The status of some southern African nominal species of *Cucumaria* (s.e.) referable to a new genus and their ecological isolation

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A full history of four nominal species of southern African dendrochirotid holothurians, namely *Cucumaria jägeri* Lampert, *Semperia (= Cucumaria) sykion* Lampert, *C. insolens* Théel and *C. sinorbis* Cherbonnier, is given and the confusion in their taxonomic status discussed. Morphological differences and habitat selection indicate that the latter three are valid sister species. *C. jägeri* is relegated to the synonymy of *C. sykion*, a well-established name which it threatens. Since none of the three species is referable to the genus in which it is currently classified, a new genus *Pseudocnella* is erected to accommodate them. It is suggested that the Mediterranean *Ocnus syracusanus* (Grube) be also classified in the new genus. A key to the three southern African species is given, their synonymy detailed, additional notes provided, and the geographic distributions mapped. Although *P. sykion* and *P. sinorbis* have an identical geographical range it is demonstrated that the two species are ecologically isolated and thus prevented from any interspecific competition. *P. insolens* is sympatric with *P. sinorbis* over a wide area, often occupying the same habitat in a single locality. However, morphological and other evidence points to subtle niche differences between them. A provisional cladogram is proposed to show the possible relationships of the four species included in the new genus.

'n Volledige geskiedenis van vier nominale spesies van Suider-Afrikaanse Holothuroidea, naamlik *Cucumaria jägeri* Lampert, *Semperia (= Cucumaria) sykion* Lampert, *C. insolens* Théel en *C. sinorbis* Cherbonnier, word gegee en die verwarring ten opsigte van hulle taksonomiese status word bespreek. Morfologiese verskille en habitat-seleksie dui daarop dat die drie laasgenoemdes geldige susterspesies is. *C. jägeri* is tot die sinonomie van *C. sykion,* 'n goed gevestigde naam wat dit bedreig, verwys. Aangesien geeneen van die drie spesies na die genus waarin hulle tans geklassifiseer word, verwys kan word nie, is 'n nuwe genus geskep om hulle te akkommodeer. Daar word voorgestel dat die Mediterreense *Ocnus syracusanus* (Grube) ook in die nuwe genus geplaas word. 'n Sleutel tot die drie Suider-Afrikaanse spesies word verskaf, hulle sinonomie word uiteengesit, addisionele gegewens word voorsien en hulle geografiese verspreiding gekaarteer. Alhoewel *P. sykion* en *P. sinorbis* 'n identiese geografiese verspreiding het, word daar gedemonstreer dat die twee spesies ekologies geïsoleer is, en dus enige tussenspesie-kompetisie vermy. *P. insolens* is simpatries met *P. sinorbis* oor 'n wye gebied en bewoon dikwels dieselfde habitat in 'n enkele lokaliteit. Nogtans dui morfologiese en ander gegewens op subtiele nisverskille tussen hulle. 'n Voorlopige kladogram word voorgestel om die moontlike verwantskap tussen die vier spesies in die nuwe genus aan te toon.

Introduction

The identity of four Southern African nominal species of dendrochirotid holothurians, namely, *Cucumaria jägeri* Lampert, 1885; *Semperia sykion* Lampert, 1885; *C. insolens* Théel, 1886; and *C. sinorbis* Cherbonnier, 1952, is particularly confused. This stems largely from Deichmann's (1948) error in regarding Théel's *C. insolens* as a growth stage of *sykion*. Cherbonnier (1952) clarified the matter but Panning (1962) subsequently supported Deichmann's view. Since there has been a considerable difference of opinion concerning the identity of the four nominal species, their full history is here detailed, the taxonomic status discussed and the complete synonymy of each recognized species included. Further, a key and some additional notes are provided and the zoogeographic distribution, ecology and relationships of the species outlined.

Lampert (1885) described *Cucumaria jägeri* from Natal and *Semperia sykion* from Algoa Bay in the southern Cape Province. Regrettably he did not illustrate the new species. Théel (1886) listed and diagnosed the two nominal species from Lampert's descriptions but transferred *sykion* to the genus *Cucumaria* commenting that the occurrence of podia also in the interambulacra did not warrant a new genus. At the same time Théel described *C. insolens from Simon's Bay in the Cape Province.*

Ludwig (1888), Vaney (1908), and several other workers subsequently identified C. insolens from Southern African shores. However, *C. sykion* was recognized only in 1923 by H.L. Clark from material collected at East London, Port Elizabeth and Natal. Clark, however, was unable to assign any southern African form to *C. jägeri,* a species he recognized with reservation, stating that it is very close to *C. sykion* in spicule form, doubting the significance of pedicel arrangement.

Deichmann (1948) recognised *C. sykion* but regarded *C. jägeri* as a 'faded *sykion*', relegating it, though with some doubt, to the synonymy of that species. She also considered Théel's *C. insolens* as a growth stage of *C. sykion*, thus listing it also as a synonym of the latter species. Panning (1949), unaware of Deichmann's paper, identified a form from Zanzibar, with some reservation, as *C. jägeri*, and referred it to the genus *Stereoderma*. In the same paper he referred *C. sykion,* without examination, to his newly erected genus *Pseudocnus* with *Cucumaria köllikeri* Semper as type species and *C. insolens* to *Ocnus* Forbes with *O. brunneus* Forbes as type species.

Cherbonnier (1952) did not accept Panning's revision. He therefore retained *sykion* and *insolens* in the genus

Cucumaria and described a new species, *C. sinorbis*, from Table Bay and Port Edward (Natal), while clearly tabulating the differences between these three endemic southern African species. He further considered Panning's identification of *C. jägeri* to be wrong as the description did not correspond with that of the type given by Lampert.

Later, Panning (1952) corrected his error by now redescribing *C. jägeri* from two specimens from Port Elizabeth (the type locality of *C. sykion*) as a subspecies of *Pseudocnus dubiosus* (Semper) but now making no mention of *C. sykion* which he included also in *Pseudocnus* in 1949. In 1962, however, in his reassessment of this genus, Panning recognized *P. dubiosus jaegeri*, but now, clearly following Deichmann (1948), regarded *C. insolens* as a growth stage of *C. sykion* which he also included in his *dubiosus* group. However, in this revision, he changed the designation of the type species of *Pseudocnus* to *Cucumaria dubiosa* Semper, since he now regarded *C. köllikeri* as a subspecies of *P. dubiosus*.

In the present paper *C. sykion*, *C. insolens* and *C. sinorbis* are treated as distinct species, whereas *C. jägeri* is relegated to the synonymy of *C. sykion*. Since these three valid southern African sister species cannot be classified in any existing dendrochirotid genus, a new genus *Pseudocnella* is erected to accommodate them. *Cucumaria syracusana* Grube, 1840, from the Mediterranean Sea, may be included as a fourth species in the new genus.

Previous records of the species and of the material examined by the writer are expressed in terms of latitude/longitude degree squares as expounded by Day (1967) for the polychaetes. The following symbols are used to indicate regions and depth records: C = Cape Province, M = Mozambique, N = Natal, SWA = South West Africa (Namibia), T = Transkei, i = intertidal, s = shallow (0–100 m).

Pseudocnella gen. nov.

Diagnosis: Small to medium-sized, usually barrel-shaped species, up to 95 mm long along ventral surface, mouth and anus directed dorsally. Tentacles 10, of more or less equal size, occasionally one or two reduced. Pedicels usually restricted to ambulacra, 2–7 rows ventrally and 2–6 rows dorsally; numerous interradial papillae (papulae). Calcareous ring simple, without posterior prolongations to radial plates but both radial and interradial plates with long anterior projections. Spicules of body wall a superficial layer of incomplete baskets, developed as cross-shaped rods with dichotomously branched arms, and an inner dense layer of round to oval, usually fir-cone-shaped, knobbed plates made up of more than one layer of calcareous material; in one species (*P. sykion*) baskets present in juveniles only while in another (*P. insolens*), buttons present in addition to knobbed plates.

Type species: *Cucumaria sinorbis* Cherbonnier, 1952 (designated herein).

Other species included: *Semperia sykion* Lampert, 1885; *Cucumaria insolens* Théel, 1886; ?*Cucumaria syracusana* Grube, 1840.

Remarks: The three southern African species included in this subgenus are united by the presence of interradial papillae (papulae) and a superficial layer of incomplete baskets appearing as dichotomously branched X-shaped rods. It is noteworthy that the latter character, not observed before in *C. sykion*, only occurs in juveniles of the species (< 25 mm in length). Although Panning (1949), in his revision of the family Cucumariidae, did not assign any such forms to *Pseudocnus*, these were included by him in 1962, in his reassessment of the genus, but the diagnosis of the genus was not amended accordingly. However, contrary to the rules of zoological nomenclature, the type species designation changed from *Cucumaria köllikeri* Semper to *C. dubiosa* Semper. Both F.W.E. Rowe and D.L. Pawson (pers. comm.) are of the opinion that the type species of *Pseudocnus* should stand as originally designated and do not favour expanding the diagnosis of the genus to also take in the southern African forms with incomplete baskets.

An examination by the writer of reasonably identified specimens of *Pseudocnus köllikeri* and *P. dubiosus* indicate that both species are characterized not only by the absence of delicate baskets but also of interradial papillae. Further, the body wall deposits of both species comprise exclusively knobbed plates composed of only a single layer of calcareous material. In addition to this, *P. dubiosus* has the two ventral-most tentacles reduced. This combination of characters hence restricts *Pseudocnus* to include only such forms. The southern African species with their more or less equal tentacles, interradial papillae, delicate baskets, and plates composed of more than one layer of calcareous material, cannot be classified in *Pseudocnus* nor in any other nominal dendrochirotid genus. *C. insolens* has been referred to *Trachythyone* Studer at least twice (see Christie & Moldan 1977; Branch & Branch 1981) but this is inadmissible since in *T. muricata* Studer, 1896, the type species of this genus, the two ventral-most tentacles are markedly reduced and only smooth plates occur in the body wall. None of the southern African species here considered can be referred to *Ocnus* since this genus, as defined by its type species (*O. brunneus* Forbes), is also characterized by reduced ventral tentacles. In addition it has only two rows of pedicels per radius and no interradial papillae. Thus, in conformity with current generic distinctions within the family Cucumariidae, a new genus *Pseudocnella* is here erected for the southern African species since *Semperia*, used for *sykion* by Lampert, is preoccupied, having been used by Crosse (1867) for the Mollusca.

Pseudocnella is most closely allied to *Pseudocnus*, *Trachythyone* and *Ocnus* amongst the Cucumariidae. It differs from *Pseudocnus* in the presence of interradial papillae, incomplete baskets, and complex knobbed plates made up of more than one layer of calcareous material; from *Trachythyone* in the equal size of the tentacles and the absence of smooth plates from the

body wall; and from *Ocnus* in the presence of interradial papillae and the more or less equal size of the tentacles.

The Mediterranean *Cucumaria syracusana* Grube may also be classified within the new genus since it shares characters with each southern African species of *Pseudocnella*. It resembles *P. sykion* in its body form and denticulate plates, *P. sinorbis* also in its body form and the presence throughout life of similar baskets, and *P. insolens* in possessing buttons in addition to plates. This combination of characters suggests that it is probably congeneric with the others. Although *P. syracusana* lacks interradial papillae of the type possessed by the others, its pedicels are nevertheless also scattered in the interambulacra and hence it cannot belong in *Ocnus* in which it is currently classified. Perhaps some other similar species, formerly classified in *Ludwigia* by Panning (1949) but provisionally referred to *Ocnus* by Rowe (1970), may also be transferred to *Pseudocnella*. Although Panning (1962) suspected that *Cucumaria capensis* Théel also belonged in *Pseudocnus*, this species can best be classified in *Ocnus* because of its reduced ventral tentacles, ambulacral restriction of the pedicels and the absence of interradial papillae.

Key to the species of *Pseudocnella* gen. nov.

1. Small to medium-sized species; spicules of body wall include, besides incomplete baskets and complex knobbed plates, a layer of regular to irregular knobbed buttons ..... 2.

   Medium-sized species; spicules of body wall include only incomplete baskets and complex knobbed plates; buttons absent ..... 3.

2. Small species (less than 40 mm long) with minute interradial papillae (papulae); baskets nearly always with finely branched, spinose or knobbed extremities; denticles of knobbed plates borne on a projecting 'handle' .... *Pseudocnella insolens* (Théel, 1886)

   Medium-sized species without interradial papillae but pedicels may be scattered in the interambulacra; baskets with smooth rounded extremities; denticles of knobbed plates never borne on a projecting 'handle' .. .. *Pseudocnella syracusana* (Grube, 1840).

3. Incomplete baskets present as a superficial layer throughout life; knobbed plates rarely with one end denticulate; interradial papillae well developed, seldom fully retracted; colour variable, usually light, never black or dark olive green in life..... ..... *Pseudocnella sinorbis* (Cherbonnier, 1952).

   Incomplete baskets present only in juveniles (up to 25 mm long) and sometimes in anal region of slightly larger individuals; knobbed plates often (20%) with one end denticulate; interradial papillae short, strongly retractile; colour always black or a very dark olive green in life, at least dorsally..... ..... *Pseudocnella sykion* (Lampert, 1885).

***Pseudocnella insolens* (Théel) comb. nov.**
(Figures 1a, 2, 5a–c)

Cucumaria insolens Théel, 1886: 70, pl.4, fig.5; Vaney, 1908: 431; 1910: 431; 1912: 27; H.L. Clark, 1923: 411; Bright, 1937: 63; 1938: 87; Stephenson, 1948: 266; Cherbonnier, 1952: 480, pl.39, figs. 1–23; Day, 1959: 502, 545; 1974: 192; Morgans, 1959: 425, 426; 1962: 301, 307, 311; Day, Field and Penrith, 1970: 83.
Semperia insolens Ludwig, 1887: 1231, 1236.
Cucumaria leonina var. ***africana*** Britten, 1910: 240.
Cucumaria sykion Deichmann, 1948: 346 (partim), pl.19, figs. 1 and ?2.
Pseudocnus dubiosus africanus Panning, 1962: 64, figs. 7–9.
Trichythyone (sic) ***insolens*** Christie and Moldan, 1977: 280.
Trachythyone insolens Branch and Branch, 1981: 247, figs., pl.156.

Diagnosis: See Théel, 1886: 70; Cherbonnier, 1952: 480.
Holotype and locality: BMNH, Simon's Bay (Cape Province).
Previous records: SWA(26/15/i); C(29/16/i to 29/17/i, 33/17/i,s to 34/21/i,s, 33/25/i).
Material examined: SWA(26/15/i); C(29/16/i to 29/17/i,s, 33/17/i,s to 34/19/i,s, 34/21/i, 33/25/i to 33/26/i); 438 spec.
Distribution (Figure 6): Luderitz (South West Africa) to Port Elizabeth, 0–40 m.
Habitat: Stones, sand, coarse and khaki sand, shells and *Phyllochaetopterus* debris. Often cryptofaunic but buried in sand; common in dredgings, from intertidal zone to about 40 m.

Description: Specimens small (Figure 1a), 3–40 mm in length. Live colouration generally black to yellow dorsally and yellowish ventrally; some specimens greyish brown, orange or even rust-coloured. Brood pouches (mamelons) present on dorsal surface of only four specimens dredged from Saldanha Bay. In three specimens more numerous mid-dorsally and on the left dorsal interradius, extending to level of anus, absent from most of right dorsal interradius as well as ventrally except at extreme anterior end; in fourth specimen entire dorsal surface, excepting anal region, beset with pouches.

Calcareous ring (Figure 2g) composed of 10 weakly fused pieces. Baskets only occasionally complete, up to 0,06 mm in diameter; incomplete baskets (Figures 2a, 5a and b) numerous, 0,02–0,04 mm. Buttons (Figures 2b, 5b and c) 0,07–0,15 mm, regular with 10 marginal knobs and four holes to quite irregular with about 12 marginal knobs and up to 10 holes. Fir-cone-shaped plates (Figures 2c and 5c) 0,16–0,45 mm long.

Remarks: This species is adequately described by both Théel (1886) and Cherbonnier (1952); only some of the more salient features are here recorded. Brood pouches were first observed in the species by Cherbonnier. In the present specimens the embryos within the pouches are usually orientated anterior end outwards. The

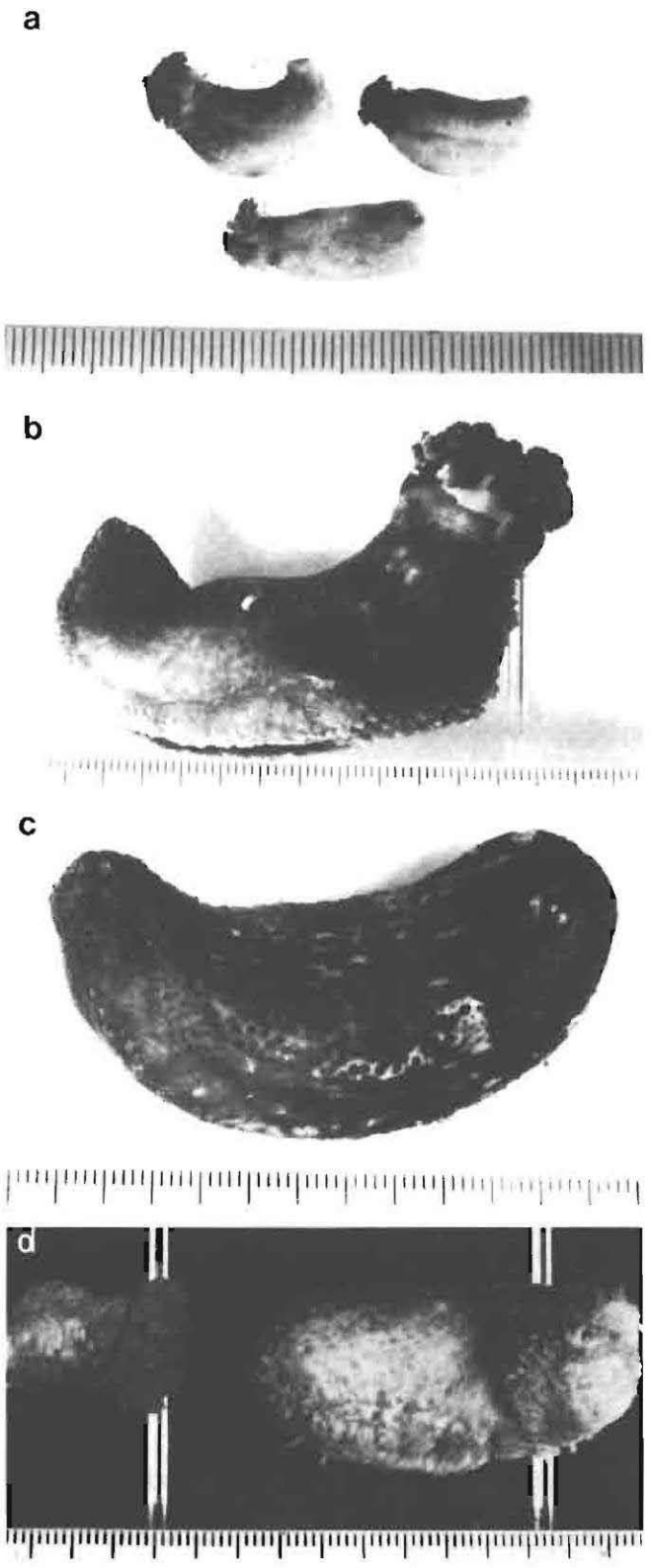

Figure 1 Southern African species of *Pseudocnella*. (a) *P. insolens* (Théel). (b) *P. sykion* (Lampert). (c) Same as (b) (tentacles retracted). (d) *P. sinorbis* (Cherbonnier).

integument of each embryo is covered with scales developed as large, weakly formed, smooth plates with 3–4 large circular fenestrae. Such plates appear to be derived from simple rods with dichotomously branched extremities. Pedicel end plates are also an early development, each beginning as three Y-shaped rods with dichotomously branching arms, the branches of each rod eventually uniting with those of the adjacent rods to form simple end plates with oval fenestrae. Branched rods of a slightly different nature and arranged in two circles around the base of each pedicel are the probable precursors of pedicel deposits (rods and plates) (Figure 2d). The baskets apparently develop later, beginning as short X-shaped rods which later become dichotomously branched and ornamented with spines or nodules, initially one only at each point of bifurcation of the arms, more being acquired later.

In a juvenile (3 mm) from Luderitz a few fenestrated plates of the embryo still persist. It is difficult to say whether these disappear later or are the precursors of the typical fir-cone-shaped plates which are already present but with only short projections instead of 'handles'. The baskets in this specimen are mostly incomplete and smooth as in *P. sinorbis*. In a slightly larger juvenile (3,5 mm) from Cape St. Francis, the fir-cone-shaped plates are numerous, simple, but with clear signs of becoming multi-layered. The buttons, however, are well formed and apparently acquired after baskets and plates.

There is no evidence of brood pouches in forms examined from the intertidal zone. Their presence in forms dredged at 15 m perhaps indicates that adults migrate into deeper waters during the breeding season, leaving only juveniles in the intertidal zone. During the non-breeding season, however, both adults and juveniles may be found in the intertidal zone. It does not seem likely that two varieties of the species or sibling species exist.

Of the three southern African species here assembled under *Pseudocnella, P. insolens* is the least typical. In its size, brooding habit, absence of anal teeth, reduction of some tentacles, weakly fused radial and interradial plates of the calcareous ring, and in the presence of pedicel end plates, and buttons in addition to baskets and fir-cone-shaped plates, it stands apart from the others in the group.

Deichmann's (1948) error in considering this species as a growth stage of *P. sykion* was probably a result of the presence in her material of *P. sinorbis*, whose superficial layer of deposits (incomplete baskets) is reminiscent of that of *insolens* whereas the inner layer (knobbed plates) is of the *sykion* type. This species was probably mistaken to represent an intermediate stage between the presumed juvenile *insolens* stage and the adult *sykion* stage. What lends support to this assumption is that the incomplete baskets of *P. sykion* illustrated by her are not like those of *P. insolens* but of *P. sinorbis,* whereas the knobbed plate is definitely of the *insolens* type.

There appears to be no basis for both Deichmann's (1948) and subsequently Panning's (1962) intimations that *sykion* and *insolens* are conspecific, one being a growth stage of the other. Since Lampert's types are lost we must draw inferences from a comparison of the description of the holotype of *C. sykion* with the species described by Théel (1886) as *C. insolens* and locally

recognized as such.

According to Lampert (1885) the holotype of *C. sykion* measured 50 mm in length and 20 mm in breadth. These dimensions are typical of medium-sized specimens of *P. sykion*. The maximum length of 438 specimens of *P. insolens* examined by the writer, is 40 mm and the maximum breadth 12 mm. In fact 40 mm is also the length recorded for the species by various workers, except H.L. Clark (1923) who gives a figure o£ 47 mm. Lampert described the retractor muscles of the type as consisting of several strands. This feature is characteristic of the species locally known as *C. sykion* and not present in any other species here considered. Further, Lampert only mentions one kind of deposits in *sykion*, namely knobbed plates of which the superficial ones are stated to be spinose. Such plates are typical of *P. sykion* as we know it (Figures 4a and 5d). In *P. insolens*, on the other hand, there are not only knobbed plates but also a superficial layer of incomplete baskets developed as cross-shaped rods with bifurcating arms (Figures 1a and 5a), and a layer of knobbed buttons (Figures 1b and 5b, c). Lampert also quite categorically states that there are no end plates in the pedicels of his type. Such plates always occur in the pedicels of *P. insolens*. From the above it is clear that Lampert's *C. sykion* is not conspecific with Théel's species but the same species recognized by both H.L. Clark (1923) and Cherbonnier (1952) as *P. sykion* and locally referred to as this species. The question that one species might represent a growth stage of the other is ruled out by the fact that whereas the small *P. insolens* is brood-protecting the larger *P. sykion* is not.

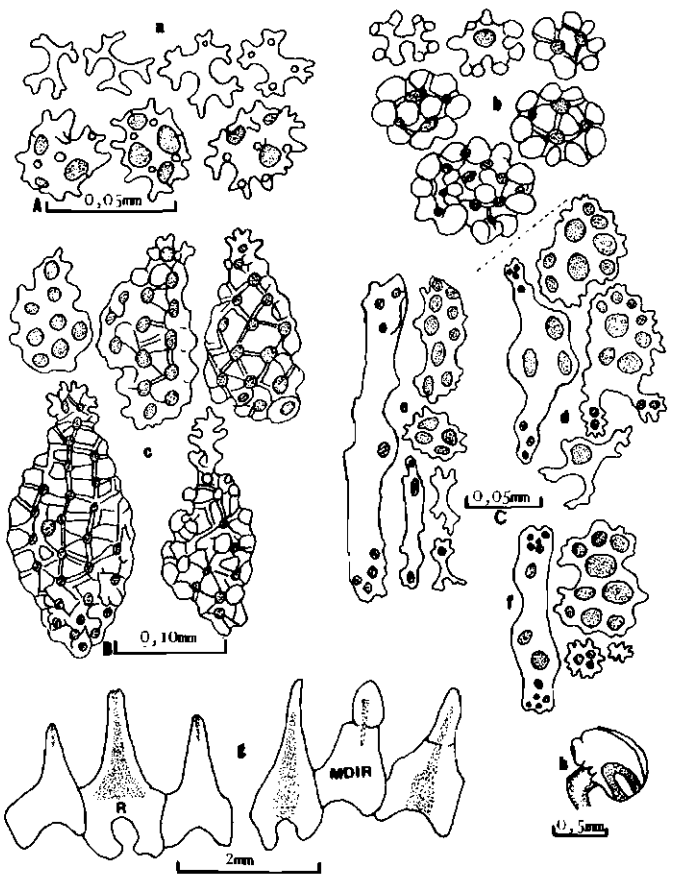

Figure 2 *Pseudocnella insolens* (Théel). (a) Baskets from dorsal body wall (various stages); (b) buttons from dorsal body wall (various stages); (c) plates (various stages); (d) pedicel spicules; (e) tentacular spicules; (f) introvert spicules; (g) parts of calcareous ring of two specimens; (h) madreporic body. b&c — Scale A; MDIR — mid-dorsal interradial plate; R — radial plate.

Cucumaria leonina var. *africana*, described by Britten (1910) from Luderitz, was referred to the synonymy o£ *P. insolens* by H.L. Clark (1923) after examination of syntypes housed in the Museum of Comparative Zoology, Harvard, U.S.A. Although Panning (1962) treats Britten's variety as a subspecies of *Pseudocnus dubiosus*, following Clark, it is here retained as a synonym of *P. insolens*.

Pseudocnella sinorbis (Cherbonnier) comb. nov.

(Figures 1d, 3, 5e and f)

Cucumaria sykion Deichmann, 1948: 346 (partim), pl.19, figs. 3 and 4; ?Plietz and Robinson, 1974: 60, pl.326.

Cucumaria sykion (insolens stage) Deichmann, 1948: 372 (Station G), 373 (Station W) (non Station Ag).

Cucumaria sinorbis Cherbonnier, 1952: 482, pl.38, figs. 1–13, pl.39, figs. 24–31.

Diagnosis: See Cherbonnier, 1952: 482.

Syntypes and locality: Mus. Nat. Hist.(Paris); Table Bay and Port Edward (Natal).

Previous records: C(33/18/?i, ?34/23/i); N(27/32/i, 31/30/i).

Material examined: C(34/20/i to 34/22/i, 34/24/i to 33/28/i); N(31/30/i, 27/32/i); M(24/35/i); 106 spec.

Distribution (Figure 6): Table Bay to Jangamo, south of Inhambane (Mozambique); intertidal.

Habitat: Cryptofaunic, usually buried in sand; also found in soft detritic conglomerates of stones, sand, shells, etc.

Remarks: The largest specimen in the present material measures 95 mm along the ventral surface. The live colouration is nearly always light, ranging from white to off-white to grey or greyish-brown. Some specimens collected from the south coast are pale brown, orange or even rust coloured. As the species is always concealed, either living buried in sand or in detritic conglomerates, dark forms are rarely encountered.

The species (Figure 1d) can readily be separated from the congeneric *P. sykion* (Lampert) by its lighter colouration, rough skin, large interradial papillae frequently equalling the size of the dorsal pedicels, fewer rows of pedicels (2–4), and the presence, throughout life, of a continuous layer of incomplete baskets, which are always smooth, quite unlike those of *P. insolens*. Such baskets (Figures 3a and 5f) (0,024–0,055 mm) have rounded incurved extremities, a feature overlooked by Deichmann (1948). Since similar baskets also occur in juveniles of *P. sykion*, preserved juveniles of both species can be separated on the size of the baskets (0,015–0,037 mm in *P. sykion*) and on the basis of

knobbed plates which, in *P. sinorbis* (Figures 3d and 5e), are rarely denticulate, measuring 0,07–0,35 mm in length. Complete baskets (Figure 3c), up to 0,05 mm in diameter, are sometimes present in juveniles.

Pseudocnella sinorbis shows a more or less identical distributional pattern to *P. sykion* (Figure 6). However, both species occupy different ecological niches (see ecological notes). The occurrence of *P. sinorbis* as far north as Mozambique extends its northward range. Besides *P. sykion* the species shares some affinities with the Mediterranean *P. syracusana,* differing from it in the presence of equal tentacles, interradial papillae, absence of buttons, and the rarity of denticulate plates.

Pseudocnella sykion (Lampert) comb. nov.

(Figures 1b, c, 4 and 5d)

Semperia sykion: Lampert, 1885: 250.

Cucumaria sykion: Théel, 1886: 266; H.L. Clark, 1923: 412; Stephenson, Stephenson and du Toit, 1937: 359, 363, 381; Stephenson, Stephenson and Bright, 1938: 18; Eyre, and Stephenson, 1938: 18; Eyre, Broekhuysen and Crichton, 1938: 96, 110; Stephenson, 1944: 306, 317, 348; 1948: 266; Deichmann, 1948: 346 (partim) (non ***C. sykion, insolens*** stage); Cherbonnier, 1952: 483, pl.40, figs. 1–18; Kalk, 1958: 223, 238; Macnae and Kalk, 1958: 130; Day, Field and Penrith, 1970: 83; Day, 1974: 192; Jackson, 1976: 14, 15; Branch and Grindley, 1979: 169; Branch and Branch, 1981: 247, figs.

Cucumaria jägeri Lampert, 1885: 249; H.L. Clark, 1923: 413.

non ***Stereoderma jägeri*** Panning, 1949: 422.

Pseudocnus dubiosus jägeri Panning, 1952: 126, figs. 6–9.

Pseudocnus dubiosus jaegeri Panning, 1962: 66, figs. 10 and 11; Pawson, 1969: 37 (passim).

? **Black holothurian** Day, Millard and Harrison, 1952: 412.

Diagnosis (From Lampert, 1885; Cherbonnier, 1952; modified herein): Barrel-shaped species up to 60 mm long (Figure 1b and c). Colour a very dark olive green to black. Pedicels in 4–7 rows. Interradial papillae (papulae) minute, strongly retractile. Anal teeth present. Stone canal and polian vesicle single; each retractor muscle composed of 4–7 strands. Spicules an external layer of minute, smooth, incomplete baskets, present only in juveniles under 25 mm (Figure 4h); adults with only densely packed round to oval knobbed plates, often (20%) with one end denticulate, but denticles never borne on a projecting 'handle' (Figures 4a, b and 5d).

Holotype and locality: Lost; Algoa Bay (Cape Province).

Previous records: C(34/18/i to 33/28/i); T(32/28/i, 31/29/i); N(29/30/i to 31/30/i, 27/32/i); M(26/32,33).

Material examined: C(34/19/i to 33/28/i); T(32/28/i to 31/29/i); N(30/30/i to 27/32/i); M(24/35/i); 357 spec.

Distribution (Figure 6): Cape Agulhas to Jangamo, south of Inhambane, Mozambique; intertidal.

Habitat: Common under stones, in pools and in rock crevices; adults usually exposed, juveniles cryptofaunic.

Remarks: This species is rediagnosed to separate it from

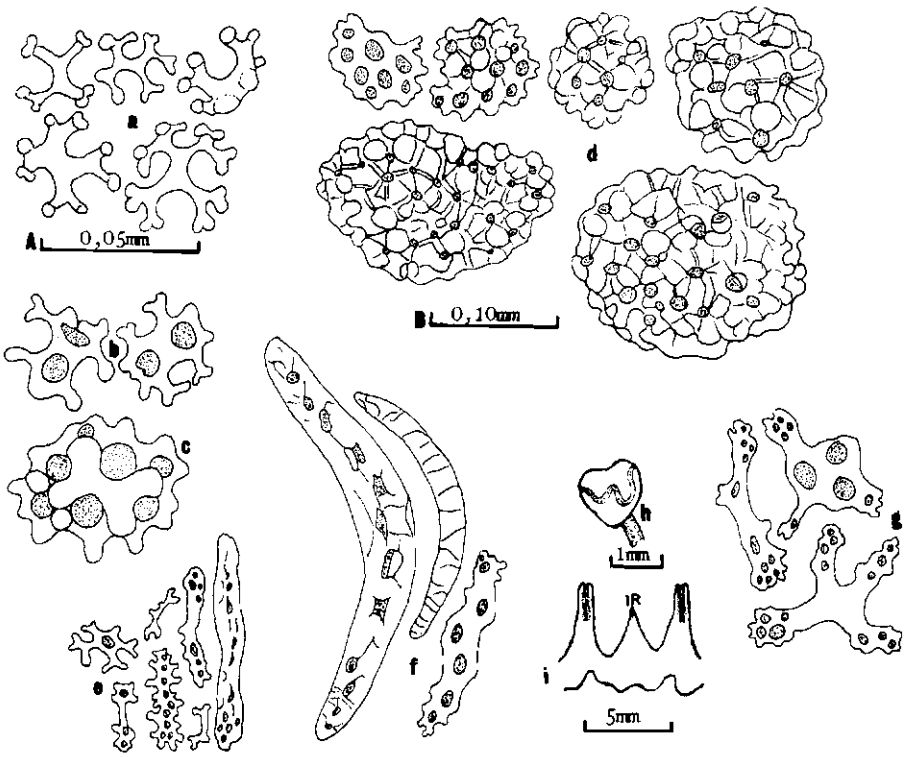

Figure 3 *Pseudocnella sinorbis* (Cherbonnier). (a) Incomplete baskets from oral region; (b) baskets from ventral body wall; (c) complete basket; (d) plates from dorsal body wall; (e) introvert spicules; (f) tentacular rods; (g) pedicel spicules; (h) madreporic body; (i) part of calcareous ring. a–c Scale A; d–g Scale B. IR — interradial plate.

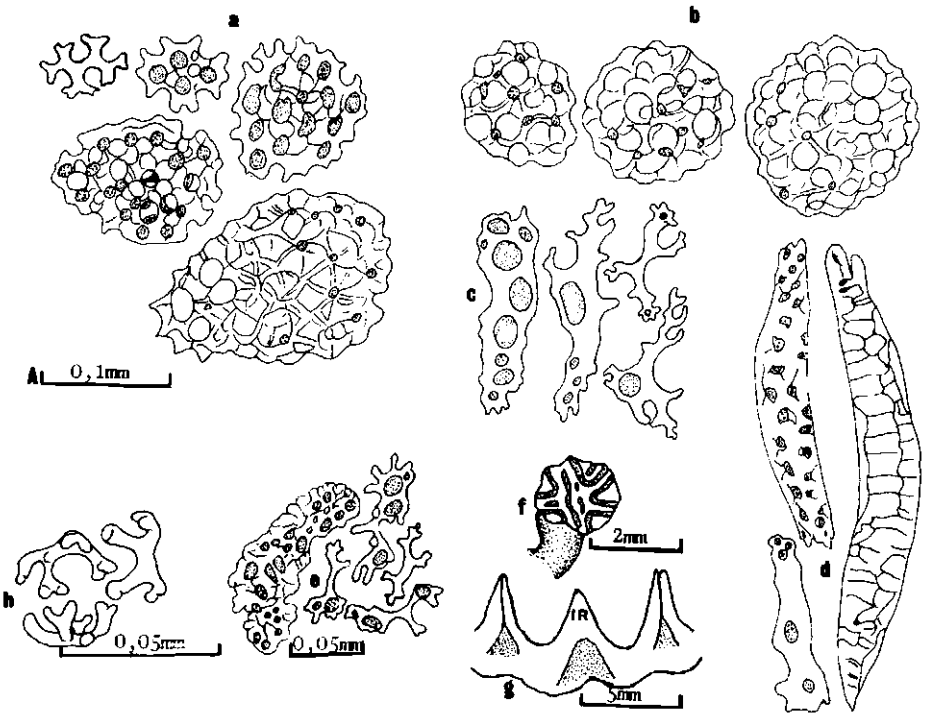

Figure 4 *Pseudocnella sykion* (Lampert). (a) Plates from dorsal body wall (various stages); (b) spherical plates from dorsal body wall; (c) pedicel spicules; (d) tentacular spicules; (e) introvert spicules; (f) madreporic body; (g) part of calcareous ring; (h) incomplete baskets (from juvenile). a–d Scale A. IR - interradial plate.

the sympatric *P. sinorbis* with which it has been confused on numerous occasions. Since it lives mostly exposed, only dark forms are encountered. This probably also explains the loss of baskets in adults and their presence in juveniles which are always concealed. The baskets (Figure 4h) are smaller (0,015–0,037 mm) than those of the juveniles of *P. sinorbis* (0,024–0,055 mm) and may persist in the anal region of slightly larger individuals or sporadically in the entire integument. Rarely some adults ('freaks' or ?hybrids) contain baskets. The plates (Figures 4a, b and 5d) measure 0,10–0,25 mm, with the non-denticulate rounded ones resembling those of *P. sinorbis*.

Since Lampert's (1885) description, *C. jaegeri* has only been recognized by Panning (1952, 1962). However, one can hardly discern from Panning's descriptions the differences between his *jaegeri* and Lampert's *sykion*. The structure, except for the retractor muscles which are said to be in single strands, does not differ from our knowledge of the structure of *P. sykion*. It is therefore probable that Panning had *sykion* in front of him which he identified as *jaegeri*. What lends support to this assumption is that in 1962, following Deichmann (1948), he regarded *sykion* and *insolens* as being conspecific. It is regrettable that even as late as 1962 Panning overlooked Cherbonnier's (1952) paper which clearly resolved the confusion initiated by Deichmann (1948). The writer was able to verify all of Cherbonnier's observations.

As suspected by both H.L. Clark (1923) and Deichmann (1948), Lampert's *sykion* and *jaegeri* are probably conspecific. The plump knobbed bodies as those described for *jaegeri* by Lampert are only found in *P. sykion* and *P. sinorbis (cf.* Figures 4b and 3d; 5d and e) amongst the cucumariids of Natal (the type locality of *jaegeri*). However, while *P. sinorbis* has well developed interradial papillae that are rarely completely retracted (Figure 1d) and a superficial layer of delicate baskets throughout life (Figures 3a and 5f), *P. sykion* has minute highly retractile papillae (Figures 1b and c) and baskets only in juveniles (< 25 mm in length) (Figure 4h). Since Lampert's *jaegeri* measured 45–55 mm in length and presumably had no interradial papillae (as these were not described), it must have been a faded *sykion* with fully retracted papillae. Hence both Lampert's *sykion* and *jaegeri* must be regarded as being conspecific.

Although *P. jaegeri* has page priority, for the sake of stability of nomenclature, the long established name *sykion* is preferred since its description is in greater detail, the species has been recognized many times in the past, and since it is the name that has been in common usage by both marine biologists in southern Africa and holothurian specialists who worked particularly on southern African material. Further, Deichmann (1948) as first reviser, though with some doubt, lists *jaegeri* as a synonym of *sykion*. To prevent further confusion, a specimen of *P. sykion* from East London, labelled as neotype (SAM A 23444), is deposited in the South African Museum, Cape Town.

Figure 6 illustrates the distribution around the coast of the three southern African species of *Pseudocnella*. *P. insolens* extends from Luderitz on the west coast to Port Elizabeth on the south coast, being intertidal and

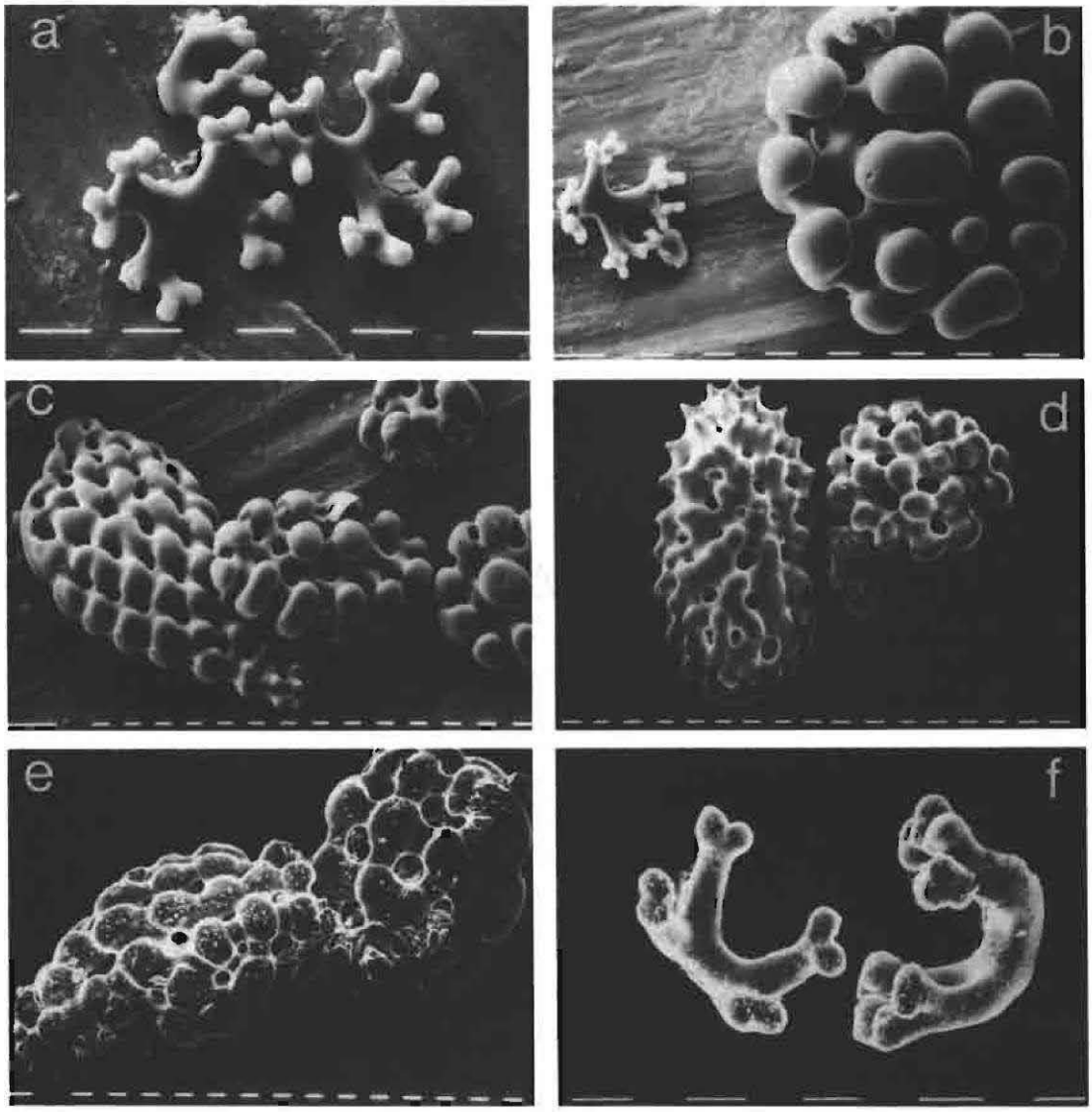

Figure 5 Scanning electron micrographs of the body wall spicules of the southern African species of *Pseudocnella*. (a) Baskets of *P. insolens;* (b) basket and button of *P. insolens;* (c) plate and buttons of *P. insolens;* (d) plates of *P. sykion;* (e) plates of *P. sinorbis;* (f) baskets of *P. sinorbis*. Scale bars = 10 μm.

subtidal to depths of about 40 m. Its occurrence on the west coast, absence from waters east of Port Elizabeth, and its brood-protecting habit, suggest that it is a cold-water species. In fact brood-protection is characteristic of many Antarctic, sub-Antarctic and New Zealand dendrochirotid holothurians.

P. sykion and *P. sinorbis*, on the other hand, are south and east coast warm-water species, restricted to the intertidal zone, the former extending from Cape Agulhas to Jangamo in southern Mozambique and the latter from Table Bay to Jangamo. Despite their identical distributional range both species are ecologically isolated. *P. sykion* lives exposed on rocky shores where it is usually wedged in narrow crevices or occurs in great abundance around the bases of rocks, from the lower part of the littorina zone to the lower balanoid zone. *P. sinorbis*, on the other hand, is almost always concealed, living buried in sand as happens on the south coast or in detritic conglomerates on the east coast. It is often cryptofaunic but always buried in sand. It is possible that this ecological niche separation between the two sympatric sister species obviates competition between them and ensures their continued co-existence. However, research into their feeding habits, behaviour and reproductive biology is still needed in support of this assumption.

The cold-water *P. insolens*, however, co-exists with the warm-water *P. sinorbis* in a wide area from Table Bay to Port Elizabeth, often occupying the same habitat in a single locality. Although it is not certain whether each species is utilizing the environmental resources in a different way, the degree of morphological differences between them, their different breeding habits and temperature tolerances, might suggest so. Hence there may be subtle niche differences between them and perhaps even different feeding habits, thus allowing them to co-exist in areas of ecological overlap. However, only research into aspects of their biology will help support this speculation.

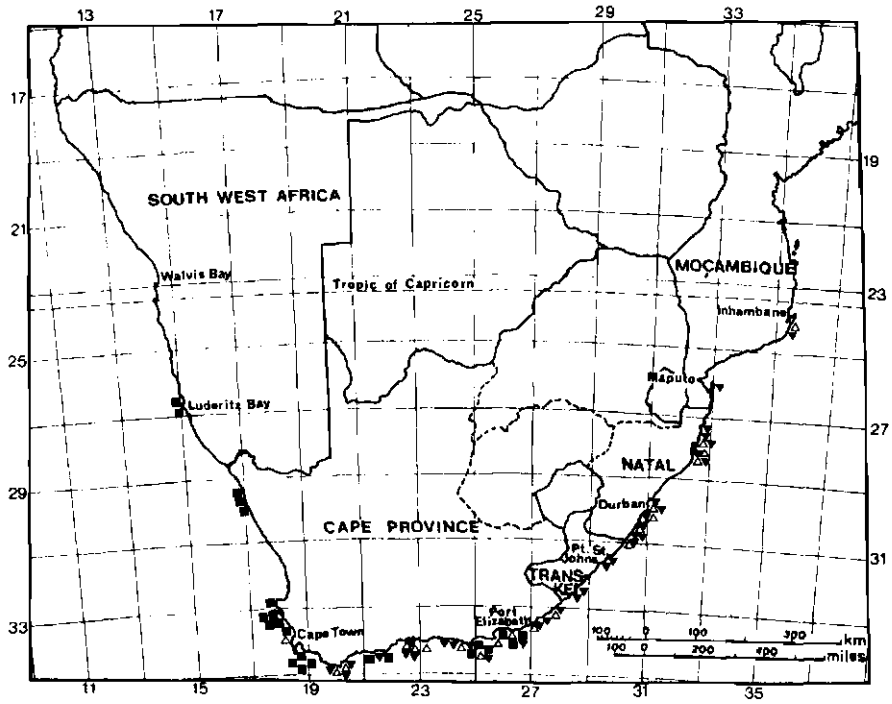

Figure 6 Distribution of the three southern African species of *Pseudocnella*. ■ *P. insolens* (Théel), ▼ *P. sykion* (Lampert) and △ *P. sinorbis* (Cherbonnier).

Although *P. insolens* and the Mediterranean *P. syracusana* differ substantially from their congenors *P. sykion* and *P.sinorbis*, there is little doubt that all four species are interrelated. The high endemicity of the southern African marine fauna, the restriction of several species to the West Indian Ocean and some evidence of speciation by geographic isolation, suggest that, although southern Africa is a region of secondary colonization, there was nevertheless a later development of an active evolutionary centre. This view was expressed by Millard (1978) for the hydroids and more recently by Thandar (1984: unpublished Ph.D. thesis) for the holothurians. Thus the endemicity, wide areas of sympatry, and some evidence of ecological niche separation suggest that the three southern African species of *Pseudocnella* speciated out within this region. Lack of evidence of any spatial separation of populations in the past, perhaps supports the idea of sympatric speciation by ecological isolation. It appears that the common ancestor of all four species was a form not unlike *P. sinorbis* which thus appears closest to the ancestral form. Perhaps it had equal tentacles, well developed interradial papillae, complete baskets and non-denticulate plates. The probable evolution and relationships of the four species is represented in a provisional cladogram (Figure 7) in which each dichotomy indicates at least one character divergence.

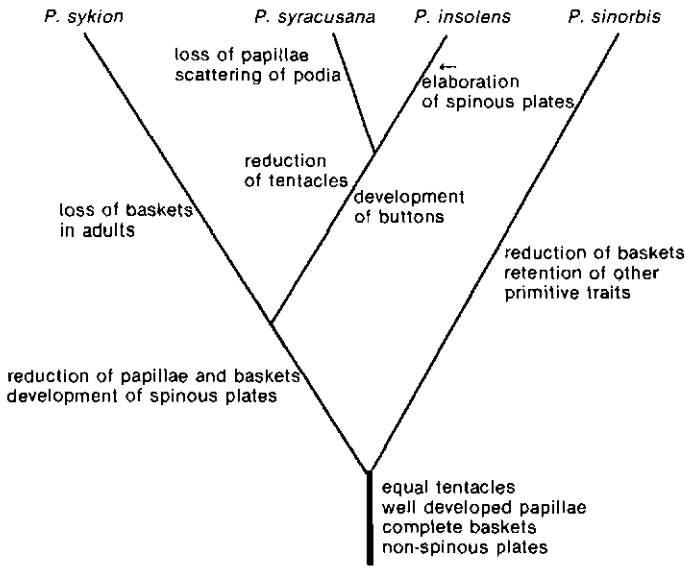

Figure 7 Provisional cladogram to show relationships and character divergence of the four species of *Pseudocnella*.

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