The phyllophorid holothurians of southern Africa with the erection of a new genus

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The southern African dendrochirotid holothurians of the family Phyllophoridae (sensu Pawson & Fell, 1965) are revised and a new genus Thyronia is erected to accommodate Thyone articulata Vanney, 1908, which possesses only slender spectacle-shaped rods as body wall deposits. In addition, Thyone proceracorona Cherbonnier, 1952 and T. turrisolida Cherbonnier, 1954, are declared junior subjective synonyms of T. aurea (Quoy & Gaimard, 1833); Havelockia imperfecta Cherbonnier, 1970 is transferred to the genus Thyone, and T. venusta Selenka, 1868 (synonym T. okenii Bell, 1884) is recorded for the first time from southern Africa. These changes bring the total number of phyllophorid holothurians now known from southern Africa to five genera and 11 species. All species are keyed, briefly described and/or discussed, and their local distributions mapped.

Introduction
In their revised classification of the dendrochirotid holothurians, Pawson & Fell (1965) concluded that the traditional classification of dendrochirotid holothurians, based on tentacle numbers, concealed some important evolutionary trends and hence, on the bases of the calcareous ring and spicules, proposed a new classification of the dendrochirotids by regrouping the various subfamilies of the then known 10-tentacled Cucumariidae Ludwig, 1894 and the polytenaculate Phyllorhidae Oestergren, 1907 so that they became intermixed; assembled the subfamilies Sclerodactylinae Panning, 1949 and Cladolobininae Heding & Panning, 1954, in the family-group taxon, the Sclerodactylidae, and diagnosed two more families, the Placothuroidae and Paracucumidae for some small groups of plated forms. Later, Pawson (1970) erected the family Heterothyoniidae for another small group of plated forms from New Zealand. Thus the dendrochirotid holothurians today comprise the following seven families: Placothuroidae Pawson & Fell, 1965; Paracucumidae Pawson & Fell, 1965; Heterothyoniidae Pawson, 1970; Psolidae Perrier, 1902; Phyllophoridae Oestergren, 1907; Sclerodactylidae Panning, 1949 and Cucumariidae Ludwig, 1894. Six of the seven families are well keyed by Pawson & Fell (1965) and all families are diagnosed by Pawson (1982).

The families Placothuroidae, Paracucumidae and Heterothyoniidae are southern in distribution and not yet known from southern African waters, south of 23°2'S latitude. The family Psolidae is poorly represented by only four species, all of which are well documented and keyed by Deichmann (1948), in her revision of the southern African holothurians, there being no subsequent additions to this family. Of the three remaining families, the Sclerodactylidae is represented by seven species and has recently been treated by Thandar (1989b); the Cucumariidae by about 20 species but is in need of revision; and the Phyllophoridae, the subject of this investigation, by 13 nominal species — 11 belonging to the 10-tentacled subfamily Thyoniinae and one each to the polytenaculate subfamilies, the Phyllophorinae Oestergren, 1907 and the Spermocellinae Heding & Panning, 1954.

Not all 11 nominal species of the Thyoniinae are valid. In this paper Thyone proceracorona Cherbonnier, 1952 and T. turrisolida Cherbonnier, 1954 are declared synonyms of T. aurea (Quoy & Gaimard, 1833), while several other species described by Cherbonnier (1954, 1970) from single specimens and/or juveniles require verification based on new material. This paper, in addition, records T. venusta Selenka 1868, from the east coast, transfers Havelockia imperfecta Cherbonnier, 1970 to the genus Thyone and erects the genus Thyoniina to accommodate Thyone articulata Vanney, 1908. Hemithyone semperi (Bell, 1884) recorded by Pearson (1910) from Querimba, northern Mozambique, is here excluded since only species occurring south of the tropic of Capricorn (23°2'S latitude) are considered. Thus only 11 phyllophorid species distributed over five genera, are currently known from southern Africa.

Material and Methods
Material for this investigation was obtained on loan from the University of Cape Town (UCT) and the South African Museum (SAM) and accumulated over several years through collection trips undertaken by the author and the Zoology Department of the University of Durban-Westville (UDW). Paratypes or fragments of the body wall and introvert of the holotypes described by Cherbonnier (1952a, 1954 and 1970) were obtained from the Paris Museum of Natural History (PMNH).

The specimens were studied by conventional methods.
outlined by other workers such as Deichman (1948) and Rowe & Doty (1977). The spicules were removed with antiformin (see Mahoney 1966), washed in distilled water several times and illustrated with a camera lucida. For scanning electron microscopy the spicules were passed through several changes of absolute alcohol and then transferred, together with a little alcohol, onto a specimen stub to which they normally stick once the alcohol evaporates. They were then sputter-coated with gold for 5 min at 30–40 mA and photographed, using a Philips SEM 500.

To indicate records and material examined, Day’s (1967) method of using latitude/longitude degree squares, is utilized. The following symbols are used to indicate regions and depth records C = Cape Province, M = Mozambique, N = Natal, SWA = Namibia, T = Transkei, i = intertidal, s = shallow (0–99 m), d = deep (100–499 m), vd = very deep (500+ m).

List of southern African phyllophorid holothurians here recognized

Thyoninae

Stolus buccalis (Stimpson, 1856)
Thyone aurea (Quoy & Gaimard, 1833)
Thyone avenusta Cherbonnier, 1970
Thyone kirta Cherbonnier, 1970
Thyone imperfecta Cherbonnier, 1970
Thyone propinqua Cherbonnier, 1954
Thyone venusta Selenka, 1868
Thyonina articulata (Vaney, 1908)

Phyllophorinae

Seleniella paradoxsa Cherbonnier, 1970

Semperiellinae

Neothytonidium arthroprocessum Thandar, 1989

Key to the subfamilies and southern African species of the family Phyllophoridae

1. Tentacles 10, ventralmost two considerably smaller than the rest ....................................................Thyoninae Panning, 1949......2

   Tentacles 15–25, usually in two or three rings ..............10

2. Spicules of body wall exclusively in the form of slender, smooth, slightly curved rods or ‘spectacles’ with one or more perforations at each end .................................................................Thyonina articulata (Vaney, 1908)

   Spicules of body wall either in the form of knobbed buttons (plates), tables or their derivatives, or spicules absent .................................................................3

3. Spicules only knobbed buttons, often quite regular with 10–12 marginal knobs and four holes; tables absent from body wall .................................................................Stolus buccalis (Stimpson, 1856)

   Spicules 2–4 pillared tables or their derivatives, often reduced with age or altogether wanting .................................4

4. Small species, less than 30 mm long; colour in life brown, violet at both ends; no spicules in body wall and pedicels; subtropical species .........................................................Thyone venusta Selenka, 1868.

   Size and colour variable; body wall spicules tables or derivatives of tables, sometimes reduced to spectacle-shaped rods generally ornamented with one or more nodules; if spicules lost (in specimens >30 mm long), pedicel end plates nearly always present ...............................5

5. Tentacle spicules include rosettes or rosette-shaped deposits .................................................................6

6. Medium-sized species up to 110 mm long; tables well-formed, discs large (0.08–0.10 mm), circular to subrectangular, with 10–20 holes; spire low ending in an irregular crown; pedicels supported by elongate (0.08–0.12 mm), curved rods with a two-pillared spire ending in one or two teeth, spire often reduced .........................................................Thyone imperfecta (Cherbonnier, 1970).

   Small species up to 30 mm long; table discs small (0.04–0.09 mm), circular to oblong, pierced by usually only four large holes but sometimes also four or more smaller marginal ones; spire reduced or ending in one or more clusters of teeth; pedicels supported by two-pillared tables or curved spired rods .........................................................7

7. Table discs circular to subcircular (0.05–0.09 mm), pierced by up to 16 holes; spire low, ending in two clusters of teeth; pedicels with two-pillared oblong tables with spire similar to that of body wall tables ........................................Thyone avenusta Cherbonnier, 1970.

   Table discs oblong, usually pierced by only four holes, rarely more; spire either well developed, terminating in two clusters of teeth, or reduced or absent; pedicels with curved, spired rods with four central perforations and one at each extremity .........................................................8

8. Table discs lobed (0.04–0.05 mm); spire well developed, low (0.013 mm), often arched and with two clusters of teeth; pedicel rods elongate (0.010–0.12 mm) with an arched spire bearing three or more teeth .........................................................Thyone propinqua Cherbonnier, 1970.

   Tables reduced to minute, smooth plates without spires; pedicel rods elongate (0.08–0.10 mm), curved with a low (0.01–0.03 mm), often reduced spire .........................................................Thyone infusca Cherbonnier, 1954.

9. Medium-sized to large species, up to 130 mm long; tables well developed only in juveniles, with both small (0.03–0.08 mm) regular discs to large (0.07–0.16 mm) irregular ones, but always ornamented with conspicuous nodules; tables severely reduced with age to minute nodular plates or spectacle-shaped rods; spicules generally absent in adults except for pedicel end plates .........................................................Thyone aurea (Quoy & Gaimard, 1833)

   Small species, less than 30 mm long; tables well developed with smooth, circular to oval discs (0.07–0.09 mm) perforated by up to 20 holes, spire low (0.03–0.04 mm) .........................................................Thyone hirta Cherbonnier, 1970.
10. Calcareous ring whole or compound but never forming a tubular structure; posterior paired prolongations of the radials composed of a mosaic of small pieces; body wall spicules in the form of tables, plates and/or rosettes. Thyone articulata, Thysonina, 1907. Selenkiella paradoxa Cherbonnier, 1970.

Calcareous ring tubular and together with the posterior paired prolongations of the radials composed of a mosaic of small pieces; body wall spicules generally include tables or their derivatives, or short, thick perforated rods as in the southern African form. Thyone articulata, Thysonina, 1907. Selenkiella paradoxa Cherbonnier, 1970.

Family Phyllophoridae Oestergren, 1907

Diagnosis (modified from Pawson, 1982:815): Dendrochirotid holothurians without a test. Tentacles 10-25 (usually 10 or 20), well branched. Pedicels either restricted to the ambulacra or scattered, but fewer and usually papilliform dorsally. Calcareous ring complex, often tubular, with long or short posterior processes, both ring and processes always composed of a mosaic of small pieces. Spicules usually plates or buttons, rods, tables or derivatives of tables.

Remarks: The complex calcareous ring in combination with knobbled buttons, tables or their derivatives as body wall spicules, is the chief diagnostic feature of this family. However, in the enigmatic Cladolabella virgo Heding & Panning, 1954, slender spectacle-shaped rods are present, whereas in another, Thysonina articulata (Vaney, 1908), slender spectacle-shaped rods occur. The spinous rods of C. virgo can be derived from tables as are those of some species of Cladolabes. However, the rods of N. arthroprocessus and, especially, those of T. articulata do not appear to be table derivatives.

Subfamily Thyoninae Panning, 1949

Diagnosis (modified from Panning, 1949:461): Small to medium-sized phyllophorids, rarely more than 100 mm long. Body soft. Pedicels numerous, usually scattered all round, but often most crowded ventrally. Tentacles 10, ventral two always reduced. Calcareous ring tubular with long paired posterior processes to radial plates. Spicules of body wall usually in the form of tables or plates (buttons), or absent.

Remarks: This subfamily was originally classified within the family Cucumariidae by Panning (1949). It is the largest of the three phyllophorid subfamilies and represented in southern Africa by three genera and nine species. The genus Thyone is here erected to accommodate the endemic Thyone articulata Vaney, 1908.

The subfamily contains all 10-tentacled phyllophorids with scattered pedicels and usually tables or buttons (plates) as body wall spicules. In some species of Thyone, however, spicules may be secondarily reduced or lost, while in the monotypic Hemithyone, peculiar, circular to oval bodies occur, and in Thyonina slender spectacle-shaped rods are found.

Genus Stolus Selenka, 1867


Diagnosis (modified from Panning, 1949: 462): Tentacles 10, ventral two much reduced. Calcareous ring conspicuously tubular with the radials carrying long paired prolongations, both ring and prolongations finely broken into a mosaic of numerous pieces. Spicules of body wall only in the form of knobbed plates ('buttons'), often quite regular with 10–12 marginal knobs and four holes.

Type species: Stolus sacellus Selenka, 1867 (by subsequent designation Panning, 1949: 462 = Thyone buccalis Stimpson, 1856).

Remarks: This genus is represented in southern Africa by its type species, a well-known Indo-West-Pacific form recently redescribed by James (1966).

Stolus buccalis (Stimpson, 1856)

(Figures la, 2 and 10a)


Thyone rigida Semper, 1868: 66.

Thyone sacellus Theel, 1886: 138; H.L. Clark, 1923: 415; Mitsukuri, 1912: 227, fig. 43; Erwe, 1913: 360, pl. 5, fig.7.

Thyone sacellus Branch and Branch, 1981: 247.

Pseudothyone buccalis Panning, 1949: 457, fig. 53.

Stereoderma murrayi Bell, 1883: 61, pl. 15, fig. 6.

Stolus buccalis Clark and Rowe, 1971: 182 (dist.), pl. 29, fig. 14; James, 1966: 285, 1 text-fig., 1 pl.

Diagnosis: Length up to 80 mm (Figure la). Colour in life reddish brown to purple. Polian vesicles one or more; stone canals numerous. Buttons of body wall with 10–12 marginal knobs, rarely more, and two central knobs often linked by a 'handle' or half ring on each side. Pedicels with end plates and other jagged plates.

Previous southern African records: M(26/32,33 i).

Material examined: N(29/30/i; 30/31/i; 28/32/i), M(26/32/i; 26/33/i; 24/35/i; 23/35/i), 18 spec.

Local distribution: Mozambique into Natal as far south as Durban, 0–3 m. Figure 11.

General distribution: Throughout the Indo-West-Pacific region.

Habitat: Usually found concealed under rock or in narrow crevices.

Remarks: This well known Indo-West-Pacific species has long been recorded from Mozambique, either as Thyone sacellus by H.L. Clark (1923), T. sacellus by Branch & Branch (1981) or Stolus sacellus by Kalk (1954, 1958), Macnae & Kalk (1958) and Day (1974). The first record of
The presence of this species as far south as Durban is a noteworthy extension of its southward range.
Zoological Nomenclature (opinion 417, 1956). According to

Type species: Anaperus Troschel, 1846: 60 (partim).

Diagnosis (modified from Deichmann, 1948: 354; Pawson and Miller, 1981: 394): Small to medium-sized dendrochiroidid holothurians up to 200 mm long. Pedicels numerous, scattered, never restricted to ambulacra, often crowded ventrally. Tentacles 10, ventral two reduced. Calcareaous ring tubular, radials with long paired posterior prolongations, both ring and prolongations subdivided. Body wall spicules two- (four-)pillared tables or their derivatives, often severely reduced with age or absent. Introvert with rosettes only, tables only, or both tables and rosettes, or plates and rods.

Type species: Holothuria fusus Muller, 1776 (by original designation Jaeger 1833).

Remarks: Although the genus Thyone has been attributed to Oken, 1815, Pawson and Miller (1981) point out that Oken’s work (1815–1816) was placed on the Official Index of Rejected Works by the International Commission on Zoological Nomenclature (opinion 417, 1956). According to these authors the name Thyone must therefore be attributed to Jaeger (1833) who was the first to validate the name in accordance with the requirements of the International Code of Zoological Nomenclature.

Thyone currently contains approximately 40 species, including the seven known from southern Africa. It is possible that not all southern African species are valid for T. propinqua may prove to be identical to Havelokkia venustella while some others like T. hirta and T. infusca are separated on minute characters and warrant a re-examination based on more material. Since the spicules of many species of Thyone change or disappear with growth, adults and juveniles may be referred to different species.

Only four of the seven species are represented in the material at hand. The key is thus based partly upon this material and fragments of the types received from the PMNH and partly upon Cherbonnier’s descriptions. The dimensions of the spicules of those species not personally examined by the author are taken from Cherbonnier’s illustrations. They are hence based on a small sample and are therefore approximate.

Thyone aurea (Quoy and Gaimard, 1833) (Figures 1b and c, 3, 4, 10b and c)

Holothuria aurea Quoy and Gaimard, 1833: 120, pl. 7, figs. 15–17.

Cladolabes aureus Brandt, 1835: 74.


Thyone proceracorona Cherbonnier, 1952a: 492, pl. 44, figs. 1–16; syn. nov.

Thyone turrisolida Cherbonnier, 1954: 117, fig. 1 (1–24), fig. 2 (14); Day, Field and Penrith, 1970: 83; syn. nov.

Diagnosis (From Deichmann, 1948 and Cherbonnier, 1952a, amended herein): Medium-sized species, up to 130 mm long. Colour in life orange to pink. Calcareaous ring tubular, broken into a mosaic of numerous tiny pieces; posterior bifurcate processes of radial plates shorter than height of ring, also compound. Spicules two-pillared tables with characteristically knobbed to spinose discs, well developed in juveniles, severely reduced in adults to slightly nodular plates with few holes or to spectacle-shaped rods or plates, or altogether absent. Pedicel tables with curved discs, reduced or lost with age; end plates well developed. Tentacles and introvert with rods and perforated plates, no rosettes.

Previous records: SWA (26/15/i,s), C(29/16/i; 29/17/i; 33/17/i,s; 33/18/i,s; 34/18/i,s). Material examined: SWA (26/15/i,s), C(28/16/i; 29/17/i; 32/18/i,s; 33/17/i,s; 33/18/i,s; 34/18/i,s), 337 spec.

Distribution: Luderitz (Namibia) to False Bay, 0–70 m. Figure 11.

Figure 2. Spicules of Stolus buccalis (Stimpson). (a)–(f) Regular 10-knobbed buttons from body wall; (g)–(k) multi-knobbed buttons from body wall; (l) and (m) smooth buttons from body wall; (n) pedicel spicules. (a–m Scale A; n Scale B).
Figure 3. Spicules and other internal structures of a 36-mm specimen of *Thyone aurea* (Quoy & Gaimard). (a) Tables, reduced tables and spectacled-shaped rods from body wall; (b) end plate from ventral pedicel; (c) tentacle spicules; (d) introvert spicules; (e) part of calcareous ring; (f) madreporite (lateral and frontal view). (a, c and d Scale A).

**Habitat:** Sand, white sand, fine sand, rock. Species often cryptofaunic or amongst *Pyura*, sometimes washed up on shore amongst *Laminaria* roots. Juveniles found in association with *Ciona* under stones at low tide.

**Remarks:** The spicules of *T. aurea* undergo tremendous reduction with growth; this has resulted not only in the confusion of this species with the locally abundant *Thyone articulata* Vaney several times but it has also led to descriptions of at least two new species (*T. proceracorona* Cherbonnier, 1952 and *T. turrisolida* Cherbonnier, 1954) from specimens which apparently represent growth stages of *T. aurea*.

In juveniles of *T. aurea* (up to 25 mm long) (Figure 1c) tables are remarkably well developed with small, oblong to large, irregular discs (Figures 4d and g, 10c) always ornamented with nodules. The smaller discs (0.03–0.08 mm) have usually four holes while the larger ones (0.07–0.16 mm) are perforated by 7–40 holes. The pedicels of juveniles are supported by tables (Figure 4h) with large (0.10–0.14 mm) curved discs and a 2–4 pillared spire of moderate height (0.03–0.06 mm). With growth all spires, except those of tables from the anal region, are reduced to knobs on the surface of discs while the discs themselves degenerate to few-holed or spectacle-shaped plates and rods (Figure 3a and 10b). In adults spicules are totally absent, except for end plates in the pedicels (Figure 3b).

Although H.L. Clark (1923) had both *T. aurea* and *T. articulata* in his material from the SAM he identified this material, with some hesitation, to *T. aurea*, thinking that the rods of his specimens were stages in the development of plates. Incidentally *T. articulata* is characterized exclusively by spectacle-shaped rods which are neither precursors of tables nor table derivatives.

Deichmann (1948), on the other hand, relegated *T. articulata* to the synonymy of *T. aurea* but drew attention to three small specimens from Table Bay (with exclusively spectacle-shaped rods in the body wall), which are obviously referable to *T. articulata*. It is therefore clear that Deichmann also confused the two species. However, her diagnosis of *T. aurea* is essentially correct and she was the first to realize that its spectacle-shaped rods are reduced tables. Cherbonnier (1952a), after examining one of the type specimens of *T. articulata*, separated the two species. However, in 1954 he described *T. turrisolida* on the basis of two small (7 mm and 12 mm) specimens which appear to be juveniles of *T. aurea*. What lends support to this assumption is that the spicules of the holotype of *T. turrisolida* (illustrated by Cherbonnier in 1954 and examined by the author from a fragment of the type) are identical to those of some juveniles of *T. aurea* determined by Cherbonnier in
1952, judging from his identification of some UCT material.

Some 220 small specimens collected by the author from the west coast have spicules identical to those of *T. turrisolida* but since these specimens are juvenile, judging from the immaturity of the gonad, and, like *T. aurea*, also orange in life and restricted to the west coast, they most probably represent juveniles of this species. Further, their introvert and tentacular spicules are identical to those of *T. aurea*. Hence there is little doubt that the two species are conspecific and hence *T. turrisolida* is here declared a junior subjective synonym of *T. aurea*.

Cherbonnier (1952a) described *T. proceracorona* on the basis of only the calcareous ring and a fragment of the anterior body wall. According to him *T. proceracorona* differs from *T. aurea* in the stronger development of the calcareous ring and the peculiar nature of the pedicel deposits. Although an examination of the holotype of *T. proceracorona* failed to reveal any spicules, except for pedicel end plates, the calcareous ring does not differ significantly from that of *T. aurea* (Figure 3e). The body wall spicules of *T. proceracorona*, illustrated by Cherbonnier, are also present in *T. aurea*, while the peculiar pedicel deposits are reduction stages of tables, many of which also occur in some growth stages of *T. aurea*. In fact, the complete tables illustrated by Cherbonnier, presumably from the pedicels, are identical to those found in juveniles of *T. aurea*. Hence *T. proceracorona* is here also regarded as a junior subjective synonym of *T. aurea*.

*T. aurea* differs from the type species, *T. fusus* (O.F. Muller), in its smaller maximum size, smaller tables and in the absence of rosettes from the introvert and elongate tables from the body wall. Its introvert spicules comprising feintly nodular plates and rods separate it from the other three groups of species in *Thyone* which either possess only rosettes, or only tables, or a combination of rosettes and tables in the introvert (see Pawson & Miller 1981).
Figure 5. Spicules and other internal structures of *Thyone avenusta* Cherbonnier. (a) Tables from anal region; (b) reduced tables from bases of pedicels; (c) introvert rosettes; (d) tentacle rosettes and rods; (e) end plate from pedicel; (f) madreporite; (g) part of calcareous ring. (a, b and e Scale A; c and d Scale B).

*Thyone avenusta* Cherbonnier, 1970  
(Figures 5 & 10d)

*Thyone avenusta* Cherbonnier, 1970: 286, fig. 4 (A–M); Day, 1974b: 94.

*Diagnosis* (after Cherbonnier, 1970, modified herein): Small species, up to 47 mm long. Colour in alcohol, brown. Radial plates of calcareous ring (Figure 5g) prolonged posteriorly to terminate in short bifurcate processes. Tables (Figures 5a and 10d) two-pillared with circular to sub-circular discs, 0.05–0.09 mm, pierced by up to 16 holes; spire low, 0.02–0.05 mm; terminating usually in two clusters of teeth. Pedicels with oblong tables (Figure 5b); introvert with rosettes (Figure 5c); tentacles with rosettes and elongate rods, usually perforated at ends (Figure 5d).

*Record*: M(23/35/i).

*Material examined*: M(23/35/i), 1 spec.; plus body wall fragment of holotype.

*Distribution*: Known only from Morrumbene, Mozambique. Figure 11.

*Habitat*: Zostera bed, mangrove; uncovered at LWS.

*Remarks*: This species was established by Cherbonnier (1970) for a single 30-mm specimen. From the UCT reference number it appears that the present specimen was collected together with the type and therefore there is no doubt as to its identity. However, there are slight differences between the two specimens. Cherbonnier describes the type as having more pedicels ventrally and no anal 'teeth'. In the specimen at hand the pedicels are uniformly distributed and anal 'teeth' are present. The table discs of the type have fewer marginal holes and the pedicel tables are not reduced. Since the holotype measured only 30 mm compared with 47 mm for the present specimen, these differences are perhaps age variations. Hence spicules in the present specimen are restricted to the posterior end whereas in the type they occurred in the entire body wall.

The tables of the present specimen bear close resemblance to those of *T. hirta* Cherbonnier from False Bay. It is a pity that Cherbonnier did not compare his material with this species. If it were not for the pedicel and tentacular deposits one would be tempted to consider them conspecific. The pedicel tables of *T. hirta*, however, have curved discs while rosettes are absent from the tentacles.

The body wall spicules of *Thyone avenusta* also closely resemble those of the holotype of *T. propingua* Cherbonnier, 1970 from the south-west Cape Province. However, the latter species has strongly curved table discs in the pedicels and a different type of tentacular deposits.

*Thyone hirta* Cherbonnier, 1970

*Thyone hirta* Cherbonnier, 1970: 288, fig. 4 (N–S), fig. 5 (A,B).


series. Body wall spicules numerous tables with multilocular ovoid discs, 0.073–0.093 mm long; spire short (0.030–0.038 mm), two-pillared, terminating in one or two clusters of teeth. Pedicels with minute plates and tables, the latter with elongate curved discs (0.090–0.105 mm) with usually four central holes and one at each extremity; spire two- (four-) pillared, 0.033–0.045 mm high. Tentacles with perforated plates and rods; rosettes absent.

Records: C(34/18/s).
Material examined: None.
Distribution: Known only from False Bay, 48–53 m.
Habitat: Sand, gravel, shelly sand, Phyllochaetopterus debris.

Remarks: Although established upon six specimens, no specimen in the present material could be referred to this species. Its body wall tables are reminiscent of those of T. avenusta Cherbonnier, 1970 and T. dura Koehler and Vaney, 1908. Its distinction from T. avenusta has already been discussed (see remarks under T. avenusta). It differs from T. dura in the form of its calcareous ring and pedicel deposits.

Regrettably the paratype of T. hirta, received from the PMNH, proved, without doubt, to be referable to Thyonina articulata (Vaney). It is therefore imperative that the remaining paratypes be re-examined to confirm their conspecificity. A direct comparison between T. hirta and other related species has still to be made.

Thyone imperfecta (Cherbonnier, 1970) comb. nov. (Figure 6)


Diagnosis (from Cherbonnier, 1970: 284): Medium-sized, synaptid-like species, holotype 110 mm long. Colour dorsally violet, ventrally maroon. Anal 'teeth' flanked by podia. Calcareous ring high, poorly calcified, posterior prolongations of radials longer than height of ring. Body wall spicules exclusively tables with circular to subrectangular discs (0.08–0.10 mm) with two large and usually two smaller central holes and 6–16 small marginal holes; spire short (0.02–0.04 mm), two-pillared, often distorted or reduced to two central knobs on surface of disc. Anal tables with larger discs and more perforations. Pedicels with elongate (0.08–0.12 mm), curved, perforated rods with an arched spire terminating in one or two blunt teeth. Tentacles with perforated rods, often forming plates, and crinkled rosette-shaped bodies.

Record: C(34/18/s).
Material examined: Dorsal and ventral body wall fragments of holotype.

Distribution: Known only from False Bay, 60–62 m. Figure 11.

Remarks: This species was established by Cherbonnier (1970) for two specimens from False Bay. Cherbonnier referred the species to Havelockia without comparing it with other species of the genus. In H. versicolor (Semper), the type species of Havelockia, the calcareous ring, as illustrated by Clark and Rowe (1971: Fig. 91b), is short and stout with only the short radial prolongations subdivided and the table discs usually perforated by eight or less marginal holes. However, the subdivided plates and the length of the radial prolongations of the calcareous ring of H. imperfecta suggest that the species belongs in Thyone. Although the fragments of the body wall of the holotype produced only rods and plates from around the bases of pedicels (Figure 6a and b), judging from Cherbonnier's drawings, the spicules of this species are also reminiscent of those of Thyone species, especially T. hirta. Hence the species is here transferred to Thyone. It differs from T. hirta in its larger table discs with a crenulate margin, spires that are frequently distorted, and the presence of rosette-shaped bodies in the tentacles.

Thyone infusca Cherbonnier, 1954 (Figure 7)


Diagnosis (from Cherbonnier, 1954:119): Small (?) species, holotype 25 mm long. Colour, in alcohol, chocolate brown. Anal 'teeth' present. Radial plates of calcareous ring broken into two series of large pieces, interradials in a single series of three large pieces; posterior prolongations of radials almost as long as height of ring. Body wall spicules smooth, elongate (0.04–0.09 mm) plates with usually four central holes and one or two minute holes at each end. Pedicel tables with elongate (0.08–0.10 mm) curved discs bearing four central holes and usually an additional hole at each end; spire short (0.01–0.03 mm), two-pillared, with 4–8 blunt teeth, or spire reduced to knobs on surface of disc. End plates of pedicels (0.120–0.165 mm) with holes gradually increasing in size peripherally. Tentacles with small perforated rods and rosettes.

Record: C(34/18/s).
Material examined: Dorsal and ventral body wall fragments of holotype.

Distribution: Known only from False Bay, 8–9 m. Figure 11.

Habitat: Rock.
Remarks: This presumably small species (Cherbonnier did not mention the state of maturity of the gonad), based upon a single 25-mm specimen, is quite unlike other southern African species of *Thyone*. The plates of the body wall appear to be reduced table discs reminiscent of those of *T. aurea* (Figure 7a). Although there is no evidence of reduction they must be regarded as such since complete tables are found in the anal region and pedicels. In similar size specimens of *T. aurea* well-developed tables are present. *T. infusca* also differs from the latter species in the structure of the calcareous ring which is composed of large pieces, especially the interradial series, and in the presence of rosettes in the tentacles. It is improbable that the two species are conspecific. Since the Cape Province coastline is noted for its high endemic fauna it does not appear likely that *T. infusca* has any close relative outside the southern African subcontinent. The occurrence of several distinct species of *Thyone* in a restricted area such as False Bay does not preclude the existence of sympatric hybrids.

*Thyone propinqua* Cherbonnier, 1970

*Thyone propinqua* Cherbonnier, 1970: 289, fig. 5 (c-k); Day, Field and Penrith, 1970: 83.

Diagnosis (from Cherbonnier, 1970: 289): Small species up to 20 mm long. Pedicels long. Anal 'teeth' present, each flanked by a single papilla. Calcareous ring with anteriorly bifid radials and spear-shaped interradials; radials with two series of elements, interradials with a single larger series. Body wall tables with a lobed disc (0.04–0.05 mm), usually perforated by four large holes, rarely more (up to eight); spire (ca. 0.013 mm) two-pillared, often arched, terminating in a few blunt teeth or conical projections. Pedicels supported by large (0.10–0.12 mm) curved rods with four central holes and one at each extremity, and an arched spire (ca. 0.018 mm) with several conical teeth; end plates 0.12–0.13 mm in diameter. Tentacles supported by large (up to 0.26 mm), curved, perforated plates and small (0.07 mm) rosette-shaped bodies.

Records: C(34/18/s; 34/22/s).

Material examined: Fragment of body wall of paratype.

Distribution: False Bay to Mossel Bay, 19–51 m. Figure 11.

Habitat: Sand and shell.

Remarks: This species was established by Cherbonnier (1970) upon two probably juvenile specimens. It is a pity that Cherbonnier did not compare his material with *Havelockia venustella* (Ludwig and Heding) with which it shares the typical *fusus*-like tables. The calcareous ring of *H. venustella* is poorly described and not illustrated. It is not clear whether Panning (1949), who referred the species to *Havelockia*, examined the holotype. The fact that *T. propinqua*, also from the south-west Cape Province, was collected from shallow water and also has pedicel spicules, suggests that it may represent a juvenile of *H. venustella* since the type measured only 20 mm. Since the calcareous ring of *H. venustella* is poorly known and since this species was recognized by Dr. Cherbonnier (judging from some UCT material identified by him), there is no justification at this stage to synonymize both species.

According to Cherbonnier, *T. propinqua* differs from *T. fusus* and other related species in the type of pedicel deposits. In a similar size specimen of *T. fusus* from N. Ireland, here examined, the disc length of the body wall tables is 0.05–0.08 mm and the spire height 0.03–0.05 mm while the corresponding dimensions of the pedicel tables are 0.10–0.15 mm and 0.028–0.043 mm. *T. propinqua*, however, has in the body wall tables with smaller discs (0.04–0.05 mm) and low spires (ca. 0.13 mm) and, while the pedicel table discs are of approximately the same size range as those of *T. fusus*, the spires are much lower.

*Thyone venusta* Selenka, 1868

*Thyone venusta* Selenka, 1868: 115, figs. 11 and 12.

*Thyone okeni* Bell, 1884: 149, pl. 9, fig. D; Clark, 1921: 167; 1946: 402, Clark & Rowe, 1971: 182 (dist.); Rowe & Doty, 1977: 226, fig. 8a; syn. nov.

Diagnosis: (from Selenka, 1868: 115, amended herein): Small species, up to 85 mm in length; colour brown to purplish brown, fading in alcohol. Calcareous ring tubular. Stone canal and polian vesicle single. Spicules absent, only pedicel end plates present except in the southern African form.

Previous southern African record: None.

Material examined: N(29/30/i), 1 spec.

Description: Specimen (mature female) without calcareous ring and associated structures. Length 26 mm, diameter 8 mm. Colour, in life, brown but dark purple anteriorly and at
tip of anus. Pedicels filamentous in life, shortening on preservation, crowded, less numerous and sparsely distributed in dorsal mid-body, decreasing in size posteriorly. Anal 'teeth' or papillae absent. Spicules, including pedicel end plates, absent.

**Distribution:** Red Sea and Natal (Figure 11); *T. okeni* has been recorded only from the West Pacific.

**Habitat:** Found under stone in rock pool at LWS.

**Remarks:** This specimen (the only record of a *Thyone* from Natal) was examined immediately on preservation. It is undoubtedly a *Thyone* but whether it is Selenka's *T. venusta* or another species is open to question. The identification is based upon the absence of deposits and upon the possibility that the Red Sea species could extend into Natal, as does *Ohshimella ehrenbergii* (Selenka). However, since many species of *Thyone* lose their deposits with growth, as happens in *T. aurea*, their absence is inconclusive. In its size, form of the pedicels and life colouration, the present specimen is quite different from *T. aurea*. The latter species is bright orange in life, reaches a fairly large size at maturity (130 mm), has thicker pedicels and is not yet known to extend east of False Bay.

Deichmann (1948) observed that both *T. venusta* and *T. venustella* Ludwig & Heding, 1935 are probably conspecific, arguing that in many species of *Thyone* the spicules are lost with age. However, the two species differ so much in form that it is certain that they are not conspecific. Further *T. venusta* is a cold-water species while *T. venustella* is distinctly tropical - subtropical.

Selenka's species, based on a single specimen, has not been found since its description in 1868. Perhaps similar forms are masquerading under different names as they possess spicules. Selenka, however, reported the presence of well developed end plates in his specimen which are absent in the Natal form, perhaps a local variation.

Bell's (1884) *T. okeni*, originally described from New South Wales but probably distributed throughout the western Pacific area (Rowe & Doty 1977) like Selenka's *T. venusta*, also possesses only end plates in the pedicels. Clark (1921, 1946) describes his *T. okeni* from Torres Strait as brownish in life and Rowe & Doty (1977) also report their specimen from Guam as being brown. It is unfortunate that none of the above workers compared their specimens with Selenka's species. Despite this, the author is inclined to think that both *T. venusta* and *T. okeni* are conspecific and hence the latter is here relegated to the synonymy of the former which has priority.

**Genus Thyone Gen. nov.**

*Thyone* Vaney, 1908b (non *Thyone* Jaeger, 1833).


**Diagnosis:** Small, cylindrical species up to 55 mm long. Pedicels numerous, scattered. Tentacles 10, ventral two reduced. Calcareous ring short tubular, radials with long paired posterior prolongations, both ring and prolongations broken into a few large pieces. Body wall spicules minute, slender, straight or slightly curved, smooth rods, expanded and often digitated at ends which have a single large and one or more smaller holes. Pedicels with end plate (up to 0.135 mm in diameter) with numerous small central holes and a single series of large marginal holes, both types sharply demarcated. Introvert with rosettes. Tentacles with simple plates and rods, often provided with spiny margins.

**Type species:** *Thyone articulata* Vaney, 1908 (designated herein).

**Etymology:** The name *Thyone* is derived from *Thyone*. The gender is feminine.

**Remarks:** The genus *Thyone* has long been restricted (Jaeger, 1833) with the designation of *T. fenus* (O.F. Muller) as type species. It therefore should include only those species with 2(4)-pillared tables or their derivatives as body wall spicules. The type species of the new genus, formerly classified in *Thyone* (s.s.), does not belong in this genus since its characteristic slender, spectacle-shaped rods are not derived from tables. Its calcareous ring, subdivided into large pieces, is also of a different form than that of the species currently classified in *Thyone* (s.s.) and resembles to some extent that of *Havelockia*. Hence for *T. articulata* the genus *Thyone* is here erected.

A complex calcareous ring in combination with simple rods as exclusive body wall deposits is not present in any other dendrochirotid and hence relating the new genus to others in the group appears problematical at this stage. It is for this reason that the genus is at present monotypic and *T. articulata* has remained in *Thyone* for so long. Amongst the Thyoniinae simple rod-like spicules are found in *Thyoneria cognata* (Lampert) (= *Stiolus cognatus* according to Pawson & Miller, 1981) from the tropical West Atlantic. However, in this species the spicules are thick and elongate, with two series of holes and there are in addition small button-like plates with usually four holes (Deichmann 1930; Caycedo 1978). Hence the new genus does not even come close to *Thyoneria*. *Hemioedema spectabilis* (Ludwig), with which Vaney (1908b) compared his species, has spicules similar to those of *T. articulata* but its calcareous ring is simple without posterior prolongations.

**Thyone articulata** (Vaney, 1908)

(Figures 1d, 8 and 10e, f)

*Thyone articulata* Vaney, 1908a: 295; 1908b: 426, pl. 4, figs. 43, 44; Cherbonnier, 1952a: 495, pl. 46, figs. 6–9; Day, Field and Penrith, 1970: 83.

*Thyone aurea* H.L. Clark, 1923: 415 (partim); Deichmann, 1948: 354 (partim), text-figs. 6–9.

**Diagnosis:** As for the genus.

**Previous records:** C(33/17)s; 33/18/s).

**Material examined:** C(33/18/s); 34/18/s; d; 34/25/s), 372 spec.

**Description:** Colour dark maroon-brown (Figure 1d). Plates of calcareous ring (Figure 8j) broken into 2(4)-radial and (1)–2 or 3 interradial series of calcareous elements; posterior prolongations of radials longer than height of ring, composed of a single series of calcarous elements. Each respiratory tree consisting of two main trunks, a short medial and a longer lateral trunk.

**Spicules:** Rods minute (0.040–0.065 mm long) (Figures 8d
and e, 10e), derived from slender forked deposits and not tables, more numerous ventrally, lost in some specimens, possibly owing to preservation and not age. Some ventral rods stouter with larger holes often along most of their length (Figure 8f), rarely forming plates. Cross-shaped rods with 1–2 holes at each extremity occasionally present. Anal region with more slender rods with a single perforation. End plates (Figure 8a and b) with rims often showing deposition of additional calcareous material.

Distribution: Saldanha Bay to Port Elizabeth, 16–162 m. Figure 11.

Habitat: Coarse khaki brown sand and shell, pebbles, stones, shelly sand, white sand, mud.

Remarks: This species was erected and diagnosed by Vaney (1908a) on the basis of two specimens taken at Saldanha Bay by the RIMSS 'Investigator', but described in a subsequent paper (Vaney 1908b). H.L. Clark (1923), in his monograph of the southern African echinoderms, overlooked Vaney's papers thus misidentifying three small specimens from Table Bay, obviously referable to *T. articulata*, as *T. aurea*.

Deichmann (1948), in her revision of the South African holothurians, took an unusual step by referring *T. articulata* to the synonymy of *T. aurea*, while drawing attention to and illustrating the spicules of the three Table Bay specimens misidentified by Clark. The reason for Deichmann's action is difficult to understand.

Cherbonnier (1952a) examined one of Vaney's types housed in Monaco and found it to be similar to his material from Table Bay. Regrettably Cherbonnier neither compared the calcareous ring of his *T. articulata* with that of the type nor did he comment on Vaney's description of its structure.

The description of the calcareous ring by Vaney (1908b) is brief and the illustration does not correspond with that of *T. articulata* given by Cherbonnier and herein (Figure 8i). Vaney mentions five radial and five interradial prolongations which are illustrated as being distally forked, each prolongation consisting of two series of calcareous elements. According to him the calcareous ring measured 10 mm in height in the type which was 45 mm in length. However, one of the specimens at hand which measures 40 mm in length has a calcareous ring which is scarcely 5 mm high.

Nevertheless, the present material so well fits Vaney's description of the spicules and end plates that there is little doubt as to its identity. *Thyonina articulata* clearly differs...
from *Thyone aurea* not only in size but also in the structure of the calcareous ring, end plates and spicules. Further, it has a short gonadal stolon and two stems to each respiratory tree. Only the spectacle-shaped rods or plates of *T. aurea* bear any resemblance to the spicules of *T. articulata* but they are of different origin, being derived from reduced tables and not from dichotomously branched rods. Since all species of *Thyone* (s.s.) have tables or their derivatives as body wall deposits there is no justification in retaining *T. articulata* in this genus.

**Note:** There are four other specimens (TRA 67H) in the UCT collection, dredged from Dassen Island on the west coast at 29 m with the bottom material also described as shelly sand. These specimens differ so much from the typical *T. articulata* in their form, texture, coloumtion and some other features that they appear to belong to another species. They are somewhat barrel-shaped, 24-42 mm in length, and yellowish with brownish blotches. The calcareous ring has one (rarely more) interradial series of elements, the end plates seldom have a complex rim and the retractors originate as 1-3 strands with the dorsal ones arising more anteriorly. However, they possess the same type of spicules (Figure 10f), pedicel end plates and calcareous ring as *T. articulata*. Since they are sympatric with the typical *T. articulata* they are here not considered a subspecies.

**Subfamily Phyllophorinae Oestergren, 1907**

**Diagnosis** (modified from Heding and Panning, 1954: 139): Dendrochirotid holothurians with 15, 20 or 25 tentacles, usually 20 in two or three circles of 15 + 5 or 10 +5 +5 respectively. Pedicels generally distributed over entire body. Calcareous ring of 10 plates, either whole or compound, but never forming a tubular structure; posterior prolongations of radials compound, composed of a few large pieces. Spicules of body wall in the form of four-pillared tables or their derivatives, or rosettes; introvert with rosettes.

**Remarks:** This subfamily is represented in southern Africa by only *Selenkiella paradoxa*, described from a single specimen from Mozambique by Cherbonnier (1970). As this species is not present in the material at hand its spicules are illustrated from a sample of the body wall of the holotype.

**Genus Selenkiella Heding and Panning 1954**


**Diagnosis:** (after Heding and Panning, 1954: 139):

Tentacles 25. Radial and interradial plates of calcareous ring compact, posterior prolongations sub-divided into a few large pieces. Body wall spicules four-pillared tables or their derivatives.

**Type species:** *Selenkiella siamense* Heding and Panning,

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**Figure 9.** Spicules from holotype of *Selenkiella paradoxa* Cherbonnier. (a) Plate and rods from ventral pedicels; (b) branched rods (rosettes) from ventral body wall; (c) 'buttons', rods, plates and tables from ventral body wall; (d) large tables from ventral body wall; (e) tables from dorsal body wall; (f) branched rods (rosettes) from dorsal body wall.
Figure 10. SEM micrographs of spicules of southern African phyllorhids. (a) Stelis buccalis (Stimpson). (b) Thyone aurea (Quoy & Gaimard), 36-mm specimen; (c) T. aurea (Q and G), juvenile (8 mm); (d) T. avenusta Cherbonnier; (e) Thyonina articulata (Vaney); (f) T. articulata (atypical form); (g) Neothyonidium arthroprocessum Thunders. (Scale bars = 10 μm).


Selenkiella paradoxa Cherbonnier, 1970

(Figure 9)

Selenkiella paradoxa Cherbonnier, 1970: 291, fig. 6 (A–P); Day, 1974b: 94.

Diagnosis (After Cherbonnier, 1970, amended herein):
Holotype 21 mm. Colour maroon. Tentacles 25 in two circles (15 + 5). Radial processes of calcareous ring subdivided into 6–8 pieces. Spicules as buttons (plates), tables and rosettes. Buttons (Figure 9c), 0.03–0.17 mm, with smooth or undulating margins and one or more holes. Tables (Figure 9d & e) with mostly irregular discs, 0.05–0.08 mm, with 4–9 holes and 2–4 pillars. Rosettes (0.020–0.035 mm) rare (Figure 9b & f), present both dorsally and ventrally.

Record: M(23/35/s).

Material examined: Fragments of dorsal and ventral body wall of holotype.

Distribution: Only known with certainty from Morrumbene, Mozambique, 3–5 m (Figure 11). However, Day (1974b) also records the species from Inhaca Island, M(26/32,33) but this record could not be confirmed.

Habitat: Sand.

Remarks: Cherbonnier (1970) commented on the differences between this species and the two others (S. siamense and S. malayense) congeneric with it. In S. siamense the radial prolongations consist of four pieces, the body wall spicules include only tables with eight or more-holed discs, and the pedicels have only plates. In S. malayense, on the other hand, the tentacles are arranged in two circles of 20 + 5, the radial prolongations subdivided into three pieces, the body wall spicules consist of only regular tables with eight-holed discs and the pedicels contain only plates. The southern African species is hence distinct from those of the Far East and this considerably increases the known distribution of the genus. Its tentacle distribution and irregular tables place it closer to S. siamense than to S. malayense. However, more specimens of the species need to be found.

Subfamily Semperelliinae Heding and Panning, 1954

Diagnosis (from Heding and Panning, 1954: 179): Dendrochirotid holothurians with 15–20 tentacles. Calcareous ring well developed, often tubular; radial and interradial plates always broken into a mosaic of small pieces, posterior prolongations of radial and/or often the interradials also subdivided. Body wall spicules 2–4 pillared tables or their derivatives; in one species (Cladolella virgo) spinous rods occur while in another (Neothyonidium arthroprocessum) short, thick perforated rods are found.

Remarks: The endemic Neothyonidium arthroprocessum recently described from False Bay by the author (Thandar 1989a) is the only known representative of this subfamily in the southern African waters. For the sake of completeness, it is briefly diagnosed below.
Genus *Neothyoniun* Deichmann, 1938


**Diagnosis:** (After Deichmann, 1938: 379, amended herein): Dendrochirotid holothurians with 20 tentacles in two circles of 10 + 10. Calcareous ring tubular, with long deeply divided posterior prolongations to radial and/or interradial plates. Body wall spicules two-pillared tables or their derivatives; short, thick rods present in the southern African species.

**Type species:** *Thyonium hawaiiensis* Fisher, 1907 (by original designation Deichmann, 1938: 379).

*Neothyoniun arthroprocessum* Thandar, 1989 (Figures 1f & 10g)

**Diagnosis:** A large U-shaped phyllophorid up to 270 mm along ventral surface. Radial plates of calcareous ring prolonged posteriorly into bifurcate processes, each united with the adjacent process of the neighbouring radial plate. Spicules short, thick, perforated rods of varying shapes, the perforations often occluded. Introvert with tables, rods and rosette-shaped bodies.

**Record:** C34/18/s).

**Distribution:** Known only from False Bay, South Africa, 70-12 m.

**Habitat:** Sand.

**Remarks:** This species (Figure 1f) has been described in detail elsewhere (Thandar, 1989a) and requires no further comments except that its spicules (Figure 10g) are so characteristic that it cannot be mistaken for another species and the holotype (mature female) possesses transverse slits (of unknown significance) in the body wall.

**Southern African nominal phyllophorid holothurians and their present disposition**

<table>
<thead>
<tr>
<th>Nominal species</th>
<th>Present disposition (this paper)</th>
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<td><em>Thyonium imperfecta</em> (Cherb, 1970)</td>
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<tr>
<td><em>Stolus sacellus</em> Selenka, 1867</td>
<td><em>S. buccalis</em> (Stimpson, 1856)</td>
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<td><em>Thyonium articulata</em> Vaney, 1908</td>
<td><em>Thyonina articulata</em> (Vaney, 1908)</td>
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<tr>
<td><em>T. aerea</em> (Quoy &amp; Gaimard, 1833)</td>
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<td><em>T. hirsia</em> Cherb, 1970</td>
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<td><em>Selenkiella paradoxus</em> Cherb. 1970</td>
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**References**


