

# A classification of the phylum Sipuncula

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## Synopsis

A classification of the phylum Sipuncula is adopted following the analysis of Cutler & Gibbs (1985) and comprises two classes, four orders and six families. This replaces the earlier classification of Stephen & Edmonds (1972) which was based on four families only. The diagnostic characters are reviewed. Seventeen genera are redefined, one new subgenus is described and twelve other subgenera are recognised.

## Introduction

The classification of the phylum Sipuncula has had a confused history. Early attempts to define higher taxa by grouping genera were, to a large extent, thwarted by incomplete, imprecise or erroneous descriptions of many species. Stephen & Edmonds (1972) classified the phylum into four families in providing the first compilation of species described prior to about 1970. However, this monograph is essentially literature-based and consequently many errors are repeated; nevertheless, it provides a useful base-line to the present revision.

The need for greater precision in defining genera has led the authors to re-examine most of the available type specimens. The definitions of genera presented below incorporate both novel observations and corrections to earlier descriptions. Where possible, nine basic characters have been checked for each species before assigning it to a genus. These characters are summarised for each genus in Table 1. A phylogenetic interpretation of the classification used here will be found in Cutler & Gibbs (1985).

## Diagnostic features of higher taxa

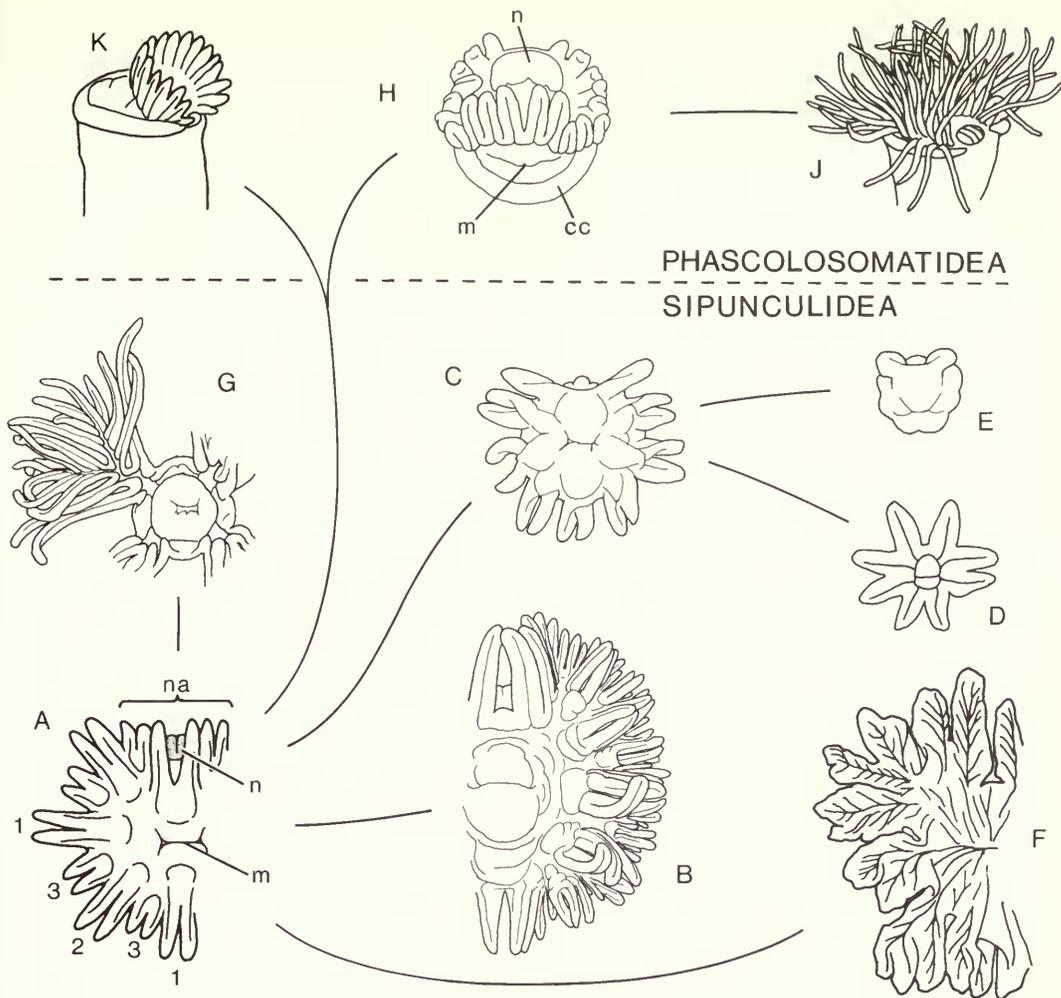
In reviewing the diagnostic characters of the phylum, particular attention has been paid to the structure of the oral disk since the arrangement of the tentacles provides a useful basis for dividing the phylum into two classes—Sipunculidea and Phascolosomatidea. Certain descriptions of tentacle arrangements are misleading or in error (see for example Stephen & Edmonds (1972) p. 16 and Table 3). No doubt these errors result from the fact that some species are not amenable to fixation in the extended state; species with long introverts are notoriously difficult to preserve with their introvert fully extended. Although dissection of the introvert is possible the details of the tentacular arrangement on a withdrawn disk are often difficult to interpret and have yet to be satisfactorily determined in some small-sized species (e.g. *Apionsoma trichocephala* Sluiter). The following summarises the distinctions of the two classes.

The sipunculan tentacular crown exhibits many diverse forms but, basically, two tentacular patterns can be recognised. In one, that of the proposed class Sipunculidea, the tentacles are arranged peripherally on the oral disk so as to encircle the centrally-placed mouth; dorsally this circle is inflexed to form an arc enclosing the nuchal organ, a feature well developed in *Thysanocardia* spp for example (see Gibbs, Cutler & Cutler, 1983, Fig. 2). In the other, that of the proposed class Phascolosomatidea, the tentacles are restricted to a dorsal arc enclosing the nuchal organ and

Table 1. Summary of characters in sipunculian genera

	Presence of anal shield	Type of tentacle arrangement	Type of introvert hook when present	Presence of banding in longitudinal muscle layer	Presence of canals or sacs in body wall	Number of retractor muscles apparent	Spindle muscle attached posteriorly	Number of nephridia	Presence of villi on contractile vessel	Number of species
<i>Sipunculus</i>	-	S	-	+ <sup>1</sup>	+	4	-	2	-	10
<i>Xenosiphon</i>	-	S	-	+ <sup>1</sup>	+	4	-	2	-	1
<i>Siphonosoma</i>	-	S	S	+ <sup>1</sup>	+	4	+	2	+/- <sup>7</sup>	10
<i>Siphonomecus</i>	-	S	S	+ <sup>1</sup>	+	2	+	2	-	1
<i>Phasclopsis</i>	-	S	-	+	-	4	-	2	-	1
<i>Golfingia</i>	-	S	S	-	-	4	-	2	-	12
<i>Nephasoma</i>	-	S	S	-	-	2	-	2	-	23
<i>Thysanocardia</i>	-	S	-	-	-	2	-	2	-	3
<i>Phascolion</i>	-	S	S	-	-	4 <sup>3</sup>	- <sup>5</sup>	1	+	25
<i>Onchnesoma</i>	-	S	S	-	-	2 <sup>4</sup>	- <sup>5</sup>	1	-	4
<i>Themiste</i>	-	(S)	S	-	-	2	-	2	+	25
<i>Aptinosoma</i>	-	P	P	-	-	4	+	2	+	6
<i>Phascolosoma</i>	-	P	P	+	-	4	+ <sup>6</sup>	2	-	36
<i>Antillesoma</i>	-	P	-	+	-	4	+	2	+	1
<i>Aspidosiphon</i>	+	P	P	-/+ <sup>2</sup>	-	2	+	2	-	45
<i>Cloeosiphon</i>	+	P	P	-	-	2	+	2	-	1
<i>Lithacrosiphon</i>	+	P	P	+	-	2	+	2	-	2

<sup>1</sup>Circular muscle layer also banded. <sup>2</sup>Present in *A. (Paraspidosiphon)*. <sup>3</sup>Often strongly fused so that number appears to be fewer (3, 2 or 1). <sup>4</sup>Column is entire but thought to be composed of two fused muscles. <sup>5</sup>Spindle muscle absent. <sup>6</sup>Unattached posteriorly in *P. pectinatum*. <sup>7</sup>Absent in some species. <sup>8</sup>Present in *P. cirratum*.



**Fig. 1.** The structure of the tentacular crown of Sipuncula: some examples illustrating the form and variation within the classes Sipunculidea and Phascolosomatidea. Solid lines indicate possible evolutionary trends. A. Generalised Sipunculidea crown such as might have been possessed by ancestral stock adults; B. *Golfingia margaritacea*; C. *Nephasoma rimicola*; D. *Onchnesoma squamatum*; E. *Nephasoma minutum*; F. *Sipunculus norvegicus*; G. *Themiste lageniformis*; H. *Phascolosoma granulatum*; J. *Antillesoma antillarum*; K. *Aspidosiphon johnstoni*. (B, E, F: after Théel, 1905.) Abbreviations: cc, cephalic collar; m, mouth; n, nuchal organ; na, dorsal arc of tentacles enclosing nuchal organ; 1,2,3, primary, secondary and tertiary tentacle pairs around disk periphery. (Modified from Cutler & Gibbs, 1985.)

there are no peripheral tentacles (Fig. 1). Thus, the two patterns have a common, perhaps homologous, feature in the dorsal arc of tentacles. In evolutionary terms, the peripheral tentacles could be interpreted as a later addition, i.e. the Sipunculidea have evolved from a Phascolosomatidea stock. However, around the margin of the oral disk in Phascolosomatidea there is a prominent ridge, the cephalic collar, and it is thought that this ridge represents a vestige of the peripheral system. If this interpretation is correct the common ancestor must have possessed a Sipunculidea-type of tentacular crown, probably a simple form, somewhat similar to that of *Thysanocardia provera* (Gibbs, Cutler & Cutler, 1983, Fig. 2B), and the peripheral tentacles were lost during an early divergence to give the Phascolosomatidea line. The Sipunculidea tentacular pattern, peripheral

circle plus nuchal arc, can perhaps be best regarded as an elaboration of simple prostomial tentacles possessed by the early protostomial stock.

The development of the tentacular crown in the Sipunculidea, as seen for example in *Golfingia* species, commences with the formation of four primary pairs of tentacles in the dorsal, ventral and lateral positions, between which secondary pairs subsequently develop to form a single ring encircling the central mouth on the oral disk (Fig. 1A). Between these pairs tertiary pairs usually develop: in the adult these may be few or very numerous; in the latter case the tentacles are accommodated in loops or 'festoons' that extend aborally on to the anterior introvert. The nuchal organ situated dorsally between the two primary tentacles thus becomes enclosed by an arc of tentacles. As a general rule, the number of tentacles increases with increasing size and age of individuals and large-sized species have more tentacles than small-sized species.

Within the class Sipunculidea a wide range of tentacular development is found. The most highly evolved crown is found in the genus *Thysanocardia*, adult specimens of which often possess well-developed festoons comprising several hundred tentacles; in some *Thysanocardia nigra* (Ikeda) the number exceeds 500 (see Gibbs, Cutler & Cutler, 1983). Large *Golfingia margaritacea* (Sars) have 100 or more tentacles (Fig. 1B) but most other Sipunculidea have around 50 or fewer with only a limited number of tertiary tentacles developing, as in *Golfingia elongata* (Keferstein) with 20–34 and *Nephasoma rimicola* (Gibbs) with 12–20 (Fig. 1C; see Gibbs, 1973). In some species only the primary tentacles appear, as in *Onchnesoma squamatum* (Kor. & Dan.) with 8 and *Nephasoma minutum* (Keferstein) with just two (Fig. 1D, E). Thus the evolution of the tentacular crown could have been not only towards greater complexity but also towards simplification, a trend, possibly neotenous, seen in several genera, notably *Nephasoma* (e.g. *N. minutum*), *Onchnesoma* (e.g. *O. steenstrupi* Kor. & Dan.) and *Phascolion* (e.g. *P. pacificum* Murina). Another variation is seen in some members of the family Sipunculidae where the peripheral tentacles have become flattened and fused to form a continuous veil-like structure, as for example in *Sipunculus norvegicus* Dan. (Fig. 1F). The crown of *Themiste* with its tentacles arising from 4–8 stems appears anomalous at first sight but, in fact, this type represents yet another modification of the basic Sipunculidea pattern. In themistids the secondary tentacles develop between the primary pairs but are borne on outgrowths of the oral disk so that with subsequent tertiary tentacle development, an erect dendritic structure results rather than the typical festoon which is contiguous with the introvert wall. In the themistid type the dorsal primary tentacles are widely spaced and do not enclose the nuchal organ (Fig. 1G).

All six genera grouped in the class Phascolosomatidea are rather similar in terms of the tentacular arrangement: with one exception, all have a single arc of up to 30 tentacles enclosing the nuchal organ (Fig. 1H, K). The exception is *Antillesoma antillarum* (Grube & Oersted) in which the tentacles are fairly numerous (Fig. 1J) presumably as a result of secondary proliferation.

One other character that separates the Sipunculidea and Phascolosomatidea is the structure of the introvert hooks on the anterior introvert, when present. In the former group these hooks are somewhat variable but generally are simple, sharply-pointed protrusions of the epidermis and scattered in their distribution; however, in the latter they have a typical recurved shape, usually an internal structure is apparent and they are closely-packed in distinct rings encircling the anterior introvert.

Definitions of orders, families and genera are given below. Four orders are recognised. In the class Sipunculidea, members of the order Sipunculiformes are distinguished by the presence of banding in the longitudinal muscle of the body wall found in five genera, all of which are placed in the family Sipunculidae. The remaining six genera within this class all have a uniform, continuous layer of longitudinal muscle tissue and form the order Golfingiiformes comprising three families — Golfingiidae, Phascolionidae and Themistidae. In the class Phascolosomatidea the genera are separated into two orders, each with a single family, on the basis of the presence (Aspidosiphoniformes: Aspidosiphonidae) or absence (Phascolosomatiformes: Phascolosomatidae) of an anal shield, a hardened thickening of the anterior trunk region. It should be noted that the structure of the anal shield is different in all three genera within the Aspidosiphonidae and it is recognised that this character may have evolved several times.

Whilst the forms of the tentacle crown and of the introvert hooks are useful characters for

dividing the 17 genera into two natural groups, here designated as classes, few other major characters are confined to one or other of these two classes (Table 1): coelomic spaces in the body wall is a feature exclusive to Sipunculidae and likewise for anal shield development in Aspidosiphonidae. Other characters are found in both classes, notably the banding of the longitudinal muscle layer in the body wall, the attachment of the spindle muscle to the posterior trunk and an increase in the volume of the contractile vessel through the development of villi in conjunction with increased tentacular volume or area. Such characters would appear to be polyphyletic in origin. There is little doubt that the basic number of introvert retractor muscles is four, arranged as dorsal and ventral pairs. Loss of the dorsal pair appears to have occurred independently in a number of generic lines. Assessing the number of retractors in any one specimen can often be problematical because fusion frequently occurs but may not be evident. In some species only one retractor is apparent in the adult form: in *Phascolion* species there is good evidence to suggest the one muscle is the result of the fusion of all four muscles (Gibbs, 1985) whilst in *Onchnesoma* the single muscle is thought to comprise only the fused ventral pair, the dorsal pair having been lost. Use of the number of retractors as a taxonomic character has to be approached with some caution since even within a single population the number is liable to variation, as noted for *Golfingia elongata* (Gibbs, 1973). Morphological variation seems to be one of the hallmarks of the phylum, a feature that may account for the survival of this small group but one that does not facilitate good taxonomy.

The present scheme of classification (Table 2) updates that given in Stephen & Edmonds (1972) and some later authors by incorporating the recent revisions of several major genera, notably, *Siphonosoma*, *Golfingia* and *Phascolosoma*. Synonymies are as given in Stephen & Edmonds (1972): any more recent changes are noted under each genus.

### Key to Families

- |   |  |   |
|---|--|---|
| 1 | Tentacles arranged in an arc encircling dorsal nuchal organ; peripheral tentacles absent; hooks complex, in distinct rings [Class <i>PHASCOLOSOMATIDEA</i> ]   | 2 |
|   | Tentacles arranged peripherally on oral disk so as to encircle central mouth; may be borne on stem-like outgrowths of oral disk or reduced in number to a single dorsal pair; hooks simple, usually scattered [Class <i>SIPUNCULIDEA</i> ] | 3 |
| 2 | Anal shield present . . . . . Fam. <i>ASPIDOSIPHONIDAE</i> (p. 55)   |   |
|   | Anal shield absent . . . . . Fam. <i>PHASCOLOSOMATIDAE</i> (p. 54)   |   |
| 3 | Longitudinal muscles of body wall gathered into separate or anastomosing bands . . . . . Fam. <i>SIPUNCULIDAE</i> (p. 48)  |   |
|   | Longitudinal muscle of body wall in a uniform continuous layer . . . . .   | 4 |
| 4 | Tentacles carried on 4–8 stem-like outgrowths of oral disk . . . . . Fam. <i>THEMISTIDAE</i> (p. 53)   |   |
|   | Tentacles not carried on disk outgrowths . . . . .   | 5 |
| 5 | A single nephridium present . . . . . Fam. <i>PHASCOLIONIDAE</i> (p. 51)   |   |
|   | Two nephridia present . . . . . Fam. <i>GOLFINGIIDAE</i> (p. 50)   |   |

### Classification

Phylum *SIPUNCULA*  
Class *SIPUNCULIDEA*

Sipuncula with tentacles encircling a central mouth on the oral disk. Introvert hooks (when present) simple, thorn-like hollow structures that are usually irregularly distributed. Spindle muscle unattached posteriorly (except in *Siphonosoma* and *Siphonomecus*).

### Order *SIPUNCULIFORMES*

Sipunculidea with longitudinal muscle in body wall gathered into bands (likewise for circular muscle in two genera—*Sipunculus* and *Xenosiphon*). Coelomic extensions – canals or sacs – in body wall (except in *Phascolopsis*).

**Table 2.** Classification of the phylum Sipuncula**Cl. Sipunculidea**

## Ord. SIPUNCULIFORMES

Fam. SIPUNCULIDAE Stephen &amp; Edmonds, 1972

*Sipunculus* Linnaeus, 1766*S. (Sipunculus)**S. (Austrosiphon)* Fisher, 1954*Xenosiphon* Fisher, 1947*Siphonosoma* Spengel, 1912*Siphonomecus* Fisher, 1947*Phascolopsis* Fisher, 1950

## Ord. GOLFINGIIFORMES

Fam. GOLFINGIIDAE Stephen &amp; Edmonds, 1972

*Golfingia* Lankester, 1885*Nephasoma* Pergament, 1946*Thysanocardia* Fisher, 1950

Fam. PHASCOLIONIDAE Cutler &amp; Gibbs, 1985

*Phascolion* Théel, 1875*P. (Phascolion)**P. (Isomya)* Cutler & Cutler, 1985*P. (Montuga)* Gibbs, 1985*P. (Lesenka)* Gibbs, 1985*P. (Villiophora)* Cutler & Cutler, 1985*Onchnesoma* Koren & Danielssen, 1875

Fam. THEMISTIDAE Cutler &amp; Gibbs, 1985

*Themiste* Gray, 1828*T. (Themiste)**T. (Lagenopsis)* Edmonds, 1980**Cl. Phascolosomatidea**

## Ord. PHASCOLOSOMATIFORMES

Fam. PHASCOLOSOMATIDAE Stephen &amp; Edmonds, 1972

*Phascolosoma* Leuckart, 1828*P. (Phascolosoma)**P. (Edmondsius)* subgen. nov.*Apionsoma* Sluiter, 1902*Antillesoma* Stephen & Edmonds, 1972

## Ord. ASPIDOSIPHONIFORMES

Fam. ASPIDOSIPHONIDAE Baird, 1868

*Aspidosiphon* Diesing, 1851*A. (Aspidosiphon)**A. (Paraspidosiphon)* Stephen, 1964*Cloeosiphon* Grube, 1868*Lithacrosiphon* Shipley, 1902Family **SIPUNCULIDAE** Baird, 1868

Characters are those of the order.

**Key to Genera**

- |   |   |                     |   |
|---|---|---------------------|---|
| 1 | Body wall circular muscle layer continuous . . . . .  | <b>PHASCOLOPSIS</b> | 2 |
|   | Body wall circular muscle layer gathered into bands . . . . .   |                     |   |
| 2 | Body wall circular and longitudinal muscle bands anastomosing, spindle muscle attached to posterior end of trunk . . . . .  |                     | 3 |
|   | Body wall circular and longitudinal muscle bands not anastomosing, spindle muscle not attached to posterior trunk . . . . . |                     | 4 |
| 3 | Four introvert retractor muscles . . . . .  | <b>SIPHONOSOMA</b>  |   |
|   | Two introvert retractor muscles . . . . .   | <b>SIPHONOMECUS</b> |   |

- 4 Gut with post-oesophageal loop; coelom extends into body wall as longitudinal canals running throughout most of trunk length . . . . . *SIPUNCULUS*  
 Gut without post-oesophageal loop; coelom extends into body wall as short diagonal canals running across the width of one circular muscle band . . . . . *XENOSIPHON*

Genus *SIPUNCULUS* Linnaeus, 1766

DIAGNOSIS. Introvert much shorter than trunk, without hooks, covered with scattered subtriangular papillae. Trunk cylindrical. Body wall contains coelomic extensions in the form of parallel longitudinal canals which extend most of trunk length. Circular and longitudinal muscle layers gathered into distinct bands. Oral disk carries tentacles arranged around the mouth sometimes modified with the development of an inter-tentacular membrane (*S. nudus* L., *S. norvegicus* Danielssen). Four introvert retractor muscles. Two protractor muscles may be developed (*S. mundanus* Sel. & Bülow). Two contractile vessels, both without villi. Gut with post-oesophageal loop, caecum on rectum, and coil attached to body wall along its entire length by many connective strands. Spindle muscle not attached posteriorly. Two nephridia. Species usually large-sized (trunk greater than 5 cm long in adults).

TYPE SPECIES. *Sipunculus nudus* Linnaeus, 1766, subsequent designation, ?Fisher 1952.

Subgenus *SIPUNCULUS* Linnaeus, 1766

*Sipunculus* (*Sipunculus*): Cutler & Cutler, 1985a: 232.

DIAGNOSIS. Nephridia anterior to anus. Spindle muscle originates on body wall anterior to anus.

TYPE SPECIES. *Sipunculus nudus* Linnaeus, 1766, subsequent designation, ?Fisher, 1952.

Subgenus *AUSTROSIPHON* Fisher, 1954, emended

*Xenosiphon* (*Austrosiphon*) Fisher, 1954: 314.

*Xenosiphon* (*Xenopsis*) Johnson, 1969: 44.

*Sipunculus* (*Contraporus*) Cutler & Cutler, 1985a: 241.

DIAGNOSIS. Nephridia posterior to anus. Spindle muscle originates from ventral surface of rectum.

TYPE SPECIES. *Sipunculus mundanus* Selenka & Bülow, 1883, monotypy.

Genus *XENOSIPHON* Fisher, 1947

DIAGNOSIS. Introvert much shorter than trunk, and without hooks but covered with scattered subtriangular papillae. Body wall contains coelomic extensions in form of short, diagonal canals limited in length to width of one circular muscle band. Circular and longitudinal muscle layers divided into distinct bands. Oral disk carries tentacles arranged around mouth. Four introvert retractor muscles and two thin protractor muscles present. Contractile vessel without villi, gut without post-oesophageal loop, caecum present on rectum and coil attached to body wall along entire length by connective strands. Spindle muscle originates on ventral wall of rectum and is not attached to the body wall posteriorly. Anus anterior to nephridiopores. Two nephridia. Contains one large-sized species.

TYPE SPECIES. *Sipunculus mundanus* var. *branchiatus* Fischer, 1895, original designation.

REMARKS. The two subgenera previously included in this genus are now assigned to *Sipunculus* (see above).

Genus *SIPHONOSOMA* Spengel, 1912

*Siphonosoma* (*Siphonosoma*): Fisher, 1950b: 805.

*Siphonosoma* (*Hesperosiphon*) Fisher, 1950b: 805.

*Siphonosoma* (*Dasmosiphon*) Fisher, 1950b: 805.

DIAGNOSIS. Introvert much shorter than the trunk with prominent conical papillae (sometimes also hooks) arranged in rings. Body wall with coelomic sac-like extensions; circular and longitudinal

muscle layers gathered into anastomosing bands. Oral disk carries tentacles arranged around the mouth. Four introvert retractor muscles. Contractile vessel with or without villi. Spindle muscle attached posteriorly. Two nephridia. Species usually large-sized (trunk greater than 5 cm long in adults).

TYPE SPECIES. *Phascolosoma australe* Keferstein, 1865, subsequent designation, Gerould, 1913.

REMARKS. The three subgenera recognised by Fisher (1950b) were distinguished by the presence or absence of transverse dissepiments and rectal caeca. These characters have been found to be subject to great variation and of limited diagnostic value: consequently, this subgeneric separation is not supportable (Cutler & Cutler, 1982).

### Genus *SIPHONOMECUS* Fisher, 1947

DIAGNOSIS. Introvert much shorter than trunk with prominent hooks and conical papillae arranged in rings. Body wall with coelomic extensions (sacs); circular and longitudinal muscle layers gathered into anastomosing bands. Oral disk carries tentacles arranged around the mouth. Two introvert retractor muscles. Contractile vessel without villi. Spindle muscle attached posteriorly. Two nephridia. Contains one large-sized species.

TYPE SPECIES. *Siphonomecus multicinctus* Fisher, 1947, original designation.

### Genus *PHASCOLOPSIS* Fisher, 1950

DIAGNOSIS. Introvert shorter than trunk with deciduous hooks (present in juvenile but lost in adult). Body wall without coelomic extensions. Circular muscle layer continuous, longitudinal muscle layer gathered into anastomosing bands. Oral disk carries tentacles arranged around the mouth. Four introvert retractor muscles. Contractile vessel without villi. Spindle muscle not attached posteriorly. Two nephridia. Contains one large-sized species.

TYPE SPECIES. *Sipunculus gouldii* Portalès, 1851, monotypy.

## Order GOLFINGIIFORMES

Sipunculidea with body wall longitudinal muscle in a continuous layer, not gathered in bands.

### Family GOLFINGIIDAE Stephen & Edmonds, 1972

Golfingiiformes with two nephridia. Tentacles not borne on stem-like extensions of oral disk.

#### Key to Genera

1	Contractile vessel with numerous villi . . . . .	<i>THYSANOCARDIA</i>	
	Contractile vessel without villi . . . . .		2
2	Four introvert retractor muscles . . . . .	<i>GOLFINGIA</i>	
	Two introvert retractor muscles . . . . .	<i>NEPHASOMA</i>	

### Genus *GOLFINGIA* Lankester, 1885

*Golfingia* (*Golfingia*): Fisher, 1950a; 549.

*Golfingia* (*Dushana*) Murina, 1975: 1085.

*Themiste* (*Stephensonum*) Edmonds, 1980: 33.

*Centrosiphon* Shipley, 1903: 173.

DIAGNOSIS. Introvert about equal to or shorter than trunk; hooks when present are usually scattered (arranged in rings in *G. elongata*). Body wall with continuous muscle layers. Oral disk carries tentacles arranged around the mouth. Four introvert retractor muscles. Contractile vessel without villi. Spindle muscle not attached posteriorly. Two nephridia. Species small- to large-sized.

TYPE SPECIES. *Golfingia macintoshii* Lankester, 1885 [= *Sipunculus vulgaris* de Blainville, 1827: Stephen, 1934], monotypy.

REMARKS. This genus now contains only those species previously assigned to the nominate subgenus *Golfingia* (*Golfingia*). It includes *Centrosiphon* Shipley, 1903: Edmonds (1980) placed the type species *C. herdmani* Shipley within the genus *Golfingia*; the *Centrosiphon* specimens recorded by Cutler & Cutler (1979) are now considered to be aberrant *Aspidosiphon*.

The subgenus *G. (Dushana)* Murina, 1975, was characterised by complete or partial fusion of the dorsal and ventral retractor muscles on one side of the body. However, it is known that such fusion of the retractors, and also reduction of the retractor number through loss of one or both dorsal retractors, are features of some *Golfingia* species, for example *G. elongata* (see Gibbs, 1973). The holotype of *G. (Dushana) adriatica* Murina shows a similar retractor arrangement (Murina, 1975, Fig. 1) to that described by Watier (1932) for aberrant *G. vulgaris*. The type species originally designated for *G. (Dushana)*, *G. scutigera* (Roule), does not differ significantly in its retractor arrangement (Roule, 1906, Fig. 95) from typical *Golfingia* species. Thus *G. (Dushana)* is no longer recognised.

#### Genus *NEPHASOMA* Pergament, 1946

*Golfingia (Phascoloides)* Fisher, 1950a: 550.

DIAGNOSIS. Introvert about equal to, or shorter than, trunk. Hooks when present usually scattered (arranged in rings in *N. rimicola* (Gibbs), in spirals in *N. abyssorum* (Kor. & Dan.)). Body wall with continuous muscle layers. Oral disk carries tentacles arranged around the mouth but tentacles may be reduced in both size and number and restricted to dorsal region. Two introvert retractor muscles often partially fused. Contractile vessel without villi. Spindle muscle not attached posteriorly. Two nephridia. Species generally small- to medium-sized (trunk less than 5 cm in length).

TYPE SPECIES. *Nephasoma marinki* Pergament, 1946 [= *Onchnesoma glaciale* Danielssen & Koren: Cutler & Murina, 1977; = *Phascolosoma lilljeborgii* Danielssen & Koren: Gibbs, 1982], monotypy.

REMARKS. This genus now contains all those species previously assigned to the *Golfingia* subgenus *Phascoloides* Fisher, 1950, since *Nephasoma* Pergament has been shown to have priority over *Phascoloides* (Cutler & Murina, 1977).

#### Genus *THYSANOCARDIA* Fisher, 1950

DIAGNOSIS. Introvert longer than trunk, without hooks. Body wall with continuous muscle layers. Oral disk carries tentacles arranged around the mouth; those enclosing nuchal organ are well developed. Two introvert retractor muscles. Contractile vessel with distinct villi. Spindle muscle not attached posteriorly. Two nephridia. Species small- to medium-sized (adults generally under 5 cm in trunk length).

TYPE SPECIES. *Phascolosoma procerum* Möbius, 1875, original designation.

REMARKS. The subgenus *Golfingia (Thysanocardia)* was recently elevated to generic rank and the number of species reduced to three by Gibbs, Cutler & Cutler (1983).

#### Family PHASCOLIONIDAE Cutler & Gibbs, 1985

Golfingiiformes with one nephridium (usually the right). Tentacles not borne on stem-like extensions of oral disk. Gut coil without well-defined axial spindle muscle.

#### Key to Genera

- 1 Anus usually situated on anterior trunk; epidermal 'holdfast' or 'attachment' papillae often present. Retractor muscles highly fused but usually 2-4 roots apparent at base of column . . . . . **PHASCOLION**
- Anus situated on distal half of introvert; epidermal 'attachment' papillae absent. Retractor muscle(s) appear as single column without separate roots . . . . . **ONCHNESOMA**

Genus *PHASCOLION* Théel, 1875

**DIAGNOSIS.** Introvert length one-half to four times that of trunk length, with or without hooks. Trunk usually with modified 'holdfast' papillae. Body wall with continuous muscle layers. Oral disk carries tentacles arranged around the mouth. Introvert retractor muscle system modified by fusion of dorsal and ventral pairs: relative size and degree of fusion defines subgenera (see below). Contractile vessel without villi (but present in *P. cirratum*). Gut coiling generally loose and without axial spindle muscle. One nephridium (usually right). Species small- to medium-sized (less than 5 cm in length) generally inhabiting mollusc shells.

**TYPE SPECIES.** *Sipunculus strombus* Montagu, 1804, monotypy.

Subgenus *PHASCOLION* Théel, 1875

*Phascolion (Phascolion)*: Gibbs, 1985: 314.

**DIAGNOSIS.** Retractor column divided for most of its length: oesophagus detaches from retractor column at a point posterior to the first separation of the retractor muscles. Dorsal retractor(s) much more strongly developed than ventral retractor(s). Contractile vessel without villi.

**TYPE SPECIES.** *Sipunculus strombus* Montagu, 1804, monotypy.

Subgenus *ISOMYA* Cutler & Cutler, 1985

*Phascolion (Isomya)* Cutler & Cutler 1985b: 820

**DIAGNOSIS.** Characters as for *P. (Phascolion)* except that dorsal and ventral retractor muscles are about equal in diameter.

**TYPE SPECIES.** *Phascolion tuberculosum* Théel, 1875, original designation.

Subgenus *MONTUGA* Gibbs, 1985

*Phascolion (Montuga)* Gibbs, 1985: 315.

**DIAGNOSIS.** Retractor column divided only at posterior end: oesophagus detaches from retractor column at a point anterior to the first separation of the retractor muscles. Contractile vessel without villi.

**TYPE SPECIES.** *Phascolion lutense* Selenka, 1885, original designation.

Subgenus *LESENKA* Gibbs, 1985

*Phascolion (Lesenka)* Gibbs, 1985: 315.

**DIAGNOSIS.** Retractor column entire with retractor muscles fused throughout whole length. Contractile vessel without villi.

**TYPE SPECIES.** *Phascolion cryptum* Hendrix, 1975, original designation.

Subgenus *VILLIOPHORA* Cutler & Cutler, 1985

*Phascolion (Villiophora)* Cutler & Cutler, 1985b: 821.

**DIAGNOSIS.** Retractor column entire with retractor muscles fused throughout whole length. Contractile vessel with numerous villi.

**TYPE SPECIES.** *Phascolion cirratum* Murina, 1968, monotypy.

Genus *ONCHNESOMA* Koren & Danielssen, 1875

**DIAGNOSIS.** Introvert much longer than trunk. Body wall with continuous muscle layers. Oral disk carries tentacles arranged around mouth but tentacles may be highly reduced in size. Introvert retractor muscle system modified by fusion to form single retractor muscle. Anus situated on

introvert. Contractile vessel rarely apparent and without villi. Spindle muscle absent. One nephridium (right). Species small-sized (trunk less than 1 cm in length).

TYPE SPECIES. *Onchnesoma steenstrupii* Koren & Danielssen, 1875, subsequent designation, Stephen & Edmonds, 1972.

#### Family THEMISTIDAE Cutler & Gibbs, 1985

Golfingiiformes with two nephridia. Tentacles borne on stem-like extensions of oral disk.

#### Genus THEMISTE Gray, 1828

DIAGNOSIS. Introvert less than trunk length. Body wall with continuous muscle layers. Oral disk carries tentacles basically surrounding mouth but extending with growth along margins of stem-like outgrowths of the oral disk. With or without hooks. Two introvert retractor muscles. Contractile vessel with villi. Spindle muscle not attached posteriorly. Two nephridia. Species small- to large-sized.

TYPE SPECIES. *Themiste hennahi* Gray, 1824, monotypy.

#### Subgenus THEMISTE Gray, 1828

*Themiste* (*Themiste*): Edmonds, 1980: 33.

DIAGNOSIS. Contractile vessel with long, thread-like villi.

TYPE SPECIES. *Themiste hennahi* Gray, 1828, monotypy.

#### Subgenus LAGENOPSIS Edmonds, 1980

*Themiste* (*Lagenopsis*) Edmonds, 1980: 33.

DIAGNOSIS. Contractile vessel with short, digitiform villi.

TYPE SPECIES. *Themiste lageniformis* Baird, 1868, original designation.

REMARKS. The subgenus *T.* (*Stephensonum*) Edmonds, 1980, was erected to include two species of *Themiste* having four, not two, retractor muscles, namely, *Themiste stephensoni* (the type species, original designation) and *T. pinnifolia*. The type material of *Themiste stephensoni* (Stephen) (described under the name *Dendrostomum* Grube, a junior synonym) in the RSME collections has been examined. The holotype (1958.23.24) has a golfingiid, not themistid, tentacle crown (as shown by dissection of the introvert) and the 'band of very short villi' on the contractile vessel (Stephen, 1942, p. 252) do not appear to be true villi but rather outpouchings of a relatively voluminous vessel. The specimen is clearly a *Golfingia* and probably *G. capensis* (Teuscher); the other type specimens comprise further *Golfingia* but also include some *Themiste* all of which have the typical number of retractors (two). Thus *T.* (*Stephensonum*) becomes a junior synonym of *Golfingia*. The species *Themiste pinnifolia* (Keferstein) is based on a single specimen, collected more than 100 years ago, which cannot be traced. No subsequent record appears in the literature, despite extensive collecting in the area of the type locality (St Thomas, West Indies). Since the generic identity of this specimen is in doubt, the species name *pinnifolia* is regarded as a *nomen dubium*.

#### Class PHASCOLOSOMATIDEA

Sipuncula with tentacles confined to an arc enclosing dorsal nuchal organ: peripheral tentacles absent. Introvert hooks recurved, usually with an internal structure and closely-packed in regularly-spaced rings (absent in *Antillesoma*). Spindle muscle attached posteriorly.

#### Order PHASCOLOSOMATIFORMES

Phascolosomatidea with anterior trunk not modified to form anal shield. Four introvert retractor muscles.

## Family PHASCOLOSOMATIDAE Stephen &amp; Edmonds, 1972

Characters are those of the order.

## Key to Genera

- |   |   |                     |   |
|---|---|---------------------|---|
| 1 | Introvert hooks absent. Contractile vessel with villi . . . . .       | <i>ANTILLESOMA</i>  |   |
|   | Introvert hooks present. Contractile vessel without villi . . . . .   |                     | 2 |
| 2 | Longitudinal muscle in body wall gathered into bands . . . . .        | <i>PHASCOLOSOMA</i> |   |
|   | Longitudinal muscle in body wall a uniform continuous layer . . . . . | <i>APIONSOMA</i>    |   |

Genus *PHASCOLOSOMA* Leuckart, 1828

DIAGNOSIS. Introvert variable in length, often equal to trunk with numerous rings of recurved hooks (absent in *P. meteori* Hérubel). Body wall with longitudinal muscle layer gathered into bands. Oral disk carries relatively few tentacles (less than 30) enclosing nuchal organ. Contractile vessel without true villi (may have bulbous vesicles). Four introvert retractor muscles; lateral pairs sometimes partially, rarely completely, fused. Spindle muscle attached posteriorly (except in *P. pectinatum*). Two nephridia.

TYPE SPECIES. *Phascolosoma granulatum* Leuckart, 1828, monotypy.

Subgenus *PHASCOLOSOMA* Leuckart, 1828

*Phascolosoma* (*Phascolosoma*): Stephen & Edmonds, 1972: 289.

?*Phascolosoma* (*Rueppellisoma*) Stephen & Edmonds, 1972: 271.

?*Phascolosoma* (*Satonus*) Stephen & Edmonds, 1972: 28 (in part).

DIAGNOSIS. Spindle muscle attached posteriorly. Introvert hook without accessory spinelets.

TYPE SPECIES. *Phascolosoma granulatum* Leuckart, 1828, monotypy.

Subgenus *EDMONDSIUS* subgen. nov.

*Phascolosoma* (*Satonus*) Stephen & Edmonds, 1972: 282 (in part)

DIAGNOSIS. Spindle muscle not attached posteriorly. Introvert hook with accessory spinelets at base.

TYPE SPECIES. *Phascolosoma pectinatum* Keferstein, 1867, monotypy.

The subgenus is named in honour of Dr Stanley J. Edmonds.

REMARKS. Stephen & Edmonds (1972) attempted to divide this large genus by creating four subgenera, *P. (Phascolosoma)*, *P. (Rueppellisoma)*, *P. (Antillesoma)* and *P. (Satonus)*, for the most part using published descriptions concerning the number of retractor muscles (four or two), presence or absence of contractile vessel villi and whether or not the spindle muscle is attached posteriorly. In examining all of the available type material, Cutler & Cutler (1983) found that the subgeneric distinctions were highly confused because many of the original descriptions contained errors. *P. (Rueppellisoma)*, comprising eight putative species each allegedly with two retractor muscles, is now considered invalid (all *Phascolosoma* are now interpreted as having four retractors), the type species, *Phascolosoma rueppellii* Grube, 1868, by original designation, being placed as *incertae sedis* since the type is lost. *P. (Antillesoma)*, formerly containing six species, now contains only the type species, *Phascolosoma antillarum* Grube & Oersted, 1858, original designation; this subgenus is sufficiently distinct as to warrant generic rank (see below). The remaining subgenus, *P. (Satonus)*, is distinguished from the nominate subgenus by the absence of a posterior attachment of the spindle muscle. This character is difficult to determine with any degree of certainty in any specimen that has been damaged internally, become macerated or has dried, as found when most of the type materials of the eight species grouped in *P. (Satonus)* were re-examined, including that of the type species, *Phymosoma nigritorquatum* Sluiter, 1882, original designation. Just one species, *Phascolosoma pectinatum* Keferstein, 1867, appears to fit the definition of *P. (Satonus)*. Since the type species of this subgenus, *P. nigritorquatum*, has uncertain

status (it may be a junior synonym of *P. (Phascolosoma) scolops* (Selenka & de Man)), it has been categorised as *incertae sedis* (Cutler & Cutler, 1983). Thus *P. (Satomus)* is invalid and the new subgenus accommodates *P. pectinatum*.

#### Genus *APIONSOMA* Sluiter, 1902

*Apionsoma* Sluiter, 1902: 42.

*Golfingia (Mitosiphon)* Fisher, 1950a: 550.

*Golfingia (Phascolana)* Wesenberg-Lund, 1959: 183.

*Fisherana* Stephen, 1964: 460.

*Golfingia (Siphonoides)* Murina, 1967: 1334.

**DIAGNOSIS.** Introvert of variable length in relation to trunk with rings of recurved hooks (absent in *A. trichocephala*) that in some species have accessory spinelets at base. Body wall with continuous muscle layers. Oral disk with tentacles enclosing nuchal organ but not mouth. Contractile vessel without villi. Four introvert retractor muscles. Spindle muscle attached posteriorly. Two nephridia, sometimes bilobed. Species small-sized (less than 2 cm in length).

**TYPE SPECIES.** *Apionsoma trichocephala* Sluiter, 1902, monotypy.

**REMARKS.** Cutler (1979) reviewed this taxon which is here elevated to generic status. It includes many species previously assigned to various *Golfingia* subgenera and *Fisherana* (see above). This genus is one that still presents problems, in particular, the precise nature of the oral disk in *A. trichocephala* remains unknown. The variations within the genus may justify the use of subgenera.

#### Genus *ANTILLESOMA* Stephen & Edmonds, 1972

*Phascolosoma (Antillesoma)* Stephen & Edmonds, 1972: 277.

**DIAGNOSIS.** Introvert variable in length, often about equal to trunk, without hooks. Body wall with longitudinal muscle layer gathered into anastomosing bands. Oral disk carries numerous tentacles (more than 30 in adults) enclosing nuchal organ. Contractile vessel with many villi. Four introvert retractor muscles, lateral pairs often extensively fused. Spindle muscle attached posteriorly. Two nephridia. Contains one small- to medium-sized species (less than 5 cm in length).

**TYPE SPECIES.** *Phascolosoma antillarum* Grube & Oersted, 1858, original designation.

**REMARKS.** This taxon was erected as a subgenus to include six *Phascolosoma* species but is now considered to be monospecific (Cutler & Cutler, 1983) and of generic rank.

### Order *ASPIDOSIPHONIFORMES*

Phascolosomatidea with the anterior trunk hardened to form a horny or calcareous anal shield. Two retractor muscles.

#### Family *ASPIDOSIPHONIDAE* Baird, 1868

Characters are those of the order.

#### Key to Genera

- |   |   |                       |   |
|---|---|-----------------------|---|
| 1 | Introvert protrudes from centre of anal shield. Shield calcareous (white) composed of numerous polygonal plates . . . . . | <i>CLOEOSIPHON</i>    |   |
|   | Introvert protrudes from ventral margin of anal shield . . . . .  |                       | 2 |
| 2 | Shield composed of single calcareous cap . . . . .  | <i>LITHACROSIPHON</i> |   |
|   | Shield composed of numerous horny (brown-black) plates. . . . .   | <i>ASPIDOSIPHON</i>   |   |

#### Genus *ASPIDOSIPHON* Diesing, 1851

**DIAGNOSIS.** Introvert usually longer than trunk with recurved hooks in numerous rings. Trunk with anal shield composed of hardened plates (occasionally inconspicuously developed). Introvert

protrudes from ventral margin of shield. Body wall either with continuous longitudinal muscle layer or with longitudinal muscle layer gathered into anastomosing, sometimes ill-defined, bands. Oral disk with tentacles enclosing nuchal organ but not mouth. Contractile vessel without villi. Two introvert retractor muscles often almost completely fused. Spindle muscle attached posteriorly. Two nephridia. Species small- to medium-sized.

TYPE SPECIES. *Aspidosiphon muelleri* Diesing, 1851, subsequent designation, Stephen & Edmonds, 1972.

#### Subgenus *ASPIDOSIPHON* Diesing, 1851

*Aspidosiphon* (*Aspidosiphon*): Cutler, 1973: 174.

DIAGNOSIS. Longitudinal muscle layer of body wall continuous, not gathered into bands.

TYPE SPECIES. *Aspidosiphon muelleri* Diesing, 1851, subsequent designation, Stephen & Edmonds, 1972.

#### Subgenus *PARASPIDOSIPHON* Stephen, 1964

*Paraspidosiphon* Stephen, 1964: 459.

*Aspidosiphon* (*Paraspidosiphon*): Cutler, 1973: 168.

DIAGNOSIS. Longitudinal muscle layer of body wall gathered into bands.

TYPE SPECIES. *Aspidosiphon steenstrupii* Diesing, 1859, original designation.

REMARKS. Earlier diagnoses of this genus contain serious errors. The tentacular arrangement is phascolosomatid (Gibbs, 1977; Gibbs, in Edmonds, 1980) and there are always two retractor muscles. Although *A. semperi* ten Broeke and *A. insularis* Lanchester are described as having four retractor muscles, the type of the former (ZMUA collection) has, in fact, two, and the type of the latter (BMNH: Reg. 1924.3.1.80) is not an *Aspidosiphon* but a *Phascolosoma* (possibly *P. perlucens* Baird). In *Aspidosiphon* species the spindle muscle is always attached posteriorly.

#### Genus *CLOEOSIPHON* Grube, 1868

DIAGNOSIS. Introvert longer than trunk with numerous rings of recurved hooks. Trunk with conspicuous anal shield composed of small rectangular calcareous plates. Introvert protrudes through centre of shield. Body wall with continuous muscle layers. Oral disk carries tentacles enclosing nuchal organ, but not mouth. Contractile vessel without villi. Two introvert retractor muscles often almost completely fused. Spindle muscle attached posteriorly. Two nephridia. Contains one medium-sized species.

TYPE SPECIES. *Loxosiphon aspergillus* Quatrefages, 1865, monotypy.

#### Genus *LITHACROSIPHON* Shipley, 1902

DIAGNOSIS. Introvert about equal to trunk with numerous rings of recurved hooks. Trunk with anal shield formed by internal calcareous conical structure. Body wall with longitudinal muscle layer gathered into bands. Oral disk with tentacles enclosing nuchal organ but not mouth. Contractile vessel without villi. Two introvert retractor muscles, often almost completely fused. Spindle muscle attached posteriorly. Two nephridia. Species small- to medium-sized (less than 4 cm in length).

TYPE SPECIES. *Lithacrosiphon maldiviense* Shipley, 1902, monotypy.

REMARKS. This genus now contains two species (see Cutler & Cutler, 1981).

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