier 1933).

Seraphs peterjungi Caze, Merle, Pacaud & Saint Martin, 2010

Plate 2E

2010 *Seraphs peterjungi* Caze *et al*., p. 445, figs. 15J to N & 19.

Type Material. Holotype – MNHN A28578. The type measures 23 mm length, with a width of 7 mm.

Type Locality. Chaussy, France Lutetian.

Diagnosis. The shell is moderately ovate and elongated, with the widest part being just below the adapical end of the aperture. The apex is moderately blunt. The surface of the shell is smooth with faint sinuous growth lines. The labial callus is well-developed and conspicuous. The labrum is not thickened and has a moderately quadrate profile. The columella is recurved backward near the base. The base of the labrum does not extend as far as the end of the columella. The anterior of the body whorl has fine axial grooves.

Distribution. Lutetian – *France* Chaussy, Val d'Oise (Caze *et al*. 2010); Grignon, Yvelines (Caze *et al*. 2010); Beynes, Yvelines (Caze *et al*. 2010); Saulx-Marchais, Yvelines (Caze *et al*. 2010); Fercourt, Oise (Caze *et al*. 2010); Parnes, Oise (Jung 1974; Caze *et al*. 2010).

Seraphs pliciferus (Bayan, 1870)

Plate 2F

1870 *Terebellum pliciferum* Bayan, p. 481, no. 25. = *Terebellum* (*Mauryna*) *placiferum* Bayan – de Gregorio 1880, p. 25. Dainelli 1905, p. 76. Dainelli 1912, p. 57, no. 140. = *Terebellum* (*Seraphs*) *pliciferum* Bayan – Jung 1974, p. 24. = *Terebellum* (*Mauryna*) *placiferum plicifera* Bayan – de Gregorio 1880, p. 25, pl. I, fig. 28, pl. V, fig. 31. de Gregorio 1896, p. 36. = *Mauryna plicifera* Bayan – Dainelli 1905, p. 76. = *Seraphs* (*Seraphs*) *plicifer* Bayan – Jung 1974, p. 24, pl. 7, figs. 1 to 17. = *Seraphs plicifer* Bayan – Quaggioto & Mellini 2008, p. 48, pl. 1, fig. 28, pl. V, figs. 23, 30 & 31.

1880 *Terebellum* (*Mauryna*) *placiferum plicifera transeuns* de Gregorio, p. 25, pl. V, fig. 23. = *Mauryna plicifera transeuns* de Gregorio – Jung 1974, p. 24.

1880 *Terebellum* (*Mauryna*) *placiferum protoelegans* de Gregorio, p. 25, pl. I, figs. 25 & 26. = *Mauryna protoelegans* de Gregorio – Dainelli 1905, p. 76. Jung 1974, p. 24.

Type Material. Lectotype – MNHN no. G2100. The type measures 33.7 mm in length, with a width of 13.9 mm.

Type Locality. Croce Grande, San Giovanni Ilarione, Italy [Lutetian].

Diagnosis. The shell is slender with variably wide axial swellings that are parallel to the undulating growth lines. The aperture is smooth with an unmargined labrum, and labium with an obsolete columella.

Distribution. OLIGOCENE – *France* Gaas, Aquitaine Basin (Jung 1974). EOCENE – Lutetian – *Italy* Croce Grande near San Giovanni Ilarione (de Gregorio 1880; Jung 1974). *Yugoslavia* (Jung 1974).

Seraphs sopitus (Brander, 1766)

Plate 2G

1766 *Bulla sopita* Brander, p. 19, pl. I, fig. 29a. Montfort 1810, p. 375. Sowerby 1821, p. 155. Reeve 1842, p. 268. Morris 1843, p. 162. de Gregorio 1894, p. 11. Dainelli 1905, p. 76. = *Terebellum sopita* Brander – Mörch 1852, p. 64. = *Terebellum sopitum* Brander – Fuchs 1870, p. 13. Zittel 1885, p. 259, fig. 354. Dainelli 1905, p. 76. = *Terebellum* (*Seraphs*) *sopitum* Solander – Cossmann 1889, p. 92. Jung 1974, p. 16. = *Terebellum* (*Seraphs*) *sopitum* Solander – Dainelli 1905, p. 76. Dainelli 1912, p. 57, no. 139. Quaggioto & Mellini 2008, p. 48, pl. 1, fig. 19, pl. V, fig. 33. = *Bulla sopita* Solander – Jung & Abbott 1967, p. 448. Jung 1974, p. 16. Caze *et al*. 2010, p. 428. = *Seraphs* (*Seraphs*) *sopitus* Brander – Jung 1974, p. 16, pl. 1, figs. 1 to 3, 6 to 11 & 14 to 19, pl. 2, fig. 8, tf. 11. = *Seraphs* (*Seraphs*) cf. *sopitus* Solander – Jung 1974, p. 16, pl. 5, figs. 3 & 4. = *Terebellum sopitum* Solander – Rusu *et al*. 2004, p. 443. = *Bulla sopitus* Brander – Pacaud 2008, p. 722. = *Terebellum* (*Seraphs*) *sopitus* Cossmann – Caze *et al*. 2010, p. 428. = *Terebellum* (*Seraphs*) *sopitum* Lamarck – Caze *et al*. 2010, p. 426. = *Terebellum sopitum* d'Orbigny – Caze *et al*. 2010, p. 426. = *Seraphs sopitus* Brander – Caze *et al*. 2010, pp. 426 & 428, figs. 6F to G & 9.

1823 *Terebellum obvolutum* Brongniart, p. 62, pl. II, figs. 15a & b. Bronn 1824, p. 50, pl. 3, no. 4. Jung 1974, p. 17.

1850 *Terebellum belemnitoideum* d'Archiac in de Tchihatcheff, p. 405. Jung 1974, p. 17, pl. 3, figs. 6 to 8.

1880 *Terebellum sopitum lanceolatum* de Gregorio, p. 23, pl. V, fig. 28. = *Terebellum lanceolatum* de Gregorio – Jung 1974, p. 17.

1880 *Terebellum sopitum fusiformopse* de Gregorio, p. 22, pl. V, fig. 29. Eames 1952, p. 74. = *Terebellum fusiformopse* de Gregorio – Eames 1952, p. 74, pl. 3, figs. 76a & b. Jung 1974, p. 17. = *Terebellum fusiformopsis* de Gregorio – Eames 1952, p. 74.

1880 *Terebellum sopitum convofusiforme* de Gregorio, p. 22, pl. V, fig. 32. = *Terebellum convofusiforme* Jung – Jung 1974, p. 45. Pacaud 2008, p. 727. Quaggioto & Mellini 2008, p. 48, pl. V, fig. 32.

1880 *Terebellum fusiformopse pectinatum* de Gregorio, p. 22, pl. 1, fig. 17. = *Terebellum pectinatus* de Gregorio – Quaggioto & Mellini 2008, p. 48, pl. 1, fig. 17. = *Terebellum pectinatum* de Gregorio – Pacaud 2008, p. 727.

1880 *Terebellum fusiforme postonicum* de Gregorio, p. 20, pl. I, fig. 18.

1880 *Terebellum sopitum perconvolutum* de Gregorio, p. 23. = *Terebellum perconvolutum* de Gregorio – Jung 1974, p. 17.

1880 *Terebellum sopitum superbum* de Gregorio, p. 23, pl. I, fig. 19. = *Terebellum superbum* de Gregorio – Jung 1974, p. 17.

1880 *Terebellum sopitum postturgidum* de Gregorio, p. 23, pl. V, fig. 33. = *Terebellum postturgidum* de Gregorio – Jung 1974, p. 17.

1896 *Terebellum convolutum roncanum* de Gregorio 1896, p. 35, pl. 3, fig. 4.

1966 *Terebellum* (*Seraphs*) *korobkowi* Bagmanov, p. 181, pl. 85, fig. 1. Jung 1974, 8, p. 18.

1966 *Terebellum* (*Seraphs*) *issaevae* Bagmanov, p. 181, pl. 83, figs. 2 to 5. Jung 1974, 8, p. 18.

1966 *Terebellum* (*Terebellum*) *paradaschensis* Bagmanov, p. 181, pl. 84, figs. 1 to 4. Jung 1974, p. 18.

Terebellum obesum Mayer – de Gregorio 1880, p. 25. Jung 1974, p. 18, pl. 4, figs. 1 to 4.

Terebellum plicatum d'Archiac & Haime – Jung 1974, p. 17.

Terebellum clava Schafhäutl – Jung 1974, p. 17.

Terebellum (*Seraphs*) *sopitum giganticum* Korobkov – Jung 1974, p. 18.

Terebellum (*Seraphs*) *sopitum daralagiosicum* Gabrielian – Jung 1974, p. 18.

Terebellum convolutum Lamarck – Wood 1829, p. 7.

Terebellum obtusum Sowerby – Jung 1974, p. 17, pl. 4, figs. 12 & 13.

Seraphs spc. 1 – Caze *et al*. 2010, p. 434, figs. 11A to C & 12A to C.

Terebellum fusiforme Lamarck – Sowerby 1821, p. 157. pl. 287, figs. 1 to 4. Brown 1849, p. 45, pl. XXX, figs. 26 and 27. de Gregorio 1894, p. 11, pl. 1, fig. 21. Dainelli 1912, p. 57, no. 138. = *Terebellum fusiform* Lamarck – Abbass 1972, p. 53, pl. V, figs. 3 & 4.

Terebellum obtusum Sowerby – d'Archic & Haime 1853, pl. 32, fig. 20. Jung 1974, p. 17.

Type Material. Lectotype – NHMUK GG21010. The type measures 26.4 mm in length.

Type Locality. Cliffs near Hordwell Village, Hampshire County [Bartonian].

Diagnosis. The shell is inflated with a teleoconch that is variable in height, which is reflected in the acuteness of the apex that ranges from blunt to moderately acute at maturity. The surface of the shell is smooth with undulating growth lines. The labrum is not thickened and is weakly calloused. The aperture is long and narrow, with a straight columella that becomes basally recurved.

Distribution. EOCENE – *The United Kingdom* Barton (Morris 1843); Cliffs near Hordwell, Hampshire County (Jung 1974). Bartonian – *The United Kingdom* Barton-on-sea, Hampshire (Morris 1843; Jung 1974); Hordwell, Hampshire County (Jung 1974); London Clays (Tennant 1847). *France* Baron, Oise (Caze *et al*. 2010). Le Limon, Seine-et-Marne (Caze *et al*. 2010); Le Guépelle, Val d'Oise (Caze *et al*. 2010); Le Quoniam, Val d'Oise (Caze *et al*. 2010); Vendrest, Seine-et-Marne (Caze *et al*. 2010); Saint-Witz, Val d'Oise (Caze *et al.* 2010). *Italy* Mont Postale (de Gregorio 1894). *Romania* (Rusu *et al*. 2004). Lutetian – *Italy* San Giovanni Ilarione (de Gregorio 1880). *France* Villiers-St-Frédéric, Yvelines (Jung 1974). Turkey Zafranboli (Jung 1974). *Armenia* Djulfa (Jung 1974). Ypresian – *Saudi Arabia* Ash Sharqiyda (Abbass 1972).

Seraphs squamosus (Martin, 1914)

Plate 3A

1914 *Terebellum* (*Seraphs*) *squamosum* Martin, p. 159, pl. 5, figs. 125 & 126. Jung 1974, p. 25. = *Terebellum squamosum* Martin – Jung 1974, p. 25. = *Seraphs* (*Seraphs*) *squamosus* Martin – Jung 1974, p. 25, pl. 6, figs. 17 to 19.

Type Material. Lectotype – RGM no. 10344. The type measures 37.1 mm in length with a width of 13.1 mm.

Type Locality. Kai Puru, Naggulan, Djokjakarta, Java [Priabonian].

Diagnosis. The shell has a stout but acute teleoconch. The greatest diameter of the shell occurs at the adapical end of the aperture. The body whorl is slightly concave at the lower half. The columella is bent to the left and backward. The callus of the labrum reaches the apex. The labrum is slightly thickened and terminates well above the columella. As a juvenile, the shell has a slight spiral groove near the apex. The adults have distinctive sculpturing on the lower half of the body whorl. The growth lines of the shell form a reticulate spiral pattern.

Distribution. EOCENE – Priabonian – *Indonesia* Kali Puru, Nanggulan, Java (Martin 1914; Jung 1974).

Seraphs striatus (von Koenen, 1889)

Plate 3B

1889 *Terebellum striatum* von Koenen, p. 39, pl. 1, figs. 7a to d. Sacco 1893, p. 21. Jung 1974, p. 28. = *Seraphs* (*Seraphs*) *striatus* von Koenen – Jung 1974, p. 28, pl. 9, figs. 1 to 4.

Type Material. Lectotype – von Koenen 1889, pl. 1, figs. 7a–d. The type measures 38.5 mm in length with a width of 10.7 mm (von Koenen 1889).

Type Locality. Lattorf, Germany [Rupelian].

Diagnosis. The shell is slender. The surface of the shell is smooth with fine spiral lines anteriorly on the body whorl. The labial callus is well-developed and extends to the shell apex. The labrum is moderately thickened and extends to the apex. The columella is recurved outward at the base.

Distribution. OLIGOCENE – Rupelian – *Germany* Lattorf (Jung 1974).

Seraphs subconvolutus (d'Orbigny, 1852)

Plate 3C

1852 *Terebellum subconvolutum* d'Orbigny, p. 8, no. 140. Fuchs 1870, p. 12. Jung 1974, p. 26. Harzhauser 2007, p. 104. Caze *et al*. 2010, p. 438. Vergneau 1967, pp. 203 & 206. = *Seraphs* (*Seraphs*) *subconvolutus* d'Orbigny – Jung 1974, p. 26, pl. 8, figs. 1 to 10, tf. 18. = *Seraphs subconvolutus* d'Orbigny – Harzhauser 2007, p. 104, pl. 4, fig. 9. Harzhauser 2009, p. 138. Caze *et al*. 2010, p. 438, fig. 14.

1852 *Terebellum subfusiformis* d'Orbigny, p. 8, no. 141. Fisher 1873, p. 377, no. 651. Jung 1974, p. 26. = *Terebellum* (*Terebellum*) *subfusiforme* d'Orbigny– Sacco 1893, p. 21, pl. 2, fig. 19. Jung 1974, p. 26.

1880 *Terebellum fusiforme saldatum* de Gregorio, p. 22, pl. V, fig. 22.

1880 *Terebellum fusiforme retractum* de Gregorio, p. 20, pl. V, figs. 24 & 25. Jung 1974, p. 17. Eames 1952, p. 74. = *Terebellum retractum* de Gregorio – Pacaud 2008, p. 727.

Terebellum convolutum Lamarck – Grateloup 1834, p. 314. d'Orbigny 1852, p. 8, no. 140. Fuchs 1870, p. 12. Jung 1974, p. 26. Caze *et al*. 2010, p. 438.

Terebellum fusiforme Lamarck – Grateloup 1834, p. 315. d'Orbigny 1852, p. 8, no. 141. Fisher 1873, p. 377. Jung 1974, pp. 2 & 18, pl. 3, figs. 4 & 5. Caze *et al*. 2010, p. 438. Harzhauser 2007, p. 104.

Seraphs volutatus Solander – Quaggioto & Mellini 2008, figs. 24 & 25.

Type Material. Lectotype – MNHN no. UBT 65-2-120 (Caze et al. 2010). The type measures 28 mm in length with a width of 6.5 mm.

Type Locality. Gaas, France [Oligocene].

Diagnosis. The shell is cylindrical with a long, narrow aperture. The labial callus is thin in contrast to the labrum, which is slightly thickened and prosocyrt below the adapical end of the aperture. Above the adapical end of the aperture the labrum runs antispiral, reaching the apex after about half a volution. The columella is slightly bent backward near the base.

Distribution. MIOCENE – Aquitanian – *Oman* Gebel Madrakah (Harzhauser 2007). OLIGOCENE – *France* Lesperon ('Grateloup' in Jung 1974); La Souys ('Magne' in Jung 1974).

Italy Tongriano of Cassinelle ('Sacco' in Jung 1974); Latterfiano ('Fabiani' in Jung 1974); Castelgomberto (Jung 1974); Mt. Della Cariolo Bei Polescella (Fuchs, 1870); Mt Castellaro (Fuchs, 1870); Mt Grumi (Fuchs 1870). Rupelian – *France* Gaas, Landes (Fuchs 1870; Jung 1974; Caze *et al*. 2010). *Italy* Veneto ('Fabiani' in Jung 1974). Chattian – *Oman* Karmah Pass, Duqm (Harzhauser 2007); Madrakah Cliff (Harzhauser 2007). EOCENE – Lutetian – *Italy* San Giovanni Ilarione (de Gregorio 1880).

Seraphs volutatus (Brander, 1766)

Plate 3D

1766 *Bulla volutata* Brander, p. 34, pl. VI, fig. 75. Montfort 1810, p. 375. = *Terebellum sopitum* d'Orbigny – Caze *et al*. 2010, p. 428.

1821 *Terebellum convolutum* Lamarck – Montfort 1810, p. 375. Sowerby 1820–1825, pl. 263, fig. 4. Sowerby 1821, p. 155. Wood 1829, p. 7. Gould 1833, p. 96. Sowerby 1839, p. 96, 104, fig. 451. Anton 1839, p. 102. Sowerby 1842, p. 255, fig. 451. Reeve 1842, p. 268, pl. 191 fig. 4. Sowerby 1846, p. 255, fig. 451. Brown 1849, p. 45, pl. XXX, figs. 24 & 25. Sowerby 1852, p. 273, fig. 451. Mörch 1852, p. 64. Pictet 1853–1857, p. 42, pl. 64, fig. 1. Chenu 1859, p. 264, fig. 1659. Fuchs 1870, p. 13. Cossmann 1889, p. 92. de Gregorio 1894, p. 11, pl. 1, figs. 14 to 20. Zittel 1885, p. 259. Dainelli 1905, p. 76. Jung 1974, pp. 16 & 18. Caze *et al*. 2010, p. 426. Effinger 1938, p. 381. = *Seraphs convolutus* Montfort, 1810, p. 375. Sowerby 1821, p. 155, pl. 286. Wood 1829, p. 7. Morris 1843, p. 162. Tennant 1847, p. 34. Caze *et al*. 2010, p. 426. = *Seraphs convolutus* Montford – Reeve 1842, p. 268. = *Terebellum convolutum* Montfort – Jung 1974, p. 17. = *Seraphs convolutus* Wood – Caze *et al*. 2010, p. 426. = *Terebellum* (*Seraphs*) convolutum Lamarck – Jung 1974, p. 17. Caze *et al*. 2010, p. 426. = *Terebellum* (*Seraphs*) *sopitum convoluta* Cossmann – Caze *et al*. 2010, p. 426. = *Terebellum sopitum convolutum* de Gregorio, 1880, p. 23, pl. I, fig. 20. = *Terebellum convolutum* de Gregorio– Jung 1974, p. 17. = *Seraphs convolutum* Lamarck – Bandel 2007, p. 137. = *Seraphs convolutus* Wood– Caze *et al*. 2010, p. 428.

Terebellum convolutum roncanum de Gregorio– Jung 1974, p. 17, pl. 3, fig. 9.

Seraphs spc. 2 – Caze *et al*. 2010, p. 434, figs. 11D, E & 12 D to F.

Bulla sopita Brander– Wood 1829, p. 7, pl. I, fig. 29a. = *Seraphs* (*Seraphs*) *sopitus* Brander– Jung 1974, p. 16, pl. 1, figs. 4, 5, 12 & 13. pl. 2, figs. 1 to 7.

Type Material. Lectotype – Brander 1766 p. 34, pl. VI, fig. 75.

Type Locality. Cliffs near Hordwell Village, Hampshire County, UK [Bartonian].

Diagnosis. The shell is inflated with a teleoconch that is variable in height, which may reach 75 mm length and 22 mm in width (Caze *et al*. 2010), which is reflected in the acuteness of the apex. The surface of the shell is smooth with undulating growth lines. The labrum is not thickened and is weakly calloused. The aperture is long and narrow, with a straight columella that becomes basally recurved.

Distribution. EOCENE – *Egypt* Mount Mokattam, near Cairo (Jung 1974). *Italy* Roncá (Jung 1974); Monte Postale (Jung 1974). *Romania* Monoster, Cluj Basin (Jung 1974). Bartionian – *France* Bois-Gouët, Loire-Atlantique (Caze *et al.* 2010); Acy-en-Multien, Oise (Caze *et al.* 2010); Caumont, Seine-et-Marne (Caze *et al.* 2010); Luzancy, Seine-et-Marne (Caze *et al.* 2010); Mary-sur-Marne, Seine-et-Marne (Caze *et al.* 2010); Ronquerolles, Val-d'Oise (Caze *et al.* 2010); Verneuil, Marne (Caze *et al.* 2010). *England* Hordwell, Hampshire County (Jung 1974; Caze *et al.* 2010). Lutetian – *France* Beynes, Yvelines (Caze *et al.* 2010); Blaye, Gironde (Caze *et al.* 2010); Boursault, Marne (Caze *et al.* 2010); Chambors, Oise (Caze *et al.* 2010); Chamery, Marne (Caze *et al.* 2010); Chaussy, Val d'Oise, (Caze *et al.* 2010); Chaussy. Seine-et-Oise, (Jung 1974); Cressay, Yvelines (Caze *et al.* 2010); Damery, Marne (Caze *et al.* 2010); Ferme de l'Orme, Yvelines (Caze *et al.* 2010); Fontenay-en-Vexin, Eure (Caze *et al.* 2010); Fresville, Manche (Caze *et al.* 2010); Gentilly, Val-de-Marne (Caze *et al.* 2010); Grignon, Yvelines (Caze *et al.* 2010); Hauteville-Bocage, Manche (Caze *et al.* 2010). Hermonville, Marne (Caze *et al.* 2010); Latinville, Oise (Caze *et al.* 2010); Montaincille, Yvelines (Caze *et al.* 2010); Montchauvet, Yvelines (Caze *et al.* 2010); Mouchy-le-Chatel, Oise (Caze *et al.* 2010); Parnes, Oise (Caze *et al.* 2010); St-Lubin-de-la-Haye, Eure (Caze *et al.* 2010); St-Thomas, Aisne (Caze *et al.* 2010); Septeuil, Yvelines (Caze *et al.* 2010); Thiveral, Yvelines (Caze *et al.* 2010); Thury-en-Valois, Oise (Caze *et al.* 2010); Ully-Saint-Georges, Oise (Caze *et al.* 2010); Vaudancourt, Oise (Caze *et al.* 2010); Venteuil-Arty, Marne (Caze *et al.* 2010); Villiers-St-Frédéric, Yvelines (Caze *et al.* 2010); Hauteville-Bocage, Manche (Caze *et al.* 2010). *Italy* Val Ciupio (Caze *et al.* 2010). *Italy* Roncá (Jung 1974); Monte Postale (Jung 1974) Ypresian – *France* Sapicourt, Marne (Caze *et al.* 2010).

Diameza Deshayes, 1865
(Seraphsinae)
Plate 4

1865 *Diameza* Deshayes, p. 572. Notes: accepted. Cossmann 1889, p. 95. Jung 1974, p. 32. Bandel 2007, p. 138. Caze *et al.* 2010, p. 426.

Type. By monotypy – *Ovula fragilis* Defrance, 1825, p. 132.

Definition. This clade has the characteristics outlined in the diagnosis, and contains *Diameza fragilis* (Defrance, 1825) and all taxa more closely related to it than to the defining members of *Seraphs* Montfort, 1810, *Miniseraphs* Jung, 1974 and *Terebellum* Röding, 1798.

Diagnosis. The shell is involute and inflated. The maximum diameter of the shell is just above the midline of height. The parietal callus is weak. The labrum is thickened and sinuous, being protocyrt on the lower part of the shell, and opisthocyrt on the upper part. The labrum extends above the apex, and there is a rudimentary basal sinus. The shell is smooth, with a few indistinct basal oblique grooves. The columella is smooth, and mostly straight near the base.

Discussion. There is only one recognised member of *Diameza*. While closely related to *Miniseraphs*, the latter lacks the acute apex of *Diameza*. However, based on overall similarities, it is likely they both share a hitherto unknown common ancestor arising in the Thanetian, Palaeocene of Europe (Jung 1974). While originally placed with Ovulidae Fleming, *Diameza* shows the rudimentary stromboidal notch and growth pattern more consistent with the Seraphsidae (Cossmann 1904; Jung 1974). The clade *Diameza* Deshayes 1865 has a restricted geological range of the Middle Eocene of Europe (Figure 6).

Occurrence	Oligocene	Eocene				Palaeocene	Taxon
	Rupelian	Priabonian	Bartonian	Lutetian	Ypresian	Thanetian	
Europe			▨	▨			*fragilis*

Figure 6: The spatiotemporal distribution of *Diameza* Deshayes, 1865, shading indicates presence.

Diameza fragilis (Defrance, 1825)

Plate 4A

1803 *Rostellaria macroptera* Lamarck, p. 220, pl. 4, figs. 5a to c.

1825 *Ovula fragilis* Defrance, p. 132. Pacaud 2008, p. 722. = *Seraphs* (*Diameza*) *fragilis* Le Renard – Caze *et al.* 2010, p. 446. = *Diameza* (*Diameza*) *fragilis* Defrance – Caze *et al.* 2010, p. 446, figs. 20A to E & 21.

1837 *Ovula intermedia* Deshayes, p. 718, pl. 95, figs. 34 to 36. Jung 1974, p. 32. Pacaud 2008, p. 722. = *Seraphs* (*Diameza*) *intermedius* Deshayes – Jung 1974, p. 32, tfs. 20 & 22 to 25. Caze *et al.* 2010, p. 446. = *Seraphs intermedius* Deshayes – Bandel 2007, p. 137.

1865 *Ovula media* Deshayes, p. 572. de Gregorio 1880, p. 27. Jung 1974, p. 32. Bandel 2007, p. 138. Caze *et al.* 2010, p. 446. = *Diameza media* Deshayes, 1865, p. 572. Cossmann 1889, p. 95. = *Terebellum* (*Diameza*) *medium* Wenz – Caze *et al.* 2010, p. 446. = *Terebellum* (*Diameza*) *media* Deshayes – Cossmann 1904, pp. 47 & 48, pl. 3, figs. 9 to 12. Jung 1974, p. 32. Caze *et al.* 2010, p. 446. = *Seraphs medium* Deshayes – Bandel 2007, p. 137.

1880 *Diameza deshayesi* de Gregorio, p. 25, pl. VI, fig. 8. Jung 1974, p. 33. Quaggioto & Mellini 2008, p. 48, pl. VI, fig. 8.

Type Material. Neotype – MNHN A28939. The type measures 6.9 mm in length.

Type Locality. Villers-Stait-Frédéric, France [Lutetian].

Diagnosis. The shell is inflated and involute. The greatest diameter of the shell is adapical to the middle of the shell. The shell is smooth with only a few oblique grooves near the base of the columella. The parietal callus is weakly developed. The labrum is thickened and sinuous, being protocyrt on the lower half, and opisthocyrt above. The labrum extends past, and covers, the apex. The columella bends backward at the base.

Distribution. EOCENE – Lutetian/Bartonian – *Italy* San Giovanni Ilarione (de Gregorio 1880; Jung 1974; Quaggioto & Mellini 2008). Lutetian – *France* Ferme de l'Orme, Yvelines (Caze *et al*. 2010); Grignon, Yvelines (Caze *et al*. 2010); Villiers-St-Frédéric, Yvelines (Caze *et al*. 2010).

Miniseraphs Jung, 1974

(Seraphsinae)

Plate 4

1974 *Miniseraphs* Jung, p. 29. Caze *et al*. 2010, p. 448. Notes: accepted.

Type. *Terebellum* (*Seraphs*) *eratoides* Cossmann, 1889 (Jung 1974, p. 448).

Definition. This genus has the characteristics outlined in the diagnosis, and contains *Miniseraphs eratoides* (Cossmann, 1889) and all taxa more closely related to it than to the defining members of *Seraphs* Montfort, 1810, *Diameza* Deshayes, 1865 and *Terebellum* Röding, 1798.

Diagnosis. The shell is stout, involute, and has maximum width above mid-height. The posterior canal is absent. The labrum is undulating, extends to the spire, and has a wide apical angle. The suture is not channelled. The shell is smooth, with faint oblique grooves near the base of the columella. The columella is bent inwards at the base.

Discussion. Geologically *Miniseraphs* is restricted to the Middle to early Eocene of Europe (Jung 1974; Caze *et al.* 2010; Figure 7). *Miniseraphs* has a strong biogeographical affinity to both *Seraphs* and *Diameza*, and is herein considered the intermediate descendant of both these complexes (Jung 1974).

The two recognised members of *Miniseraphs* can be readily differentiated by size and shape: *Miniseraphs isabella* (Deshayes, 1865) is larger and slenderer than *Miniseraphs eratoides* Cossmann 1889, while *Miniseraphs eratoides* is more basally constricted, giving an overall greater stout appearance. There is a small protuberance on the apex of *Miniseraphs eratoides* that is often lost in fossils, and is absent in *Miniseraphs isabella*.

Occurrence	Oligocene	Eocene				Palaeocene	Taxon
	Rupelian	Priabonian	Bartonian	Lutetian	Ypresian	Thanetian	
Europe				▨			*eratoides*
			▨	▨	▨		*isabella*

Figure 7: The spatiotemporal distribution of *Miniseraphs* Jung, 1974, shading indicates presence.

Miniseraphs eratoides (Cossmann, 1889)

Plate 4B

1889 *Terebellum* (*Seraphs*) *eratoides* Cossmann, p. 94, pl. 3, figs. 7 & 8. Jung 1974, p. 30. Caze *et al.* 2010, p. 448. = *Seraphs* (*Miniseraphs*) *eratoides* Cossmann – Jung 1974. p. 30, pl. 9, figs. 10 to 12, tfs. 19 & 20. Caze *et al*. 2010, p. 448. = *Diameza* (*Miniseraphs*) *eratoides* Cossmann – Caze *et al*. 2010, p. 448, figs. 20F to J & 22. = *Terebellum eratoides* Cossmann – Pacaud 2008, p. 722.

Type Material. Lectotype – MNHN A28933.

Type Locality. Chaussy, France [Lutetian]

Diagnosis. The shell possesses a large apical angle. The greatest diameter of the shell is located on the upper part of the shell. The shell is smooth with a few faint basal spiral grooves. The labial callus is thin and weakly developed. The labrum is adapically thickened, sinuous and reaches to nearly the base of the columella. It forms a small protuberance near the apex of the shell, and possesses a siphonal notch that is moderately developed. The columella is nearly straight.

Distribution. EOCENE – Lutetian – *France* Fontenay-en-Vexin, Eure (Caze *et al*. 2010); Chaussy, Val d'Oise, (Jung 1974; Caze *et al*. 2010); Hervelon, Marne (Caze *et al.* 2010).

Miniseraphs isabella (Deshayes, 1865)

Plate 4C

1865 *Terebellum isabella* Bernay – Deshayes, p. 470, pl. 92, figs. 14 to 16. Jung 1974, p. 30. Caze *et al*. 2010, p. 450. = *Terebellum* (*Seraphs*) *isabellae* Bernay – Cossmann 1889, p. 94. Jung

1974, p. 30. Caze *et al.* 2010, p. 450. = *Seraphs* (*Miniseraphs*) *isabella* Deshayes – Jung 1974, p. 30, pl. 9, figs. 13 to 18, tfs. 20 & 21.

= *Diameza* (*Miniseraphs*) *isabella* Deshayes – Caze *et al.* 2010, p. 450, figs. 20K to O & 23. = *Seraphs isabella* Deshayes – Bandel 2007, p. 137.

1880 *Terebellum pusilliusculum* de Gregorio, p. 23, p. 1, fig. 33. Jung 1974, p. 31. = *Seraphs* (*Miniseraphs*) *pusilliusculum* de Gregorio – Quaggioto & Mellini 2008, p. 48, pl. 1, fig. 33.

1953 *Terebellum* (*Seraphs*) *vertesensis* Szöts, p. 175, pl. 4, figs. 43 & 44. Jung 1974, p. 31.

Type Material. Lectotype – MNHN A28935. The type measures 13.4 mm in length.

Type Locality. Chaussy, France [Lutetian].

Diagnosis. The shell has a large apical angle and an inflated body whorl. The greatest diameter of the shell is just above the middle. The labial callus is thin, and the labrum is sinuous and thickened adapically. The labrum is abapically prosocyrt and adapically opisthocyrt. The columella is bent backward at the base and reaches down nearly to the base of the labrum. The siphonal notch is moderately developed. The shell is smooth with only a few faint spiral lines near the base.

Distribution. EOCENE – Lutetian/Bartonian – *France* Ferme de l'Orme, Paris Basin (Jung 1974); Grignon, Paris Basin (Jung 1974). *Italy* Palermo (Jung 1974); San Giovanni Ilarione (de Gregorio 1880). Lutetian – *France* Chaussy, Val d'Oise, (Jung 1974; Caze *et al.* 2010); Latinville-Saint-Peirre, Oise (Jung 1974; Caze *et al.* 2010); Cauvigny, Oise (Caze *et al.* 2010); Parnes, Oise (Jung 1974; Caze *et al.* 2010); Mouchy-le-Chatel, Oise (Jung 1974; Caze *et al.* 2010); Fercourt, Oise (Jung 1974; Caze et al., 2010); Vaudancourt, Oise (Jung 1974; Caze *et al.* 2010); Ponchon, Oise (Caze et al., 2010); Villiers-St-Frédéric, Yvelines (Caze *et al.* 2010); Bois-Gouët, Loire-Atlantique (Caze *et al.* 2010). Ypresian – *Hungary* (Szöts 1953).

Neoterebellinae new subfamily
(Seraphsidae)

Type genus. *Terebellum* Röding, 1798.

Definition. This clade has the characteristics outlined in the diagnosis, and contains *Terebellum* Röding, 1798 and all taxa more closely related to it than to the defining members of *Seraphs* Montfort, 1810 and *Diameza* Deshayes, 1865.

Diagnosis. The adult shell is evolute. Shell is typically long and narrow. The stromboidal notch is not well developed or is absent. The shell lacks a posterior canal. It is typically smooth, or with reduced sculpture where present.

Discussion. This clade is erected to hold the evolute members of the Seraphsidae.

Mauryna de Gregorio, 1880

(Neoterebellinae)

Plate 4

1880 *Mauryna* de Gregorio, p. 24. Tryon 1885, p. 103. Zittel 1885, p. 259. Savazzi 1988a, p. 256. Bandel 2007, p. 138. Notes: accepted.

Type. *Terebellum plicatum* d'Archiac & Haime, 1853 (Cossman 1904, p. 46).

Definition. This genus has the characteristics outlined in the diagnosis, and contains *Mauryna plicatum* (d'Archiac & Haime, 1853) and all taxa more closely related to it than to the defining members of *Seraphs* Montfort, 1810, *Diameza* Deshayes, 1865 and *Terebellum* Röding, 1798.

Diagnosis. The shell is moderately slender, and has an evolute growth pattern. The teleoconch has three whorls and an indistinct suture. The whorls are sculptured with axial costae. The labrum is thickened. The narrow posterior canal extends from the adapical end of the aperture to the apex, and is reflected down the dorsal side of the body whorl. The columella is straight.

Discussion. Arising in the Thanetian, the clade *Mauryna* is restricted to the Late Paleocene and the Eocene of Southeastern Asia. However, there is a significant gap in the fossil record (Figure 8). *Mauryna* was originally erected to hold the axially costate members of Seraphsidae, particularly *Mauryna plicatum* (d'Archiac & Haime, 1853) and the two synonyms *Mauryna protoelegans* (de Gregorio, 1880) (= *Seraphs pliciferum* Bayan, 1870) and *Seraphs pliciferum*. *Seraphs pliciferum* lacks the distinctive posterior canal, and has involute coiling usually associated with members of the *Mauryna* complex (de Gregorio 1880; Jung 1974).

There are currently two recognised members of *Mauryna*, namely *Mauryna plicatum* and *Mauryna costatum* Martin, 1931, which are separated by geological time and morphology, although the morphology of *Mauryna costatum* is problematic due to the quality of material. Consequently, its position within the *Mauryna* complex is tenuous.

The *Mauryna* complex demonstrates a close structural affinity to *Terebellopsis*, but *Terebellopsis* lacks the heavy plications and is structurally similar to *Semiterebellum* Cossmann, 1889 (Rostellariidae), and particularly to the Rimellidae.

Occurrence		Geological Period						Taxon
	Oligocene	Eocene				Paleocene		
	Rupelian	Priabonian	Bartonian	Lutetian	Ypresian	Thanetian	Selandian	
Asia		▨						*costaum*
						▨		*plicatum*

Figure 8: The spatiotemporal distribution of *Mauryna* de Gregorio, 1880, shading indicates presence.

Mauryna costatum Martin, 1931

1931 *Mauryna costata* Martin, p. 38, pl. 5, figs. 12 & 12a. Jung 1974, p. 49. = *Terebellum* (*Mauryna*) *costatum* Martin – Jung 1974, p. 49.

Type Material. Lectotype – Martin 1931, pl. 5, figs. 12 & 12a. The illustration of the lectotype in Martin (1931) is of poor quality, being immature and crushed. The length is 24 mm and the width is 8 mm (Martin 1931).

Type Locality. Java, Indonesia [Priabonian].

Diagnosis. At present, the validity of *Mauryna costata* Martin, 1931 is in doubt.

Distribution. EOCENE – Priabonian – *Indonesia* Kali Puru, Java (Jung 1974).

Mauryna plicatum (d'Archiac & Haime, 1853)

Plate 4D

1853 *Terebellum plicatum* d'Archiac & Haime, p. 334, pl. 32, figs. 17 & 18. Jung 1974, p. 48. Bandel 2007, p. 138. = *Mauryna plicata* d'Archiac & Haime – de Gregorio 1880, p. 24. Jung 1974, p. 48. Bandel 2007, p. 138. = *Terebellum* (*Mauryna*) *plicatum* d'Archiac & Haime – Cossmann & Pissarro 1909, p. 50, pl. 5, figs. 3 to 5. Vredenberg & Cotter 1928, p. 49. Jung 1974, p. 50. Jung & Abbott 1967, p. 448.

Type Material. Holotype – NHMUK GG21002. The type measures 35.2 mm in length, with a width of 14.1 mm.

Type Locality. Rankiot, Sind, Pakistan [Thanetian].

Diagnosis. The shell is moderately slender with a blunt apex. The teleoconch is moderately high, and consists of three whorls with an indistinct suture and sculpture consisting of weak, closely spaced axial costae that become more developed and more widely interspaced on later whorls. The body whorl has strong axial costae. The lip is thin becoming thicker posteriorly. The posterior sinus forms a canal that extends to the top of the spire and is planar in apical view. The columella is not twisted basally.

Distribution. PALEOCENE – Thanetian – *Pakistan* Ranikot, Jhirak (Vredenberg & Cotter 1928); Ranikot, Sind (Cossman & Pissaro 1909; Jung 1974).

Paraseraphs Jung, 1974

(Neoterebellinae)

Plates 5 and 6

1974 *Paraseraphs* Jung, p. 33. Bandel 2007, p. 137. Caze *et al*. 2010, p. 454.

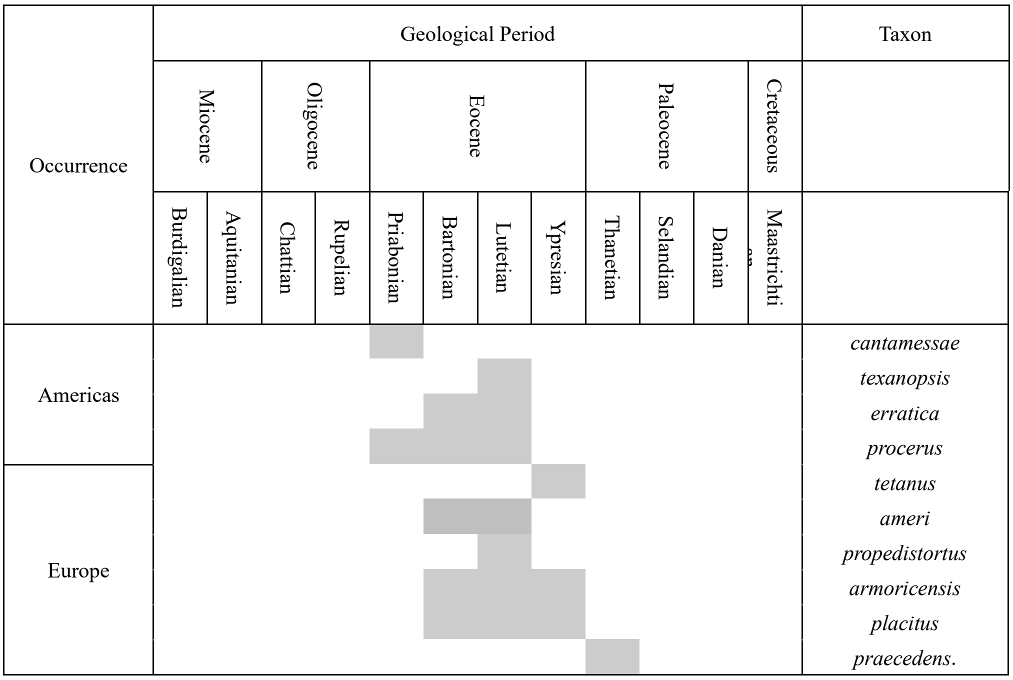
Type. *Paraseraphs tetanus* Jung, 1974 (Jung 1974).

Definition. This genus has the characteristics outlined in the diagnosis, and contains *Paraseraphs tetanus* Jung, 1974 and all taxa more closely related to it than to the defining members of *Seraphs* Montfort, 1810, *Mauryna* de Gregorio, 1880 and *Terebellum* Röding, 1798.

Diagnosis. The shell is evolute, cylindrical and smooth, with a posterior canal present. The labrum is protocyrt, with no channelled suture and a maximum diameter near the base. The adapical canal is present, and often extends to the apex. The columella is smooth and bent backward near the base.

Discussion: The clade *Paraseraphs* Jung 1974 is restricted to the Late Paleocene and to the Eocene of the tropical Americas and Europe, where it arose out of the *Seraphsinae* new subfamily. The great diversity occurred during the middle Eocene (Jung 1974; Sepkoski 2002; Caze *et al.* 2010; Figure 9). *Paraseraphs* Jung 1974 defining characteristics are a posterior canal and evolute growth pattern. *Paraseraphs* Jung 1974 likely share ancestry with the *Pseudoterebellum* new genus and *Terebellum* Röding 1798 (Jung 1974).

The species *Paraseraphs cantamessae* Maxwell *et al*., 2018 is comprised of eight specimens, which are internal casts. The new species is much narrower than the larger and more dorso-ventrally convex *Paraseraphs procerus* (Merian, 1844), which shares a similar geological record. *Paraseraphs cantamessae* is similar to other *Paraseraphs* from Europe., The new species is particularly similar to *Paraseraphs armoricensis* (Cossmann, 1897), and was likened to that taxon by Jung (1974), but occurs after that species disappears during the Bartonian. The new species is also similar to *Paraseraphs propedistortus* (de Gregorio, 1880), being slender with an acute spire, but the latter is restricted to the Lutetian of the Mediterranean. There is some uncertainty surrounding the type material of *Paraseraphs propedistortus*, with the collection supposedly destroyed during the Second World War (Malaroda 1954). Specimens purported from the de Gregorio collection remain unlabelled and are in disarray (Savazzi 1988a). However, while there appears to be some material that has survived, this does not include the types of *Paraseraphs propedistortus* (Jung 1974). The lectotype material for *Paraseraphs erraticus* (Cooper, 1894) is an incomplete shell lacking the base (Jung 1974). The type material of *Paraseraphs erraticus* is comparable to that of *Paraseraphs californicus* (Vokes, 1939), and they are herein considered the same species (Jung 1974).



Occurrence	Geological Period												Taxon
	Miocene		Oligocene		Eocene				Paleocene			Cretaceous	
	Burdigalian	Aquitanian	Chattian	Rupelian	Priabonian	Bartonian	Lutetian	Ypresian	Thanetian	Selandian	Danian	Maastrichti	
Americas					▨								*cantamessae*
							▨						*texanopsis*
						▨	▨						*erratica*
					▨	▨	▨						*procerus*
Europe								▨					*tetanus*
						▨	▨						*ameri*
							▨						*propedistortus*
						▨	▨	▨					*armoricensis*
						▨	▨	▨					*placitus*
									▨				*praecedens.*

Figure 9: The spatiotemporal distribution of *Paraseraphs* Jung, 1974, shading indicates presence.

There is some uncertainty surrounding the type material of *Paraseraphs propedistortum* de Gregorio 1880, with the collection supposedly destroyed during the Second World War (Malaroda 1954). Specimens purported from the de Gregorio collection remain unlabelled and are in disarray (Savazzi 1988a). However, while there appears to be some material that has survived, this does not include the types of *Paraseraphs propedistortum* de Gregorio 1880 (Jung 1974). The type material for *Paraseraphs erratica* Cooper 1894 is an incomplete shell lacking the base (Jung 1974). The type material of *Paraseraphs erratica* Cooper 1894 when compared with *Paraseraphs californicum* Vokes 1939 indicates close affinities, and they are herein considered the same species (Jung 1974).

Paraseraphs ameri (Abbass, 1967)

Plate 5A

1967 *Terebellum* (*Terebellum*) *ameri* Abbass, p. 61, pl. VIII, figs. 3 & 6.

Type Material. Holotype – EMC no. G363.

Type Locality. Ras El Ghorab, Egypt [Bartonian].

Diagnosis. The shell is smooth and fusiform with three whorls. The spire is acute with the final body whorl being more than 80% of the length of the shell. The aperture is narrow and the labrum is thin. There is a posterior canal, and the sutures are obsolete and linear.

Distribution. EOCENE – Bartonian – *Egypt* Ras El Ghorab (Abbass 1967). Lutetian – *Egypt* Mokattam (Abbass 1967).

Paraseraphs armoricensis (Cossmann, 1897)

Plate 5B

1856 *Terebellum cylindricum* Cailliaud, p. 42. Jung 1974, p. 34. Caze *et al.* 2010, p. 459.

1881 *Terebellum armoricum* Vasseur, pp. 174 & 245 (*nomen nudum*). Jung 1974, p. 36. Caze *et al.* 2010, p. 459. = *Terebellum armoricensis* Vasseur – Jung 1974, p. 36. = *Terebellum armoricus* Vasseur – Caze *et al.* 2010, p. 456, figs. 29A to C and 30. = *Terebellum fusiforme armorica* Vasseur – Sacco 1893, p. 21.

1897 *Terebellum armoricense* Cossmann, p. 340, pl. 8, figs. 10 & 15. Caze *et al.* 2010, p. 459. = *Terebellum armoricensis* Cossmann – Jung 1974, p. 34. = *Paraseraphs armoricensis* Cossmann – Jung 1974, p. 36, pl. 9, figs. 19 to 25, tf. 28, p. 37, pl. 11, figs. 1 to 6. Caze *et al.* 2010, p. 459.

Terebellum fusiforme Lamarck – de Gregorio 1880, p. 20. Jung 1974, p. 36. = *Terebellum fusiforme* Sowerby – Tennant 1847, p. 34. = *Terebellum fusiforme* Cuvillier – Jung 1974, p. 36.

Type Material. Lectotype - Cossmann 1897, p. 340, pl. 8, figs. 10 & 15. The type measures 73 mm in length (Cossmann 1897).

Type Locality. Bois-Gouët, France [Bartonian].

Diagnosis. The shell is slender with fine siral lines, with 2.5 nuclear whorls. The labial callus is moderately well-developed. The labrum is not thickened. The posterior canal is moderately antispiral continuing to the apex. The columella is bent backward basally.

Distribution: EOCENE – *England* London Clays (Tennant 1847). Bartonian – *France* Bois-Gouët, Loire-Atlantique (Jung 1974; Caze *et al.* 2010); Arthon, Loire-Atlantique (Caze *et al.* 2010); Blaye, Gironde (Caze *et al.* 2010). Ypresian – *Italy* northern regions (Jung 1974); San Giovanni Ilarione (de Gregorio 1880).

Paraseraphs cantamessae Maxwell, Rymer & Congdon, 2018

Plate 5C

1974 *Paraseraphs* cf. *armoricensis* Cossmann – Jung 1974, p. 37, pl. 11, figs. 1 to 6.

2018 *Paraseraphs cantamessae* Maxwell, Rymer & Congdon, p. 37, fig. 1.

Type Material. Holotype – USNM no. 135097A. The type measures 56.9 mm in length.

Type Locality. White Limestone Group, Port Antonio, Jamaica [Priabonian].

Diagnosis. The shell is very slender with slightly concave whorls. There is a distinctive elongation of the shell on later whorls. The base of the shell is anteriorly quadrate. The shell spire is acute.

Distribution. EOCENE – Priabonian – *Jamaica* Port Antonio (Jung 1974).

Paraseraphs erraticus (Cooper, 1894)

Plate 5D

1894 *Tornatina erratica* Cooper, p. 4. Jung 1974, p. 41. = *Terebellum erraticum* Cooper – Jung 1974, p. 41. = *Seraphs erratica* Cooper – Jung 1974, p. 41. = *Seraphs erraticus* Cooper – Effinger 1938, p. 381. = *Paraseraphs erraticus* Cooper – Jung 1974, p. 41, pl. 12, figs. 8 to 16, pl. 13, figs. 1 to 3.

1939 *Terebellum californicum* Vokes, p. 157, pl. 20, figs. 7, 8 & 11. Jung 1974, p. 41. Hanna & Hertlein 1949, p. 394.

Type Material. Holotype – Calacademy no 608. The length is 19.3 mm.

Type Locality. Rose Cañon, San Diego County, California, USA [Lutetian].

Diagnosis. The shell is moderately slender, the surface of the shell is smooth and the spire moderately high. The sutures of prior whorls are visible within the canal. The labrum is not thickened and the suture is indistinct. The columella is bent backward near the base.

Distribution. EOCENE – *USA* Rose Cañon, San Diego County, California (Jung 1974). Lutetian/Bartonian – *USA* California Media Creek area, Kern County, California ('Mallory' in Jung 1974). *Trinidad* Boca de Serpiente Formation of Soldado Rock (Jung 1974). Lutetian – *USA* Kern County, California (Hanna & Hertlein 1949). Domengine Beds, California (Effinger 1938).

Paraseraphs placitus Jung, 1974

Plate 5E

1974 *Paraseraphs placitus* Jung, p. 38, pl. 10, figs. 13 to 18, tf. 28. Caze *et al.* 2010, p. 456, figs. 24G to M & 28.

Terebellum fusiforme Lamarck – Morris 1843, p. 163. Jung 1974, p. 38. = *Terebellum fusiforme* Sowerby – Morris 1843, p. 163. Jung 1974, p. 38. Caze *et al.* 2010, p. 456.

Type Material. Holotype – NMB H14491. The type measures 22.7 mm in length.

Type Locality. Chaussy, Seine et Oise, France [Lutetian].

Diagnosis. Shell is moderately slender, with a protoconch of 1$^1/_2$ to 1$^3/_4$ nearly planispiral glassy whorls. The teleoconch has 2$^1/_4$ whorls, with a sculpture of faint axial striation and spiral striation on the upper whorls. The body whorl possesses a few spiral grooves basally adjoining the labium. The labrum is adapically thickened only, and continues parallel to the apex forming a posterior canal. The base of the labrum does not continue to the base of the columella. The columella is bent backward basally.

Distribution. EOCENE – Bartonian – *France* Baron, Oise (Caze *et al.* 2010); Caumont, Seine-et-Marne (Caze *et al.* 2010); Le Guépelle, Val-d'Oise (Caze *et al.* 2010). Lutetian – *France* Chaussy, Val d'Oise (Jung 1974; Caze *et al.* 2010); Fontenay-en-Vexin, Eure (Caze *et al.* 2010); Vandancort, Oise (Caze *et al.* 2010); Parnes, Oise (Jung 1974; Caze *et al.* 2010); Fercourt, Oise (Caze *et al.* 2010); Châteaurouge, Oise (Caze *et al.* 2010); Ponchon, Oise (Caze *et al.* 2010); Grignon, Yvelines (Jung 1974; Caze *et al.* 2010). Ypresian – *France* Mouchy, Paris Basin (Jung 1974). *Belgium* Sables de Wemmel (Jung 1974). *The United Kingdom* Barton (Morris 1843); Bracklesham (Morris 1843).

Paraseraphs praecedens Caze, Merle, Pacaud & Saint Martin, 2010

Plate 6A

2010 *Paraseraphs praecedens* Caze *et al.*, p. 460, figs. 29E & F.

Type Material. Holotype – MNHN Q05707. The type measures 19 mm in length, with a width of 7 mm.

Type Locality. Abbencourt, France [Thanetian].

Diagnosis. The shell is small and smooth, with a distinct suture and a short blunt teleoconch. The aperture is narrow and long.

Distribution. PALEOCENE – Thanetian – *France* Abbecourt, Oise (Caze *et al.* 2010).

Paraseraphs procerus (Merian, 1844)

Plate 6B

1844 *Terebellum procerum* Merian, p. 64. Jung 1974, p. 39. Rutsch 1939, p. 517. = *Terebellum* (*Terebellum*) *procerum* Merian – Woodring 1959, p. 192, pl. 25, figs. 5 to 7. Jung 1974, p. 39. = *Paraseraphs procerus* Merian – Jung 1974, p. 39, pl. 10, figs. 11 & 12, pl. 12, figs. 1 to 7, tf. 28. = *Terebellum procerus* Tripati & Zachos, 2002, p. 4.

Terebellum subdistortum Trechmann – Woodring 1959, p. 192. Jung 1974, p. 39.

Type Material. Holotype – NMB H14347. The type measures 71.8 mm in length.

Type Locality. Yellow Limestone Group, Jamaica [Lutetian].

Diagnosis. The shell has a high teleoconch and a moderately acute apex. The spire has three to four whorls and is slightly dorso-ventrally convex. The columella is slightly twisted at the base.

Distribution. EOCENE – Priabonian – *Panama* Gatuncillo Formation (Woodring 1959; Jung 1974; Tripati & Zachos 2002). *Jamaica* Claremont Formation of Claremont, St. Ann (Jung 1974). *USA* Florida Crystal River Formation, Taylor County (Jung 1974). *Lesser Antilles* St Bartholomew Formation of St Bartholomew Island (Jung 1974). *Trinidad* Boca de Serpiente formation (Rutsch 1939). Lutetian/Bartonian – *Jamaica* Yellow Limestone Group (Jung 1974). *Haiti* Plaisance Limestone (Jung 1974). *Spain* Santa Maria Formation Manresa, Barcelona Province (Jung 1974).

Paraseraphs propedistortus (de Gregorio, 1880)

Plate 6C

1880 *Terebellum fusiforme propedistortum* de Gregorio, p. 20, pl. V, fig. 17. de Gregorio 1896, p. 38, pl. 3, fig. 6. = *Terebellum propedistortum* de Gregorio – Jung 1974, p. 38. Pacaud 2008, p. 727. = *Paraseraphs propedistortus* de Gregorio – Jung 1974, p. 38, pl. 11, figs. 7 to 17, tf. 28.

Type Material. Lectotype – de Gregorio 1880, p. 20, pl. V, fig. 17 (designated herein). The type specimens are presumed destroyed during World War Two (Jung 1974).

Type Locality. San Giovanni Ilarione, Italy [Lutetian].

Diagnosis. The shell is slender, with a high, acute apex thinly covered by shell matrix. The labrum is not thickened. The posterior canal is mostly straight, running antispirally towards the apex.

Distribution. EOCENE – *Italy* Ronca (de Gregorio 1896). Lutetian – *Italy* San Giovanni Ilarione (de Gregorio 1880; Jung 1974); Ronca (de Gregorio 1896).

Paraseraphs tetanus Jung, 1974

Plate 6D

1880 *Terebellum postconicua* de Gregorio, p. 21, pl. 1, fig. 18. = *Terebellum fusiforme postconicua* de Gregorio – Sacco 1893, p. 21. = *Terebellum postconica* de Gregorio – Cossmann 1889, p. 92. = *Terebellum postconicum* de Gregorio – Jung 1974, p. 45. Pacaud 2008, p. 727. Quaggioto & Mellini 2008, p. 48, pl. 1, fig. 18.

1974 *Paraseraphs tetanus* Jung, p. 34, pl. 9, fig. 26, pl. 10, figs. 1 to 10, tfs. 12 & 26 to 28. Bandel 2007, p. 137. Pacaud 2008, p. 722. Caze *et al.* 2010, p. 438, figs. 24A to F, 25 & 26.

Terebellum fusiforme Deshayes – Jung 1974, p. 34. Caze *et al.* 2010, p. 454.

= *Terebellum fusiforme* Lamarck – Sowerby 1820–1825, pl. 231, fig. 3. Gould 1833, p. 96. Anton 1839, p. 102. Reeve 1842, p. 268, pl. 191, fig. 3. Pictet 1853–1857, p. 42, pl. 64, fig. 2. Chenu 1859, p. 264, fig. 1660. Zittel 1885, p. 259. de Gregorio 1896, p. 36, pl. 3, fig. 5. Oppenheim 1900, p. 211. Dainelli 1905, p. 72. Jung 1974, p. 34. Pacaud 2008, p. 727. Baciu & Hartenberger 2001, p. 442. = *Terebellum* (*Terebellum*) *fusiforme* Lamarck – Jung 1974, p. 34

Paraseraphs placitus Merle – Caze *et al.* 2010, p. 438.

Type Material. Holotype – NMB H15409. The type measures 28.7 mm in length.

Type Locality. Cuise-Lamotte, Oise, France [Ypresian].

Diagnosis. The shell is smooth and slender, with a protoconch of 1 $^1/_2$ to 1$^3/_4$ whorls. The teleoconch has 2$^1/_2$ to 3 whorls. The labial callus is well-developed and the labrum is not thickened. The posterior canal is antispirally bent and does not extend to the apex. The columella is basally bent backward. The labrum does not reach the base of the columella.

Distribution. EOCENE – *Italy* Ronca (de Gregorio 1896). Ypresian – *France* Monampteuil, Aisne (Caze *et al.* 2010); Aizy-Jouy, Aisne (Caze *et al.* 2010); Saint-Gobain Aisne (Caze *et al.* 2010); Sapicourt, Marne (Caze *et al.* 2010); Cuise-Lamotte, Oise (Jung 1974; Caze *et al.* 2010); Gan, Pyrenees-Atlantiques (Caze *et al.* 2010). *Italy* Roncá (Jung 1974).

Paraseraphs texanopsis Garvie, 2013

Plate 6E

2013 *Paraseraphs texanopsis* Garvie, p. 169, pl. 1, figs. 10 to 12.

Type Material. Holotype – UT(Austin) no. NPL7075. The type measures 53.3 mm in length, with a width of 14.2 mm.

Type Locality. 1 km east of Augusta Houston County, Texas [Lutetian].

Diagnosis. The shell is smooth and slender, with an high, acute apex thinly covered with shell matrix. The posterior canal is mostly straight, running antispirally towards the apex and reflected at termination. The teleoconch has four whorls. The labial callus is well-developed and the labrum is not thickened. The columella is basally bent backward. The labrum does not reach the base of the columella.

Distribution. EOCENE – Lutetian – *The United States of America* Weches Formation east of Augusta Houston, Texas (Garvie 2013).

Pseudoterebellum new genus

(Neoterebellinae)

Plate 8A to C

Type. *Terebellum diversiornatum* Eames, 1952, p. 74, pl. 3, fig. 77.

Definition. This genus has the characteristics outlined in the diagnosis, and contains *Pseudoterebellum diversiornatum* (Eames, 1952) and all taxa more closely related to it than to the defining members of *Seraphs* Montfort, 1810, *Paraseraphs* Jung, 1974 and *Terebellum* Röding, 1798.

Diagnosis. The shell is evolute, lacking a posterior canal, and is widest near the posterior. The labrum of the shell is protocyrt. The suture is channeled. The columella is smooth.

Discussion. This clade arose in the early Ypresian of the middle east (Figure 10). Members of the complex may have radiated east via the Tethys during the Ypresian into the Indonesian region of the south-western Pacific, and contained the forebearer of the modern clade *Terebellum*. However, there is a significant geological discontinuity in the geological record from the period of extinction of *Pseudoterebellum* at the end of the Eocene, to the appearance of *Terebellum* during the mid-Oligocene.

Jung (1974) described the holotype of *Pseudoterebellum diversiornatum* as an incomplete juvenile internal cast with problematic affinities. Additional weight to the generation of the new clade is provided by Eames (1952), who noted that the description of *Pseudoterebellum diversiornatum* belonged to an as yet undefined subgenus of *Terebellum*. A defining feature of *Pseudoterebellum* is the width being widest posteriorly.

Occurrence		Geological Period					Taxon
	Oligocene	Eocene				Paleocene	
	Rupelian	Priabonian	Bartonian	Lutetian	Ypresian	Thanetian	
Europe					▨		*diversiornatum*
					▨		*saudiensis*
			▨	▨			*oympiae*

Figure 10: The spatiotemporal distribution of *Pseudoterebellum* new genus, shading indicates presence.

Pseudoterebellum diversiornatum (Eames, 1952)

Plate 7A

1952 *Terebellum diversiornatum* Eames, p. 74, pl. 3, fig. 77.

Type Material. Holotype – NHMUK no. G68239. The type measures 42.2 mm in length.

Type Locality. Zinda Pir, Ghazij Shales, Western Punjab, Pakistan [Ypresian].

Diagnosis. The shell is sub-elliptical, with a short conoidal teleoconch that is one-seventh of the length of the shell. The teleoconch whorls are flat with linear sutures. The height of the whorls is proportionally slightly less than that of the width of the whorl. The teleoconch has fine straight axial costae, numbering ten per mm, that are slightly wider than the interval. They fade on the penultimate whorl, with the only ornamentation being ten spiral bands. The body whorl is oliviform and smooth, with the greatest width above the middle with sides slightly convex. The base of the aperture is narrow with no columnar folds.

Distribution. EOCENE – Ypresian – *Pakistan* Ghazij Shales, Western Punjab (Eames 1952).

Pseudoterebellum oympiae (Rolando, 2001)

Plate 7B

2001 *Terebellum oympiae* Rolando, p. 42, fig. 2.

Type Material. Holotype – MGPD no. 28168. The type measures 20.9 mm in length (Rolando 2001).

Type Locality. Watumurag Village, 4 km west of Nanggulan, Yogyakarta Province, Java, Indonesia [Lutetian].

Diagnosis. The shell is smooth and evolute, anteriorly quadrate and widest at the posterior. The spire is blunt. The sutural canal is well developed. The labrum is developed and prosocyrt. The aperture is narrow and approximately one-half the length of the shell.

Distribution. EOCENE – Bartonian – *Indonesia* Yogakarta Province, Java (Ronaldo 2001).

Pseudoterebellum saudiensis (Abbass, 1972)

Plate 7C

1972 *Terebellum saudiensis* Abbass, p. 53, pl. V, figs. 1 & 2.

Type Material. Holotype – ASU no. S.53. The type specimen measures 25 mm in length (Abbass 1972).

Type Locality. Ash Sharqiyda, Saudi Arabia [Ypresian].

Diagnosis. The teleoconch is narrow and comprises a third of the shell height. The suture is diminished and linear. The teleoconch possesses 6 axial cords separated by narrower grooves. The body whorl is narrow, with straight sides that contract anteriorly. The aperture is narrow, and the labrum is parallel to the sides of the body whorl.

Distribution. EOCENE – Ypresian – *Saudi Arabia* Ash Sharqiyda (Abbass 1972).

Terebellum Röding, 1798

(Neoterebellinae)

Plates 7 and 8

1753 *Terebellum* Klein, p. 38. Sowerby, 1820–1825, pl. 263. Mörch 1852, p. 63. Adams & Adams 1858, p. 263. Maxwell *et al.* 2018b, p. 63. Excluded – pre-Linné (1758).

1798 *Terebellum* Röding, p. 135. p. Horst & Schepman 1908, p. 223. Maxwell *et al.* 2018b, p. 63. Type: *Terebellum nebulosum* Röding, 1798 (= *Bulla terebellum* Gmelin, 1791 = *Conus terebellum* (Linné, 1758) = *Terebellum terebellum* (Linné, 1758)). Eames 1952, p. 72. Bandel 2007, p. 137. = *Terebellum* Lamarck, 1799, p. 69. Lamarck 1801, p. 72. Rafinesque 1815, p. 145. Bowdich 1822, p. 42, no. 10. Bronn 1824, p. 11, no. 29. Cronch 1827, p. 38. Gould 1833, p. 96. Anton 1839, p. 102. Cuvier 1834, p. 66. Gray 1847, p. 132. Cuvier 1868, p. 32. Fisher 1873, p. 377. Zittel 1885, p. 259. Cossmann 1889, p. 92. Maxwell *et al.* 2018b, p. 63. Type: *Bulla terebellum* Linné, 1758 (= *Terebellum terebellum* (Linné, 1758)). = *Terebellum* Montfort 1810, p. 379. Type: *Terebellum subulatum* Lamarck, 1801 (= *Terebellum terebellum* (Linné, 1758)). = *Terebrina* Rafinesque, 1815, p. 145. Maxwell *et al.* 2018b, p. 63. Synonymized - Emendation of *Terebellum* Lamarck, 1799.

1848 *Lucis* Gistel, p. 171. p. 72. Maxwell *et al.* 2018b, p. 63. Type: *Lucis subulatum* Lamarck, 1801 (= *Terebellum terebellum* (Linné, 1758)).

1848 *Artopoia* Gistel, pl 7, fig. 8. p. 72. Maxwell *et al.* 2018b, p. 63. Type: *Artopoia* (*Terebellum*) *subulata* (Lamarck, 1810) (= *Terebellum terebellum* (Linné, 1758)). = *Artopoja* Gistel – Paetel, 1888, p. 315. Maxwell *et al.* 2018b, p. 63. Notes: synonymised emendation of original name *Artopoia* Gistel, 1848 (Jung 1974).

Type. Lectotype – *Conus terebellum* Linné, 1758 (Winckworth 1945, p. 144)

Definition. This genus has the characteristics outlined in the diagnosis, and contains *Terebellum terebellum* (Linné, 1758) and all taxa more closely related to it than to the defining members of *Seraphs* Montfort, 1810, *Paraseraphs* Jung, 1974 and *Pseudoterebellum* new genus.

Diagnosis. The shell is convolute, with an evolute growth pattern. The shell lacks a posterior canal. It is typically smooth, or with greatly reduced sculpture where present, and is widest near the anterior of the shell. The labrum of the shell is protocyrt, and there is a channeled suture between the whorls. The aperture is long and narrows anteriorly, with a smooth columella. The labium is calloused and extends just above the apex. The basal sinus is present, but shallow.

Discussion. The geological record indicates that *Terebellum* arose during the beginning of the Neogene, which places the direct ancestor during the Oligocene (Figure 11). The earliest record of *Terebellum terebellum* comes from the early Miocene of Saipan. We propose that the species arose in the Indonesian region and the clade's ancestor resides there. The clade expanded during the early to mid-Miocene to incorporate a maximum of three species during the Langhian from India to Indonesia. Examples of *Terebellum terebellum* from the Miocene of Java show little or no variation from the more recent specimens, as does the trace colouration in preserved material (Cox 1948). The Martin (1928) specimen from the Early Pliocene classified as *Terebellum papilliferum* Martin, 1916 is probably a representative of *Terebellum terebellum*. Sepkoski (2002) gave the Thanetian to the Holocene for the geological range for *Terebellum*, but there is no evidence for this clade below the lower Miocene. Jung (1974) proposed the unknown ancestor of *Terebellum terebellum* arose in the regions of India or Pakistan during the late Oligocene.

Jung (1974) argued that *Terebellum cinctum* Martin, 1916 should be treated as a *nomen dubium*, as the unique bands noted by Martin (1916) were taxonomically irrelevant. However, the spiral threads are a characteristic peculiar to *Terebellum cinctum*, and support the taxonomic divergence. Jung (1974) also suggested that *Terebellum cinctum* may be a stouter and larger form of *Terebellum papilliferum*, which is rejected based on gross morphology. This study proposes that *Terebellum cinctum* is a valid taxon, and that these spiral bands are a distinguishing feature unique to this taxon. Martin (1916) provided two specimens from Puntuk Tedjo, Res Djokjokarta, Java as belonging to *Terebellum cinctum* from the lower Miocene; however, these specimens lack the defining characteristic of *Terebellum cinctum*, the spiral threads, and therefore should be treated as *Terebellum terebellum* (Jung 1974).

The taxon *Terebellum obtusum* Sowerby, 1840 is considered synonymous with *Terebellum terebellum* by some workers (Kulkarni *et al.* 2010); however, the lack of defined sutures is a clear distinguishing feature from the phenotypically stable *Terebellum terebellum*. Dey's (1961) references to *Terebellum terebellum* are not considered as *Terebellum obtusum* due to the geological time scale, with *Terebellum obtusum* restricted to the Miocene.

Distinguishing *Terebellum papilliferum* from *Terebellum terebellum* can be problematic, and it may be included as a synonym of that species. Jung (1974) noted that this species was not stratigraphically unique, and was similar to *Terebellum terebellum*, but reserved judgment on validity until further material became available.

Hanley (1860) studied an undated handwritten copy of Linné's *Museum Ulricæ*, and it shows that Linné first intended that name '*terebellum*' be used for *Conus nussatella* Linné, 1758 (Conidae Fleming, 1822). This was changed prior to publication into the taxon we now associate with this epaulet. Both Linné (1758, 1767) and Gmelin (1791) provide sound *Terebellum*

terebellum descriptions under *Conus terebellum* Linné, 1758 (= *Terebellum terebellum*) and *Bulla terebellum* Linné, 1767 (=*Terebellum terebellum*).

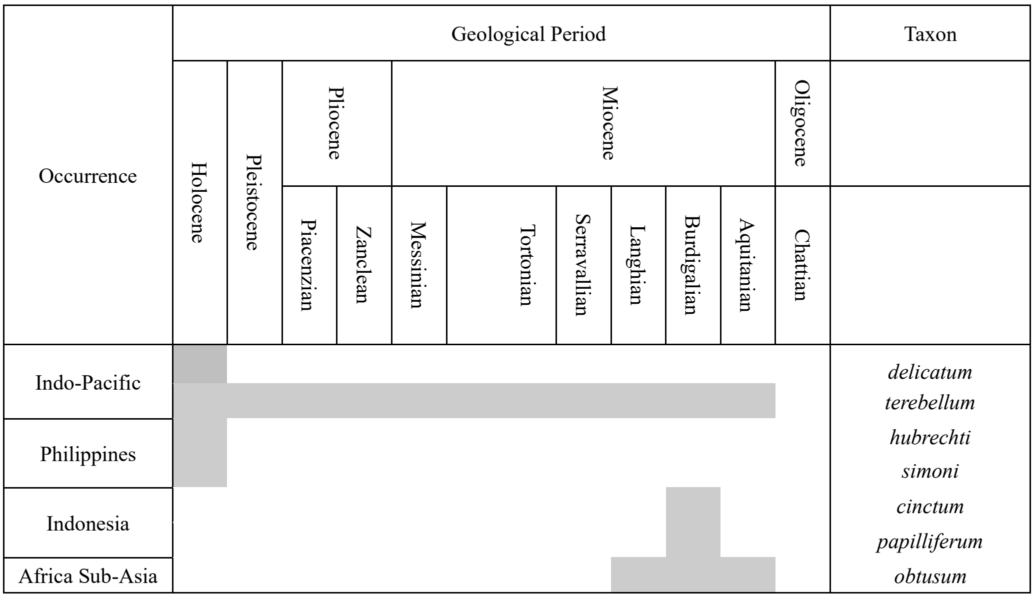


Figure 11: The spatiotemporal distribution of *Terebellum* Röding, 1798, shading indicates presence.

The shell of *Terebellum delicatum* differs from other members of *Terebellum* by having a central mid-columella ridge, a character that is lacking in all other members of the complex, which typically have the columella ridge commencing at the posterior join of the labrum and the body whorl. Furthermore, the new species lacks the marginal black line on the anterior lip typical in other *Terebellum* at maturity. The new species, together with *Terebellum delicatum* and some other forms of *Terebellum terebellum*, share the similar soft brown colouration and brown dots that have white half-moon shading. This colour pattern should not be used as a basis for species identification.

A number of Turritellidae Lovén, 1847 have been wrongly assigned to *Terebellum*: *Turritella burdenii* Tuomey & Holmes, 1857, *Turritella constrictum* Emmons, 1858, *Turritella etiwanensis* Toumey & Holmes, 1857, *Turritella exaltata* Conrad, 1841, *Turritella striatum* Tuomey & Holmes, 1857 (Tuomey & Holmes 1857; Emmons 1858; Harris 1890; Jung 1974).

Terebellum cinctum Martin, 1916

Plate 7D

1916 *Terebellum cinctum* Martin, p. 248, pl. 2, fig. 53. Jung 1974, p. 42, pl. 13, figs. 4 to 6.
Type Material. Holotype – RGM St. 10337. The type measures 34.7 mm in length.

Type Locality. Kembang Sokkoh, West Progo Mountains, Java, Indonesia [Recent].

Diagnosis. The shell is smooth and narrow, with a blunt teleoconch. There is a carina above the defined suture, with distinct incised spiral lines being the only sculpture on the teleoconch. Basal sculpture not known. Labial callus moderately developed.

Distribution. MIOCENE – Burdigalian – *Indonesia* Kembang Sokkoh, West Progo Mountains, Java (Jung 1974).

Terebellum delicatum Kuroda & Kawamoto in Kawamoto & Tanabe, 1956

Plate 8B

1956 *Terebellum terebellum delicatum* Kuroda & Kawamoto in Kawamoto & Tanabe, p. 87, pl. 10, fig. 91. Maxwell *et al.* 2018b, p. 64. = *Terebellum t. delicatum* Kuroda & Kawamoto – Kira 1959, p. 34. = *Terebellum terebellum delicatum* Kuroda & Kawamoto – Habe 1961, p. 58, pl. 17, fig. 1. = *Terebellum t. delicatum* Kuroda & Kawamoto – Kira 1962, p. 34. = *Terebellum terebellum delicatum* Kuroda & Kawamoto – Habe 1964, p. 58, pl. 17, fig. 1. Kreipl & Poppe 1999, p. 10, pl. 8, fig. 5. = *Terebellum terebellum* forma *delicatum* Kuroda & Kawamoto, 1961 – Jung & Abbott 1967, p. 449, pl. 321, figs. 9 & 10. = *Terebellum delicatum* Kuroda & Kawamoto, 1961 – Liverani 2014, p. 15, pl. 132, figs. 1 to 4. = *Terebellum delicatum* Kuroda & Kawamoto, 1961 – Poppe & Tagaro 2016, p. 93, pl. 8, fig. 6. = *Terebellum delicatum* Kuroda & Kawamoto in Kawamoto & Tanabe, 1956. Maxwell *et al.* 2018b, p. 64, figs. 1i to k & 2a to d.

Type Material. Lectotype – Hagi no. HH-Mo000214. The type measures 29.0 mm in length, with a width of 6.5 mm.

Type Locality. Kurae, Hagi, Japan [Recent].

Diagnosis. The shell is smooth, ovately rotund and quadrate at the base. The sutures are well-developed, and the labrum is protocyrt. The spire is blunt, and the aperture extends for three-quarters the length of the shell. There is a distinctive central axial mid-columella ridge that may not be evident in sub-adults. The species lacks the anterior lip marginal black line at maturity. The shell background colour is usually tan with circular white spotting, with a single dark smaller spot within each larger white one such that their circumferences touch, resulting in a white crescent shape partially surrounding the darker spot (Maxwell *et al.* 2018b).

Distribution. Specimens of *Terebellum delicatum* have been found in southwest Japan, Vietnam, Philippines, and recently in Queensland, Australia (Maxwell *et al.* 2018b). While first-hand collecting records from material examined indicates that the species has been found periodically intertidally in Queensland, this contrasts with reports of a more restricted range to deeper waters in the Philippines (Poppe & Tagaro 2016; Maxwell *et al.* 2018b). Records from Mozambique

(Maxwell *et al.* 2018b) need to be confirmed, as they are located well outside the Western Pacific rim where the species is known to occur. New Records: *Japan*. Kurae, Hagi (Hagi City Museum). *Vietnam* Nha Trang area, 24.0–37.0 mm (Maxwell *et al.* 2018b). *Australia* Bowen Sand Flats, 29.5 mm (Maxwell *et al.* 2018b); Buchans Point, 19.0–27.0 mm (Maxwell *et al*. 2018b); Dingo Beach, Queensland (Maxwell *et al.* 2018b); Saunders Beach (Maxwell *et al.* 2018b); Torres Straits (Maxwell *et al.* 2018b); Wonga Beach (Maxwell *et al.* 2018b). *Mozambique* Nacala Bay, 32.0–37.0 mm (Maxwell *et al.* 2018b).

Terebellum hubrechti Poppe & Tagaro, 2016

Plate 8C

2016 *Terebellum hubrechti* Poppe & Tagaro, p. 92, pl. 8, figs. 1 to 4. Maxwell *et al.* 2018b, p. 64, figs. 1l & m.

Type Material. Holotype – Conchology Inc.. The type measures 33.2 mm in length and has a width of 10 mm.

Type Locality. Caubian, Philippines [Recent].

Diagnosis. Shell is smooth and ovately rotund. The aperture is moderately straight, wide and quadrate basally. The labrum is thickened, and the suture is distinct.

Distribution. HOLOCENE – Philippines, Caubian (Poppe & Tagaro 2016).

Terebellum obtusum Sowerby in Grant, 1840

Plate 7E

1840 *Terebellum obtusum* Sowerby in Grant, p. 329, pl. 26, fig. 31. = *Terebellum obtusum* Sowerby – d'Orbigny 1852, p. 52, no. 880. Eames 1952, p. 73. Jung 1974, p. 43, pl. 13, figs. 12 to 18. = *Terebellum subulatum obtusum* Sowerby – Jung 1974, p. 43. Kulkarni *et al.* 2010, p. 325.

1840 *Terebellum obtusum* Sowerby – Harzhauser 2009, p. 137, pl. 3, figs. 11 to 13. Kulkarni *et al.* 2010, p. 325.

2010 *Terebellum* (*Terebellum*) *terebellum* – Kulkarni *et al.* 2010, p. 325, fig. 2q.

Type Material. Holotype – BNHM no. G21000. The type measures 42.2 mm in length.

Type Locality. Soomrow, Cutch, India [Langhian].

Diagnosis. The shell is moderately slender, with a short teleoconch of 2 ½ whorls. The labral callus is well-developed. The columella is recurved posteriorly. Sutures are not well defined.

Distribution. MIOCENE – Langhian – *India* Kachchh, Gurjarat (Kulkarni *et al*. 2010); Kutch, Gaj Beds (Jung 1974). Kutch, Soomrow (d'Orbigny 1852). Aquitanian – *Tanzania* Ras Tipuli, Lindi Bay (Harzhauser 2009).

Terebellum papilliferum Martin, 1916

Plate 7F

1916 *Terebellum papilliferum* Martin, p. 248, pl. 2, figs. 51 & 52. Jung 1974, p. 43, pl. 13, figs. 7 to 11.

Type Material. Lectotype – RGM No. St.10339. The type measures 28.0 mm in length.

Type Locality. Gunung Spolong, West Progo Mountains, Java, Indonesia [Burdigalian].

Diagnosis. The fusiform shell is moderately slender, with a low teleoconch and a smooth surface. The columella is nearly straight, and the suture is well-defined. The columella callus continues as a carina above the suture. The labrum is slightly thickened and without a stromboidal notch.

Distribution. MIOCENE – Burdigalian – *Indonesia* Gunung Spolong, West Progo Mountains, Java (Jung 1974).

Terebellum simoni Dekkers, Maxwell & Congdon, 2019

Plate 8D

2019 *Terebellum simoni* Dekkers, Maxwell, & Congdon, p. 16, pl. 1, figs. 1 to 3.

Type Material. Holotype – MNHN no. IM-2000-33613. The type measures 44.6 mm in length.

Type Locality. Bohol Island, Philippines [Recent].

Diagnosis. Shell slender, solid, and porcelainous in texture. The size is average relative to the three other recent species in the genus. The adult shell measures 33 to 50 mm in shell length. The protoconch is indistinct, and the apex of the shell always white. A distinct curved incised sutural band runs from the apex. The teleoconch has three whorls, the body whorl being the predominant feature of the shell that comprises about 90 % of the total shell length. The channel at the suture is deep and clearly visible. Above the channel is a thickened yellowish band of 1 mm maximum width. The anterior sinus is deeply incised. The body whorl is smooth, with the exception of rather coarse growth lines. The aperture is large, triangular, and bordered by a slightly thickened labrum. The columella has a well-marked callus, golden-yellow at the posterior end, becoming white at the anterior end. All shells have a golden-yellow ground colour with 4 evenly spaced darker bands of about 2 to 3 mm wide (Dekkers *et al*. 2019).

Distribution. HOLOCENE – Philippines, Bohol (Dekkers *et al*. 2019).

Terebellum terebellum (Linné, 1758)

Plate 8B

1684 Bonanno, p. 120, no. 57. Langii 1722, pp. 44 & 77.

1688 *Rhombus angustus nebulatus* Lister, IV, cap. 6, no. 736, fig. 30.

1688 *Rhombus angustus fasiatus* Lister, IV, cap. 6, no. 736, fig. 31.

1688 *Rhombus angustus punctatus* Lister, IV, no. 737, fig. 32.

1705 *Strombus terebellum* Rumphius, pl. 30, fig. S.

1711 *Strombus terebellum* Rumphius, pl. 30, fig. S.

1713 Petiver, p. 3, pl. 13, fig. 24.

1741 *Strombus terebellum* Rumphius, pl. 30, fig. S. Issel & Tapparone Canefri 1876, p. 362.

1742 D'Argenville, pl. 14, fig. G. = *Terebra alata* D'Argenville – Reeve 1842, p. 267. Issel & Tapparone Canefri 1876, p. 362.

1742 Gualtieri, pl. 23, fig. O.

1753 *Terebellum pullum* Klein, p. 38, no. 101, spc. 1. Reeve 1842, p. 267. Issel & Tapparone Canefri 1876, p. 363.

1753 *Terebellum folium* Klein, p. 38, no. 101, spc. 2.

1753 *Terebellum punctatum* Klein, p. 38, no. 101, spc. 3, pl. 2, fig. 49. Reeve 1842, p. 268. Issel & Tapparone Canefri 1876, p. 363.

1753 *Terebellum album* Klein, p. 38, no. 101, spc. 4.

1753 *Terebellum striatum* Klein, p. 38, no. 101, spc. 5, pl. 2, fig. 49.

1753 *Terebellum flammeum* Klein, p. 38, no. 101, spc. 6.

1753 *Terebellum fasciatum* Klein, p. 38, no. 101, spc. 7.

1753 *Terebellum patens* Klein, p. 38, no. 101, spc. 8.

1758 *Conus terebellum* Linné, p. 718, no. 284. Linné 1760, p. 718, no. 284. Reeve 1842, p. 268. Hanley 1860, p. 63. Cox 1948, p. 31. Dey 1961, p. 67. Cernohorsky 1965, p. 15. Jung & Abbott 1967, p. 452. Ladd 1972, p. 57. Jung 1974, p. 44. Kohn 1976, p. 43. = *Conus terebellum* Mawe, 1823, p. 116, pl. 20, fig. 7.

= *Bulla terebellum* Linné, 1767, p. 1185, no. 388. Born 1778, p. 192. Gmelin 1791, p. 3428, no. 22. Lamarck 1801, p. 72. Montfort 1810, p. 379. Sowerby 1820–1825, pl. 263. Oken 1835, p. 456. Anton 1839, p. 102. Reeve 1842, p. 268. Tryon 1885, pp. 131 & 145. Issel & Tapparone Canefri 1876, p. 363. Eames 1952, p. 72. Woodring 1959, p. 191. Dey 1961, p. 67. Cernohorsky 1965, p. 15. Jung & Abbott 1967, p. 452, pl. 323. Ladd 1972, 532, p. 57. = *Strombus terebellum* Rumphius – Reeve 1842, p. 267. = *Seraphs terebellum* Woodward – Issel & Tapparone Canefri 1876, p. 363. = *Seraphs terebellum* Montfort – Melvill & Standen 1901, p. 381. Melvill 1909, p. 93. = *Seraphs terebellum* Linné – Tate 1890, p. 212, pl. 4, fig. 5. Pilsbry 1895, p. 55. Melvill & Standen 1899, p. 166. = *Strombus terebellum* Linné – Melvill & Sykes 1897, p. 44. Hunter 1967, 15(9). = *Terebellum terebellum* Linné – Mörch 1852, p. 64. Cox 1931, p. 7. Oostingh 1935, p. 58. Solem 1958, p. 220. Dey 1961, p. 67. Perron 1978, p. 469. Rippingale & McMichael 1961, p. 60, pl. 6, fig. 2. Abbott 1962, pp. 1 to 3. Nuttall 1965, p. 170. Lewis & Taylor 1966, p. 280. Wilson & Gillett 1971, p.

40, pl. 18, fig. 11. Hinton 1972, p. 10, pl. 5, figs. 27 to 30. Cernohorsky 1972, p. 83, pl. 20, fig. 5. Jung 1974, p. 44, pl. 14, figs. 1 to 11, tf. 13. Dance 1974, p. 75. Kohn 1976, p. 43. Hinton 1977a, p. 13, no. 10. Hinton 1977b, p. 10, no. 12. Taylor 1978, p. 3. Mastaller 1978, p. 131. Wagner & Abbott 1978, p. 09-657. Tantanasiriwong 1978, p. 8, fig. 99. Wilson & Gillett 1979, p. 76, pl. 14, fig. 11. Walls 1980, pp. 15, 55, 56 & 190, fig. 4, p. 10, fig. 1, p. 11, fig. 1. Abbott & Dance 1982, p. 83. Mienis 1984, p. 56. Short & Potter 1987, p. 34, pl. 16, fig. 12. Clavier & Carrigue 1990, p. 9. Jones *et al.* 1990, p. 112. Woodward 1993, p. 28. Drivas & Jay 1998, p. 13 and 15. Kreipl *et al.* 1999, pp. 10 & 19, pl. 8, figs. 2, 3, 10 & 11. de Bruyne 2003, p. 91. Smith 2003, p. 255. Lee & Chao 2004, p. 38. Slack-Smith & Bryce 2004, p. 228. Bandel 2007, p. 137. Pacaud 2008, p. 722. Al-Ansi & Al-Khayat 1999, p. 308. Brown 2011, p. 248. Al-Yamani *et al.* 2012, p. 159, pl. 134. Maxwell *et al.* 2018b, p. 64, figs. 1a to h & 2e to g. = *Terebellum* (*Terebellum*) *terebellum* Wissema – Cox 1948, p. 31. = *Terebellum* (*Terebellum*) *terebellum* Linné – Beets 1950, p. 244. Cernohorsky 1965, p. 15, pl. 4, fig. 25. Jung & Abbott 1967, p. 445, pls. 319 to 321 & 324 to 326. Ladd 1972, p. 57, pl. 15, fig. 4. Springsteen & Leobrera 1986, p. 68, pl. 15, fig. 6a. = *Terebellum terebellum* Gabbi, 1999, p. 128. = *Terebellum terebellum terebellum* Linné – Okutani 2000, p. 189, pl. 94, fig. 1. Kulkarni *et al.* 2010, p. 325, fig. 2q.

1773 *Avena marina* Martini, pl. 51, figs. 568 & 569. Reeve 1842, p. 268. Issel & Tapparone Canefri 1876, p. 363.

1788 *Terebellum punctatum* Chemnitz, p. 124, pl. 146, figs. 1362 & 1363. Tryon 1885, pp. 131 & 143. Issel & Tapparone Canefri 1876, p. 363. Pilsbry 1895, p. 55. Martin 1899, p. 195, pl. 31, fig. 452. Oostingh 1935, p. 59. Dey 1961, p. 67. = *Terebellum punctatum* Bowdich 1822, pl. XI, fig. 14. = *Terebellum punctatum* Reeve – Issel & Tapparone Canefri 1876, p. 363. Oostingh 1935, p. 59. Cox 1948, p. 31. Jung & Abbott 1967, p. 452. Cernohorsky 1972, p. 83. = *Terebellum* (*Terebellum*) *punctatum* Chemnitz – Horst & Schepman 1908, p. 223. = *Terebellum sabulatum punctata* Melvill, 1909, p. 94. = *Terebellum punctatum* Martin – Cox 1948, p. 31. = *Terebellum punctatum* Beets, 1950, p. 244. = *Terebellum punctatum* Van Der Vlerk – Dey 1961, p. 67.

1798 *Terebellum nebulosum* Röding, p. 135, no. 1690. Woodring 1959, p. 191. Jung & Abbott 1967, pp. 449 & 452, pl. 321, fig. 11. Ladd 1972, p. 57. Cernohorsky 1972, p. 83. Wagner & Abbott 1978, p. 09-655. Walls 1980, p. 190. = *Terebellum nebulosum* Blainville – Tryon 1885, p. 141. = *Terebellum (Terebellum) terebellum nebulosum* Röding – Springsteen & Leobrera 1986, p. 68, pl. 15.

1798 *Terebellum lineatum* Röding, p. 135, no. 1691. Perry 1811, pl. 37, no. 1. Woodring 1959, p. 191. Jung & Abbott 1967, pp. 449 & 452, pl. 321, figs. 1, 2 & 14. Cernohorsky 1972, p. 83. Wagner & Abbott 1978, p. 09-655. Walls 1980, p. 190. = *Terebellum (Terebellum) terebellum lineatum* Röding – Springsteen & Leobrera 1986, p. 68, pl. 15, fig. 6d. =

Terebellum terebellum lineatum Röding – Kreipl *et al.* 1999, pp. 10 and 19, pl. 8, figs. 1 and 6.

1798 *Terebellum punctulatum* Röding, p. 135, no. 1692. = *Terebellum punctulorum* Röding – Jung & Abbott 1967, pp. 449 & 452, pl. 321, figs. 3, 5 & 6. Cernohorsky 1972, p. 83, Walls 1980, p. 190. = *Terebellum punctulovem* Röding – Wagner & Abbott 1978, p. 09-656. = *Terebellum terebellum punctulorum* Röding – Kreipl *et al.* 1999, pp. 10 & 19, pl. 8, figs. 4, 7 & 8. Poppe & Tagaro 2016, pl. 8, fig. 5. = *Terebellum* (*Terebellum*) *terebellum punctulorum* Röding – Springsteen & Leobrera 1986, p. 68, pl. 15, fig. 6c.

1807 *Terebellum album* Link, p. 99. Jung & Abbott 1967, pp. 449 & 452. Cernohorsky 1972, p. 83. Wagner & Abbott 1978, p. 09-652. Walls 1980, p. 190.

1807 *Terebellum variegatum* Link, p. 99. Jung & Abbott 1967, p. 452. Cernohorsky 1972, p. 83. Wagner & Abbott 1978, p. 09-657. Walls 1980, p. 190.

1801 *Terebellum subulatum* Lamarck, p. 72. Montfort 1810, p. 379. Sowerby 1820–1825, pl. 263, figs. 1 & 2. Lamarck 1822, p. 410. Cronch 1827, p. 38, pl. XX, fig. 1. Gould 1833, p. 96. Brown 1835, 1836, p. 67, pl. XI, fig. 4. Anton 1839, p. 102. Sowerby 1839, p. 104, fig. 452. Sowerby 1842, p. 270, fig. 452. Reeve 1842, p. 267, pl. 291, figs. 1 & 2. Sowerby 1846, p. 270, fig. 452. Adams & Reeve 1848, p. 36, pl. 9, fig. 6. Gray *et al.* 1850, p. 36, pl. 9, fig. 6. Sowerby 1852, p. 290, fig. 452. Adams & Adams 1858, p. 263. Chenu 1859, p. 264, figs. 1656 to 1658. Reeve 1860, p. 94, pl. 1, fig. 6. Cuvier 1868, p. 32, pl. XV, fig. 9. Tryon 1883, p. 192, pl. 59, fig. 66. Tryon 1885, pp. 131 & 145, pl. 11, figs. 27 to 30. Issel & Tapparone Canefri 1876, p. 363. Martens 1889, p. 189. Pilsbry 1895, p. 55. Rogers 1908, p. 122. Melvill 1909, p. 93. Cox 1931, p. 7. Oostingh 1935, p. 58. Rippingale & McMichael 1961, p. 60. Dey 1961, p. 67. Cernohorsky 1965, p. 15. Jung & Abbott 1967, pp. 449 & 452. Cernohorsky 1972, p. 83. Dance 1974, p. 75. Wagner & Abbott 1978, p. 09-657. Walls 1980, p. 190. Eames 1952, p. 72. = *Terebellum sabulatum* Lamarck – Montfort 1810, p. 379. Jung & Abbott 1967, p. 452. Wagner & Abbott 1978, p. 09-656. = *Terebellum subulatum* Chemnitz – Mörch 1852, p. 64. Adams & Adams 1858, p. 263. = *Terebellum subulatum* Cooke 1885, p. 64. Cooke 1927, p. 98. Allan 1950, p. 102, pl. 14, fig. 7. Beets 1950, p. 244.

1811 *Terebellum spirale* Perry, pl. 37, no. 1. Jung & Abbott 1967, p. 452. Cernohorsky 1972, p. 83. Wagner & Abbott 1978, p. 09-657.

1885 *Terebellum maculosum* Adams – Tryon 1885, pp. 131 & 141.

1961 *Terebellum ubulatum* Tyron – Dey 1961, p. 67.

1976 *Terebellum pseudodelicatum* Ogasawara, p. 62, pl. 3, figs. 1, 2 & 6.

Terebellum terebra Bosc – Issel & Tapparone Canefri 1876, p. 363.

Terebellum terebellum delicatum Kuroda & Kawamoto – Kira 1962, p. 34, pl. 15, fig. 1. Cernohorsky 1965, p. 15. Jung & Abbott 1967, pp. 449 & 453, pl. 321, figs. 9 & 10.

Ogasawara 1976, p. 62. Kreipl *et al.* 1999, pp. 10 & 19, pl. 8 fig. 5. Okutani 2000, p. 189, pl. 94, fig. 2. = *Terebellum delicatum* Habe – Cernohorsky 1972, p. 83. = *Terebellum delicatum* Kuroda & Kawamoto – Wagner & Abbott 1978, p. 09-653. Walls 1980, p. 190. *Terebellum spc.* Al-Khayat & Al-Ansi 2008, p. 550.

Type Material. Lectotype – CLS no. P–Z 0010819. The shell is 37.5 mm in length.

Type Locality. Designated herein as Cebu Island, Philippines [Recent].

Diagnosis. The shell is oblong fusiform, with approximately seven whorls. The protoconch is low and smooth, with fine longitudinal spirals. The teleoconch is moderately high, with six whorls and moderately straight sides. The base of the shell has incised spiral lines. The aperture is high, narrow and ovately elongate, becoming basally wider, and the labrum is moderately calloused continuing as a carina above the suture. The suture of the shell has a well-defined incised canal. The operculum is diminished, triangulate and horny.

This taxon is highly variable in colour and size throughout its range, but remains morphologically consistent. There are five colour forms recognised:

- typical colour - brown to yellowish brown, with maculations of varying intensity;
- *Terebellum terebellum* form *punctulatum* Röding, 1798 – shell with dots covering the entire surface;
- *Terebellum terebellum* form *nebulosum* Röding, 1798 – shell with three spiral bands of colour;
- *Terebellum terebellum* form *lineatum* Röding, 1798 – shell with strong zig-zag lines over the surface;
- *Terebellum terebellum* form *album* Link, 1807 – shell white.

Distribution. The species *Terebellum terebellum* was first recorded from the early Miocene of Saipan and the Marianas and later in the Pliocene of India. Currently, this taxon ranges from the Red Sea throughout the tropical Indo-Pacific, and is especially common throughout the Philippine and Micronesian archipelagos (Jung & Abbott 1967). It is possible that the distributional records for *Terebellum terebellum* includes examples of all extant taxa. HOLOCENE – *Israel* Sinai (Mienis 1984); Eilat, Gulf of Aqaba (Jung & Abbott 1967). *Sudan* Port Sudan (Mastaller 1978). *Kuwait* Mahboula (Al-Yamani *et al.* 2012). *Mozambique* off dock, Nacala (Jung & Abbott 1967). *Tanzania* 1.6 km north of Bawi Island (Jung & Abbott 1967); 2.4 km west south west of Ras Nungwi (Jung & Abbott 1967); Between Ukombe and Chumbe Islands (Jung & Abbott 1967). *Comoros Islands* Mayotte (Jung & Abbott 1967). *Madagascar* 3–5 km south of Nosy Iranja (Jung & Abbott 1967). *Réunion* (Drivas & Jay 1998). *Mauritius* (Jung & Abbott 1967). *Seychelles* (Melvill 1909); Amirante Islands (Melvill 1909); Baie Ternay, West Mahé Island (Jung & Abbott 1967); Seychelles Bank (Lewis & Taylor 1966). *Oman* (Jung & Abbott 1967) Gulf of Oman (Melvill & Standen 1901). *Qatar* Alhadid (Al-Khayat & Al-Ansi 2008); Halut Al-Asere (Al-Ansi & Al-Khayat 1999), Hadeed (Al-Ansi & Al-Khayat 1999). *Maldives* Fadiffolu Atoll (Jung &

Abbott 1967); Addu Atoll (Jung & Abbott 1967). *Chagos Archipelago* Cargodos (Melvill 1909). *Andaman Islands* Port Blair (Melvill & Sykes 1897). *Thailand* 40 km northwest of Phuket Island (Jung & Abbott 1967); Phuket, Bay of Bengal (Tantanasiriwong 1978). *Myanmar* Mergui Archipelago (Martens 1889). *Malaysia* Kudat Bay (Jung & Abbott 1967); Semporna (Jung & Abbott 1967). *China* (Adams & Reeve 1848). *Taiwan* Kenting National Park (Lee & Chao 2004). *Philippines* throughout the archipelago (Jung & Abbott 1967); Luzon Island (Jung & Abbott 1967); Cebu Island (Jung & Abbott 1967); Leyte Island (Jung & Abbott 1967); Mindanao Island (Jung & Abbott 1967); Sanga-Sanga Island (Jung & Abbott 1967); Sibutu Islands (Abbott 1962). *Japan* Bay of Yedo (Pilsbry 1895); Nagasaki (Pilsbry 1895); Yobuko (Pilsbry 1895); Baso Peninsula, Honshu (Jung & Abbott 1967); Tatsugahama, Honshu (Jung & Abbott 1967); Southern Kyushu (Jung & Abbott 1967); Okinawa Island (Pilsbry 1895; Jung & Abbott 1967). *Marianas* North side of Apro Harbor, Guam Island (Jung & Abbott 1967); Guam (Smith 2003). *Micronesia* Throughout the archipelago (Jung & Abbott 1967); Truk (Jung & Abbott 1967); Yap Island (Jung & Abbott 1967). *Palau* (Jung & Abbott 1967). *Marshall Islands* Eniwetak Atoll (Jung & Abbott 1967); Bikini Atoll (Jung & Abbott 1967); Kwajalein Atoll (Jung & Abbott 1967). *Indonesia* Ambon Island (Horst & Schepman 1908; Jung & Abbott 1967); Sunda Straits (Jung & Abbott 1967); Aoeri Islands, Geelvink Bay (Jung & Abbott 1967); Japen Island (Jung & Abbott 1967); Schouten Island (Jung & Abbott 1967); Java (Horst & Schepman 1908); Banka (Horst & Schepman 1908); Ceram (Horst & Schepman 1908). *Papua New Guinea* Finschhafen Bay (Jung & Abbott 1967); Matapi Island, 8 km from Rabaul (Jung & Abbott 1967); Rabaul Harbour (Jung & Abbott 1967); Kumbun, near Kandrain (Jung & Abbott 1967); Port Moresby (Hinton 1972). *Solomon Islands* Atao District, Malaita Island (Jung & Abbott 1967); Florida Island (Solem 1958); Roviana Lagoon, New Georgia (Jung & Abbott 1967). *American Samoa* Tutuila (Jung & Abbott 1967; Brown 2011). *Australia* Broome (Jung & Abbott 1967); Dampier Archipelago (Slack-Smith & Bryce 2004); Cape Leveque (Jung & Abbott 1967); Murray Island, Torres Straits (Melvill & Standen 1899); Lizard Island (Jung & Abbott 1967); Palm Island (Rippingale & McMichael 1961); Kenn Reef, Coral Sea (Hunter 1967); One Tree Reef (Jones *et al.* 1990). *New Caledonia* Chesterfield Reef, Coral Sea (Clavier & Carrigue 1990; Caze *et al*. 2010); Poindimié (Caze *et al*. 2010); Poum (Caze *et al*. 2010); Thio (Caze *et al*. 2010); Yaté (Caze *et al*. 2010); Belep (Caze *et al*. 2010). *Noumea* (Jung & Abbott 1967); Ile des Pins (Caze *et al.* 2010; Jung & Abbott 1967); Ouvea Island (Jung & Abbott 1967); Canala (Caze *et al*. 2010); Balabio Island (Caze *et al*. 2010); Nord Lagoon (Caze *et al*. 2010); Île Ouen-Baie du Prony (Caze *et al*. 2010); Baie de St Vincent (Caze *et al*. 2010); Atoll de Surprise (Caze *et al*. 2010); Grand Récif Sud (Caze *et al*. 2010). *Vanuatu* Aoré Island (Jung & Abbott 1967; Caze *et al.* 2010); Baldwin Bay (Caze *et al*. 2010); Belmoul Lagoon (Caze *et al*. 2010); Palikulo Bay (Caze *et al*. 2010); SE corner of Santo (Caze *et al*. 2010); Segond Channel (Caze *et al*. 2010); Tangoa Island (Caze *et al*. 2010); West Tutuba Island (Caze *et al*. 2010); West Aésé Island (Caze *et al*. 2010). *Fiji* (Cernohorsky 1965; Jung &

Abbott 1967). *Tonga* Tongatapu Island (Jung & Abbott 1967) *French Polynesia*? Marquesas Islands (Jung & Abbott 1967). QUATERNARY – *Tanzania* Dar es Salaam (Jung & Abbott 1967; Jung 1974). *Indonesia* Belitung Island (Jung & Abbott 1967; 1974); Bunyu Island, East Borneo (Jung & Abbott 1967; Jung 1974). PLEISTOCENE – *Red Sea* cast bed below reef Limestone near Mharak Village, Farasan Kebir (Cox 1931). *Madagascar* Espirit Limestone, Aldabra Atoll (Taylor 1978). PLIOCENE/ PLEISTOCENE – *Indonesia* Nias Island, off Sumatra (Dey 1961; Jung & Abbott 1967; Jung 1974); Biliton Island, off Sumatra (Dey 1961). NEOGENE – *Indonesia* Java ('Oostingh' in Jung & Abbott 1967; Jung 1974); Saonek Besar (Dey 1961; Jung & Abbott 1967; Jung 1974). PLIOCENE – *Indonesia* Java (Cox 1948; Dey 1961); Winongm Tegal, Java (Martin 1899). Tjipamali, Java (Oostingh 1935); Sumatra (Cox 1948; Dey 1961; Jung & Abbott 1967; Jung 1974); North Kutei, Borneo (Jung & Abbott 1967, Jung 1974); Boenjoe Island, Borneo (Beets 1950). *Timor* (Cox 1948); East Ceram (Jung & Abbott 1967; Jung 1974). *Red Sea* Farasan Islands (Dey 1961). *India* Gaj (Dey 1961); Sind (Dey 1961). *Malaysia* Dent Peninsula (Cox 1948; Nuttall 1965). MIOCENE – *Indonesia* Java (Cox 1948; Dey 1961; 'Martin' in Jung & Abbott 1967; Jung 1974). *India* Quilon, Kerala (Dey 1961). *Japan* Sunakozaka Formation, Asano-gawa at Higashi-Ischise, Kanazawa City, Ishikawa Prefecture (Ogasawara 1976). Aquitanian – *Marianas* Saipan Island (Ladd 1972).

3.2 Discussion

In Seraphsidae, the basal sinus of the labrum was not fully developed. The shape and morphology reflect a burying habit, thus the development of the basal sinus is redundant. Furthermore, the lack of evolutionary progression with the basal sinus, coupled with a burial habit, led to the diminishment of the cephalitic tentacle on the eyestalk in modern taxa. Significantly, the earliest ancestors of the clade were involute and were not able to detect the level of shell burial, leaving the shell exposed. This thesis divided the clade to indicate an evolutionary shift in one lineage, the aminal evolved a final evolute growth habit, enabling the development of a posterior canal with a posterior filament that provided information on shell burial orientation/depth. Later evolutionary advances included the loss of the posterior canal and the development of a channelled suture, which served the same purpose.

The cladistic arrangements obtained within the Seraphsidae indicated that there was a need to differentiate and organise the subclade into distinct inclusive clades so as to provide an improved understanding of the evolutionary patterns within the group, notwithstanding the limited morphological structural elements. The different sub-clades provided enough distinctive characteristics to enable the delineation of two distinct clade sets representing two phylogenetically constrained growth patterns. The first set, *Seraphsinae* new subfamily, comprises the clades within the Seraphsidae that have an involute terminal growth pattern. In contrast, the second set erected, *Neoterebellinae* new subfamily, contains those clades within the Seraphsidae that have an evolute terminal growth pattern. The terminal growth pattern has causal importance as it provides for differential life history characteristics associated with burial in particular. The evolute pattern enables the shell to develop a subsutural canal that contains a filament, allowing the organism to detect if it is buried, unlike the involute shell form that lacks this anterior burial detection. The ability to detect if the anterior of the shell is buried provides the organism with improved burial coverage. This improved burial detection maybe seen as a slight evolutionary advantage which maybe reflected in the continuity of the *Neoterebellinae* new subfamily and the current radiation *Terebellum* Röding, 1798 in particular (Savazzi 1991).

The extinction of all members of the *Seraphsinae* new subfamily indicates an evolutionary dead end for the involute clade. Much of the decline in the *Seraphsinae* new subfamily can be attributed to climate change within their known distribution patterns due to shifts in sea temperature, sea level fluctuations associated with interglacial cycles and continental drift (Petuch 2004). This spatiotemporal extinction pattern is also mirrored in other extant families in Stromboidea, namely the Strombidae (Petuch 1991, 1994), Rimellidae (Squires 2013) and Rostellariidae Gabb, 1868 (Dall 1915).

The lack of evolutionary progression on the development of a basal sinus on the labrum in the *Seraphsinae* new subfamily meant that the animal lacked sensory detection found in its sister clade *Neoterebellinae* new subfamily. In *Diameza*, there is the development of a long posterior elongation of the labrum that would have contained an extension of the mantle. However, the involute phylogenetic constraint faced by this clade primarily led to a lack of sensory external detection on burial. This lack of external sensory awareness, and underdevelopment of the basal sinus, may have led to the elongation of the anterior sinus, such that the labrum did not extend to the base of the shell. This would have enabled the eye peduncle, with an associated cephalic tentacle, to provide the animal with a level of external awareness. However, this would also have meant that the anterior of the shell would need to be exposed in contrast to the evolutionary trajectory of ancestors toward burial (Savazzi 1988a, 1991). Similarly, in *Miniseraphs*, there is an involute phylogenetic constraint leading to a lack of sensory external detection whilst buried. The inwardly curved base of the columella indicates an evolutionary tendency for enclosure, which is in contrast to the wide aperture of the shell.

This thesis demonstrates that, from a pluralist perspective, historical revisions of Seraphsidae are sound in terms of current species delineations (de Gregorio 1880; Jung 1974, Caze *et al*. 2010). However, the use of a pluralist approach improved the understanding of internal cladistic relationships within Seraphsidae, and resulted in the recognition of subtle structural differences, enabling the determination of novel species and the improvement of the internal cladistic arrangements among extant and extinct taxa within the group.

Chapter 4.0 Summary

This thesis argued for the erection of the clade Neostromboidae which incorporates the clades within Stromboidea that show morphological similarities in animal morphology: particularly, the tentacles are at the ends of eye peduncles (Gardner 1875), and to a lesser extent, feeding behaviour (Purchon 1977), which differentiates these from other members of the Stromboidea which have eyes at the base of the tentacles. This new arrangement regroups those organisms historically considered to be the Strombidae: conches and tibias (Gardner 1875; Walls 1980), while retaining the families erected in the modern revisions (*cf.* Bandel 2007).

Sole reliance on morphological data in existing historical revisions of taxa fails to recognise some spatiotemporally distinct species, which limits the understanding of the radiation and extent of diversity within the complex. Notwithstanding, there were some species that were morphologically distinct, such as *Seraphs kaindraperi* new species that could be delineated from more inclusive taxa. The erection of the Priabonian American *Paraseraphs cantamessae* which had been associated with the earlier Bartionian-Ypresian European *Paraseraphs armoricensis*, highlights the benefits of using spatiotemporal data to discern species, and provide more information that enables a better understanding of changes in morphological and distributional patterns. In this case, the recognition of *Paraseraphs cantamessae* provided a localised ancestor that contributes to explaining the regionalised shift in morphological form. Until that recognition, the conspecific species *Paraseraphs procerus*, with its distinctive recurved dorsal shape, made discernment of evolutionary patterns problematic. Modern revisions of extant members of the Seraphsidae remain focused on colouration and small structural differences, mirroring the historical approach taken to the extinct species (Liverani 2014; Poppe and Tagaro 2016; Dekkers *et al.* 2019). The increased evolutionary resolution, and the ability to discern new species based on limited morphological evidence, justifies the use of a pluralist approach to species conception in classical taxonomic revision, as it provides the evidence that morphology alone cannot provide such a spatiotemporal positioning.

4.1 Need for Supportive Research

While this thesis demonstrated that classical taxonomy using a pluralistic species conception is able to provide a classical revision of predominantly fossil taxa, there were some limitations in the ability to gain higher resolution of some clades. This thesis did not resolve the basal systematics within Neostromboidae which was problematic using only classical taxonomic methodology. To enable an accurate resolution of the internal cladistic arrangements within Neostromboidae, the use of extant taxa and advanced higher resolution genetic techniques are necessary. Furthermore, there is also a need to test the robustness of the pluralist approach to species recognition against molecular data. This support will give weight to the use of a pluralist classical taxonomic process, which uses all forms of evidence, such as morphological and spatiotemporal data, in the determination of extinct species, evidence that is often seen as redundant in molecular approaches to taxonomy.

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Plate 1: *Seraphs* Montfort, 1810.

A) *Seraphs andersoni* (Dickerson, 1917), California Academy of Sciences Department of Geology, no. 434 (Jung 1974, pl. 9, fig. 5).

B) *Seraphs belemnitus* (Palmer, 1953), Paleontological Research Institute Ithica, no. 29236 (Jung 1974, pl. 9, figs. 12 to 14).

C) *Seraphs caracasense* (Leymerie, 1846), British Museum Natural History, no. G50180 (Jung 1974, pl. 4, figs. 10 and 11).

D) *Seraphs chilophorus* (Cossmann, 1889), from Museum National d'Histoire Naturelle, Collectionde Paleontologie, Paris, no. A28779 (Caze *et al.* 2010, figs. 15A, B and D).

E) *Seraphs hernandoensis* (Mansfield, 1937), the United States National Museum, no. 495948 (Jung 1974, pl. 9, figs. 7 to 9).

F) *Seraphs kaindraperi* new species, the United States National Museum, no. 135098 (Jung 1974, pl. 5, figs. 3 and 4).

G) *Seraphs leukoleptus* Jung, 1974, Museum National d'Histoire Naturelle, Collectionde Paleontologie, Paris, no. A28781 (Caze *et al.* 2010, figs. 11F, H and I).

Plate 1


A


B


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D


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Plate 2: *Seraphs* Montfort, 1810.

A) *Seraphs mayeri* Jung, 1974, Naturhistorisches Museum Basel, no. H16579 (Jung 1974, pl. 8, figs. 16 to 18).

B) *Seraphs minus* (Vincent, 1913) (Jung 1974, pl. 6, figs. 9 and 10).

C) *Seraphs naricus* (Vredenberg, 1925), Central Palaeontology Laboratories, Geological Survey of India, Calcutta, no. 12614 (Jung 1974, pl. 6, figs. 20 to 22).

D) *Seraphs olivaceus* (Cossmann, 1889), Museum National d'Histoire Naturelle, Collectionde Paleontologie, Paris, no. A28577 (Caze *et al.* 2010, figs. 6H andI).

E) *Seraphs peterjungi* Caze, Merle, Pacaud and Saint Martin, 2010, Museum National d'Histoire Naturelle, Collection de Paleontologie, no. A28578 (Caze *et al*. 2010, figs. 15J, K and N).

F) *Seraphs placiferus* (Bayan, 1870), Ecole des Mines de Paris, Laboratoire Paléontologie, no. G2100 (Jung 1974, pl. 7, figs. 5-7).

G) *Seraphs sopitus* (Brander, 1766), British Museum Natural History, no. GG21010 (Jung 1974, pl. 1, figs. 1 to 3).

Plate 2

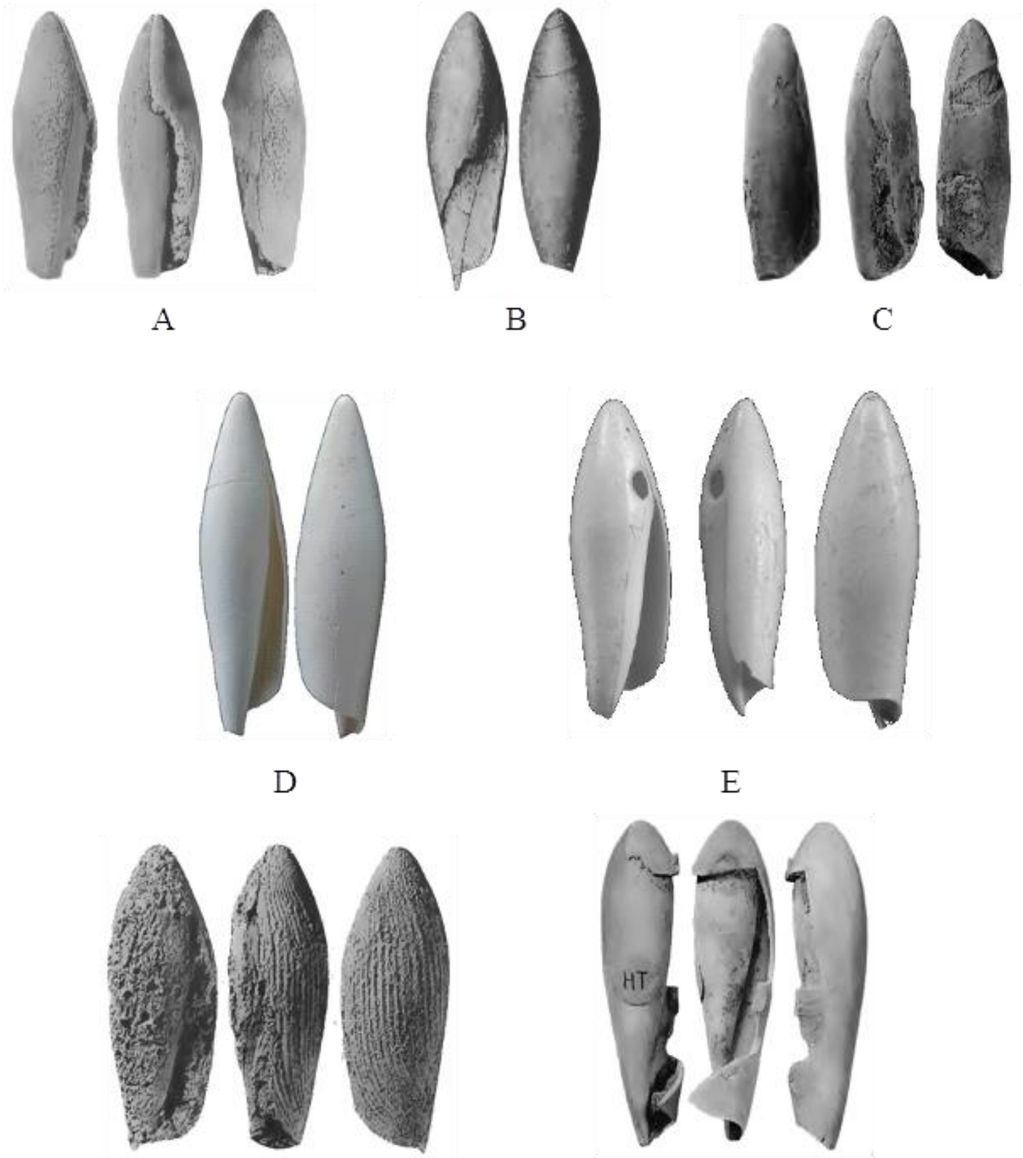

Plate 3: *Seraphs* Montfort 1810.

A) *Seraphs* s*quamosus* (Martin, 1914), Rijksmuseum van Geologie en Mineralogie, Leiden, no. St10344 (Jung 1974, pl. 6, figs. 17 to 19).

B) *Seraphs striatus* (von Koenen, 1889) (von Koenen 1889, pl. I, figs. 7A toC).

C) *Seraphs subconvolutus* (d'Orbigny, 1852), Université Bordeaux 1, Talence, no. UBT65-2-120 (Caze *et al.* 2010, figs. 14A and B).

D) *Seraphs volutatus* (Brander, 1766), Museum National d'Histoire Naturelle, Collectionde Paleontologie, Paris, no. A28776 (Caze *et al.* 2010, figs. 6A toC).

Plate 3

A

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Plate 4: *Dimeza* Deshayes, 1865, *Miniseraphs* Jung, 1974 and *Mauryna* de Gregorio, 1880.

A) *Diameza fragilis* (Defrance, 1825), Museum National d'Histoire Naturelle, Collection de Paleontologie, Paris, no. A28784 (Caze *et al.* 2010, figs. 20A, C and E).

B) *Miniseraphs eratoides* (Cossmann, 1889), Museum National d'Histoire Naturelle, Collection de Paleontologie, Paris, no. A28785 (Caze *et al.* 2010, figs. 20F to H).

C) *Miniseraphs isabella* (Deshayes, 1865), Museum National d'Histoire Naturelle, Collection de Paleontologie, Paris, no. A28783 (Caze *et al.* 2010, figs. 20M to O).

D) *Mauryna plicatum* (d'Archiac and Haime, 1853), Naturhistorisches Museum Basel, no. H15324.

Plate 4

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B

C

D

Plate 5: *Paraseraphs* Jung, 1974.

A) *Paraseraphs ameri* (Abbass, 1967), Egyptian Museum Cairo, Gastropod Section, no. G363 (Abbass 1967, p. 61, pl. VIII, fig. 6).

B) *Paraseraphs armoricensis* (Cossmann, 1897), Dumas Collection (Jung 1974, pl. 10, figs. 16 to 18).

C) *Paraseraphs cantamessae* Maxwell, Rymer and Congdon, 2018, the United States National Museum, no. 135097A (Maxwell *et al*. 2018, fig. 1).

D) *Paraseraphs californicum* (Vokes, 1939) (= *erraticus* Jung 1974), University of California Museum of Palaeontology, no. 15820 (Jung 1974, pl. 12, figs. 8 to 10).

E) *Paraseraphs placitus* Jung, 1974, Naturhistorisches Museum Basel, no. H14491 (Jung 1974, pl. 10, figs. 16 to 18).

Plate 5

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Plate 6: *Paraseraphs* Jung 1974.

A) *Paraseraphs praecedens* Caze, Merle, Pacaud and Saint Martin, 2010, Museum National d'Histoire Naturelle, Collection de Paleontologie, Paris, no. A05707 (Caze *et al.* 2010, figs. 29E and F).

B) *Paraseraphs procerus* (Merian, 1844), Naturhistorisches Museum Basel, no. H14374 (Jung 1974, pl. 12, figs. 1 and 2).

C) *Paraseraphs propedistortus* (de Gregorio, 1880), Naturhistorisches Museum Basel, no. H14509 (Jung 1974, pl. 11, figs. 12 to 13).

D) *Paraseraphs tetanus* Jung, 1974, Naturhistorisches Museum Basel, no. H15409 (Jung 1974, pl. 10, figs. 5 to 7).

E) *Paraseraphs texanopsis* Garvie, 2013, Texas Natural Science Centre, no. NPL46617 (Garvie 2013, pl. 1, figs. 10 and 11).

Plate 6

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Plate 7: *Pseudoterebellum* new genus and *Terebellum* Röding, 1798.

A) *Pseudoterebellum diversionatum* (Eames, 1952), British Museum of Natural History, no. GG68239 (Jung 1974, pl. 14, figs. 12 to 14).

B) *Pseudoterebellum oympiae* (Rolando, 2001), Geology and Paleontology Museum of Padova University, no. MGPD28168 (Rolando 2001, fig. 2).

C) *Pseudoterebellum saudiensis* (Abbass, 1972), Faculty of Science, Ain Shams University, no. S53 (Abbass 1972, pl. V, figs. 1 and 2).

D) *Terebellum cinctum* Martin, 1916, holotype from the collection of Rijksmuseum van Geology en Mineralogie, no. St10337 (Jung 1974, pl. 13, figs. 4 and 6).

E) *Terebellum obtusum* Sowerby, 1840, holotype from the collection of British Museum of Natural History, no. GG21000 (Jung 1974, pl. 13, figs. 17 and 18).

F) *Terebellum papilliferum* Martin, 1916, lectotype from the collection of Rijksmuseum van Geology en Mineralogie, no. St10339 (Jung 1974, pl. 13, figs. 9 and 11).

Plate 7

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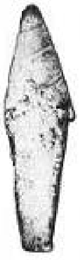
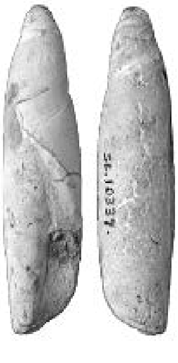
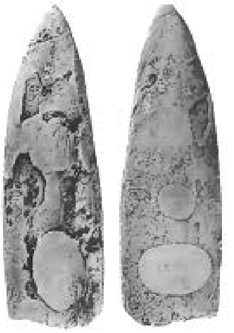


C



D



E

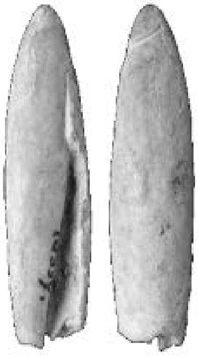


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Plate 8: *Terebellum* Röding, 1798

A) *Terebellum terebellum* (Linné, 1758), Nha Trang, Vietnam (Image V. Liverani).

B) *Terebellum delicatum* Kuroda and Kawamoto in Kawamoto and Tanabe, 1956, Nha Trang, Vietnam (Image V. Liverani).

C) *Terebellum hubrechti* Poppe and Tagaro, 2016, Caubian Deep, Bohol, Philippine (image Conchology Inc.).

D) *Terebellum simoni* Dekkers, Maxwell and Congdon, 2019, Bohol Island, Philippines (online dealer offering 2018).

Plate 8

Systematic Index