

CONTRIBUTIONS TO THE MORPHOLOGICAL DIVERSITY AND CLASSIFICATION OF THE ORDER CAVIBELONIA (MOLLUSCA: SOLENOGASTRES)

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ABSTRACT

The status of families within the order Cavibelonia is poorly understood. Here, description of new species and reexamination of type material yield new information on organizational diversity and systematic demarcations in the order. The families Drepanomeniidae and Rhipidoherpiidae are confirmed, and a new family Notomeniidae is proposed. Within Simrothiellidae, biodiversity at both the species and genus level is increased. Within Rhipidoherpiidae, as well as Proneomeniidae, the supraspecific taxa are elucidated. Of the eight species concerned, five are new: *Drepanomenia tenuitecta* n.sp. and *D. pontisquamata* n.sp. (Drepanomeniidae), *Simrothiella digitoradulata* n.sp., *S. abysseuropaea* n.sp. and *Aploradoherpia insolita* n.gen. n.sp. (Simrothiellidae). Observations on *A. insolita* confirm the independent origin of the (mesodermal) pericardioducts and (ectodermal) spawning ducts. A re-examination of the southern Norwegian *Simrothiella margaritacea* (Koren & Danielssen) revealed that specimens from the West European Basin belong to a separate species *S. abysseuropaea* n.sp. Two former *Proneomenia* species are revised and reclassified: *Thieleherpia* n.gen. is proposed for *Proneomenia thulensis* Thiele (Rhipidoherpiidae) and *Dorymenia* for *Proneomenia quincarinata* Ponder (Proneomeniidae). After re-investigation of *Notomenia clavigera* Thiele, this species is classified in the new family Notomeniidae.

INTRODUCTION

The Solenogastres are a small, still poorly known class of aplacophoran Mollusca, characterized by the mantle cover of cuticle and calcareous sclerites (scales or spicules) and by the laterally rounded body with the foot narrowed to a longitudinal pedal groove. With respect to characters of the alimentary tract (no true radula ribbon, midgut without separate digestive gland) and to the lack of special excretory organs (no emunctoria), they appear to represent a basal off-shoot of Mollusca. The arrangement of the mantle cover with cuticle and sclerites, known as the aplacophoran condition, is shared with the clearly different, paraphyletically separated Caudofoveata, and supports the primitive position of the Solenogastres (Salvini-Plawen & Steiner, 1996; Haszprunar, 2000; Salvini-Plawen, 2003).

Their generally small size (mostly between 3 and 30 mm, but up to 300 mm) and marine habitat (mostly below 50 m depth), mean that great effort and expense are required to collect them. This, as well as their organization with mainly internal systematic characters (in contrast to placophoran and conchiferan molluscs), has prevented a broader engagement and greater familiarity by scientific workers. We are thus left with a still fragmentary knowledge, not only of biological, developmental and physiological features, but even with respect to pure faunistics (biodiversity, biogeography, etc.). This incompleteness also includes several systematic descriptions that are only fragmentary when compared with the required standard, and these await supplementation or revision.

At present, about 230 species of Solenogastres have been named and new ones are under description. In addition, much material from recent collections and expeditions awaits elaboration, which will no doubt contribute to enlarging our knowledge. Despite the revised classification by Salvini-Plawen (1978), several systematic problems remain (Salvini-Plawen, 2003). New

findings reveal that additional corrections will be needed, and this is also due to supplementation and revision of earlier descriptions. This may even apply to recent publications when the state of the original material was insufficient for a comprehensive insight. In a group where we still need to improve and enlarge our comparative knowledge, all new information is valuable. This situation vindicates even fragmentary descriptions of singular, rare species as long as they are unmistakably characterized and clearly, recognizably defined against all other species.

In 1978, Salvini-Plawen introduced a new system of the Solenogastres, classifying them into the four orders Pholidoskepia, Neomeniamorpha, Sterrofulstia and Cavibelonia. Members of the Cavibelonia are mainly characterized by the elaboration of calcareous mantle sclerites, which are provided with a central cavity. These epidermal, mostly needle-shaped (acicular), hollow sclerites require a special mode of formation (Hoffman, 1949) and the order may thus represent the most advanced of the Solenogastres. This character of hollow needles is mostly combined with the presence of a thick cuticle (>35 µm) and epidermal papillae. Cavibelonia thus replace the Proneomeniidae s.l. and most of Neomeniidae s.l. in former systems (cf. Thiele, 1913; Hoffmann, 1929; Hyman, 1967).

The main character of this taxon, the hollow acicular sclerites, exhibits different arrangements, being in either radial or tangential alignment (Hoffman, 1949). The latter may be produced in a single, obliquely disposed layer, or arranged in two or more rather rectangularly intercrossing layers of low angle and almost embedded within the cuticle (termed 'skeletal' by Scheltema, 1999; Scheltema & Schander, 2000). The spicules may be either thick-walled or thin-walled. Further, spicules may be distally hooked (or barbed), asymmetrically flattened and serrate, or asymmetrically axe-like (termed 'capitate' by Arnovsky, 2000). These different elaborations, however, concern the generic level only, as demonstrated by the occurrence of a range of states within Pararrhopaliidae and Simrothiellidae (e.g. Table 3). Consequently, some or all of these characters

may be polyphyletic, as also indicated by certain sporadic findings (Salvini-Plawen, 1978; Scheltema & Kuzirian, 1991; Handl & Salvini-Plawen, 2002). However, cladistic analysis (Salvini-Plawen, 2003) suggests that this situation does not affect the monophyletic status of the taxon Cavibelonia.

There is great diversity in internal organization among Cavibelonia. Predominantly according to the types of foregut glandular organs and of the radula, 11 genus-groups or families have been defined: Acanthomeniidae, Pararrhopaliidae, Rhopalomeniidae, Amphimeniidae, Simrothiellidae, Drepanomeniidae, Strophomeniidae, Proneomeniidae, Epimeniidae, Syngenoherpiidae, Rhipidoherpiidae (cf. Salvini-Plawen, 1978). The definition of these families reflects the present knowledge of species organization. This approach suffers, however, from errors and inadequate descriptions in earlier literature and also from the gaps in knowledge of specific as well as generic diversity. The best-defined family is the Amphimeniidae (Salvini-Plawen, 1972, 1978), with 22 species within 10 genera provided with several autapomorphic characters. On the other hand, there are three monogeneric families (Drepanomeniidae, Syngenoherpiidae and Rhipidoherpiidae) and more information is required to determine whether their classification is vindicated or over-interpreted.

To establish a better foundation for the insufficiently understood status of the families within Cavibelonia, new representatives and certain type material are investigated here. The results contribute to our knowledge of both cavibelonian diversity as well as systematics at the genus and family level.

MATERIAL AND METHODS

All material comes from institutional collections, and specimens are preserved in alcohol. Mantle sclerites were isolated manually and embedded (double-slides), then drawn with camera lucida. Specimens were decalcified in Bouin's fluid, embedded in paraffin, serially cross-sectioned at 10 μm (6 μm for *Thieleherpia thulensis*) and stained with Heidenhain's Azan. One individual of *Simrothiella margaritacea* was used for preparation of a whole mount of the radula apparatus by histolysis of tissues with bleach.

Institutional abbreviations:

DMW, Dominion Museum, Wellington, New Zealand

USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA

SMNH, Swedish Museum of Natural History, Stockholm, Sweden

ZMB., Museum für Naturkunde der Humboldt-Universität, Berlin, Germany

ZMUB, Zoologisk Museum, University of Bergen, Bergen, Norway

ZMUC, Zoologisk Museum, University of København, Danmark

SYSTEMATIC DESCRIPTIONS

Order Cavibelonia Salvini-Plawen, 1978

Diagnosis: Solenogastres with acicular, generally hollow mantle sclerites; cuticle mostly thick; commonly with epidermal papillae.

Drepanomeniidae Salvini-Plawen, 1978

Diagnosis: Solenogastres with thick cuticle, sclerites as hollow needles (Cavibelonia) in one layer; type of radula unknown (vestigial), ventral foregut glandular organs epithelial; with respiratory organs, without seminal receptacles.

Genus *Drepanomenia* Heath, 1911

Diagnosis: Solenogastres-Cavibelonia with hollow needles in one layer only; opening of mouth within atrium; without radula, ventral foregut glandular organs epithelial, midgut with serial constrictions; dorso-terminal sense organ present; secondary genital opening unpaired; without seminal receptacles and copulatory stylets; secondary gills present.

Type species: *Neomenia vampyrella* Heath, 1905.

Drepanomenia tenuitecta new species

(Figures 1, 2)

Types: Holotype (USNM 1016981), 4 mm length, serial cross-sections on slides; Tasman Sea west of New Zealand (38°27'–38°30' S, 168°04'–168°07' W), Station 24-1718 of US Antarctic Research Program (USARP), 12 July 1966, 531–659 m.

Etymology: Latin *tenuis*, thin, tender, slim; *tectum*, roof, covered; referring to the rather thin mantle cuticle.

Diagnosis: Body about 4 × 1 mm with rounded body ends, cuticle moderately thick, with epidermal papillae; hollow needles in radial arrangement, mid-dorsally forming a feeble crest; pedal groove with three folds, separated from pallial cavity by mantle epithelium; mantle cavity with four respiratory folds; foregut forming proboscis with the tubular glandular organs opening at its tip; midgut with paired rostral caecum. No abdominal spicules.

Material examined: Holotype and a juvenile specimen (USNM 1016982), 1 mm in length, serial cross-sections on slides, from type locality.

Mantle: Epidermis (15 μm high) forming slender papillae which end with distal vesicle (20–25 μm diam.) filled with granules. Spicules (Fig. 1) giving the animals furry aspect are hollow, slightly curved, thin-walled needles (70–110 μm × 8–12 μm ; Fig. 1A), rising above 50–75 μm thick cuticle; all in one layer, dorsally to radially arranged, mid-dorsally forming a feeble crest; several strong, almost straight, thick-walled spicules (100–180 μm × 15–20 μm ; Fig. 1B) are sunk into the muscula-

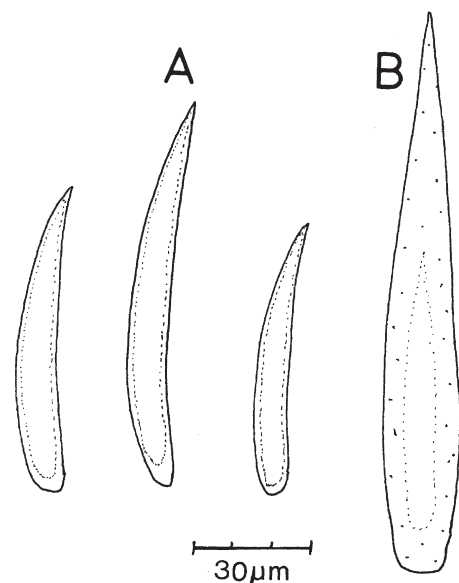


Figure 1. *Drepanomenia tenuitecta* new species: mantle sclerites. **A.** General spicules. **B.** Interspersed straight spicules.

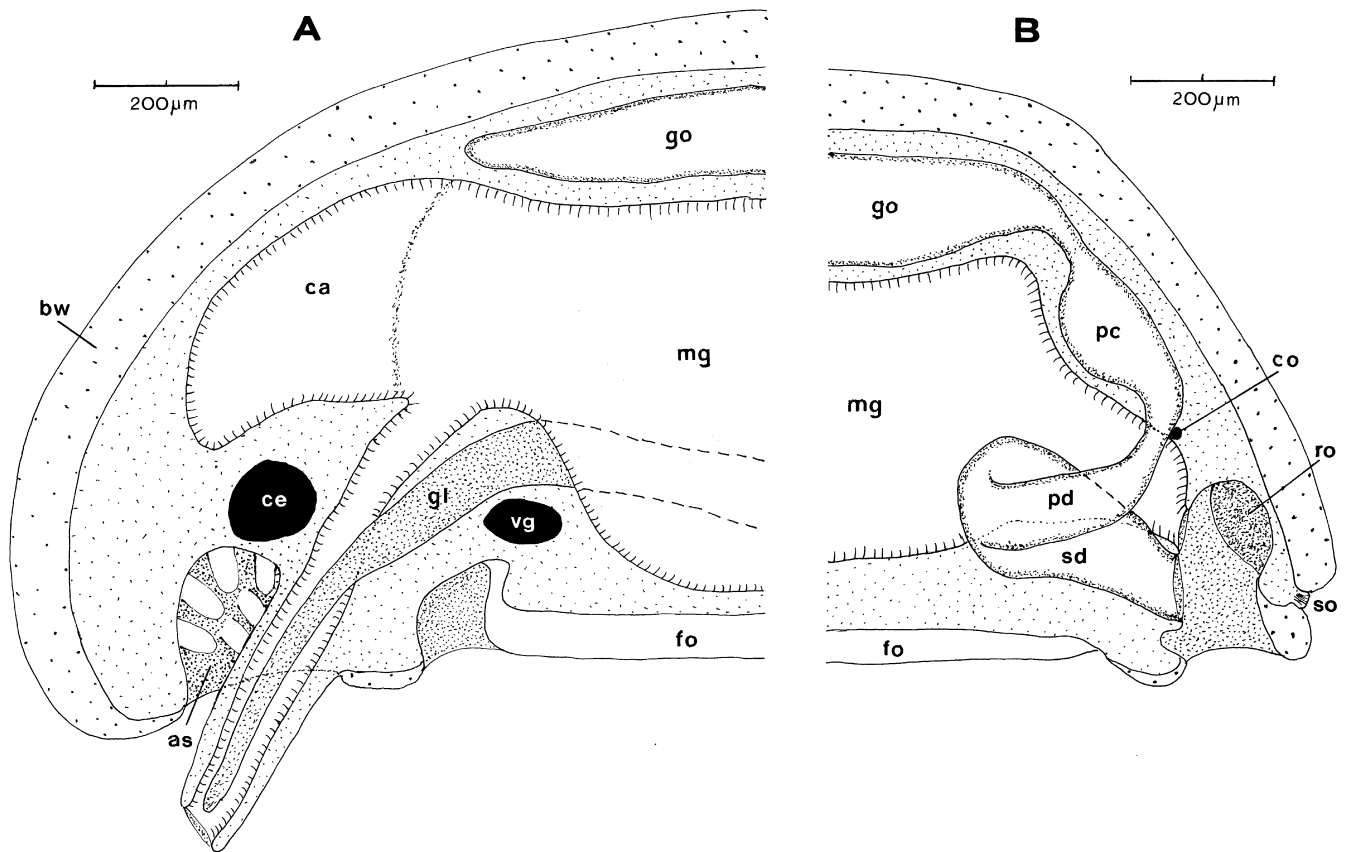


Figure 2. *Drepanomenia tenuitecta* new species, schematic organization, reconstructed from serial transverse sections: **A.** Anterior body. **B.** Posterior body. Abbreviations: as, atrial sense organ; bw, body wall (mantle and musculature); ca, midgut caecum; ce, cerebral ganglion; co, supra-rectal commissure; fo, pedal folds (foot); gl, ventral foregut glandular organ; go, gonad; mg, midgut; pc, pericardium; pd, pericardioduct; ro, respiratory organ; sd, spawning duct; so, terminal sense organ; vg, (first) ventral ganglion.

ture. No special sclerites (abdominal spicules) at anterior border of mantle cavity.

Foot and mantle cavity: Ciliated pedal pit receiving intercellularly opening pedal glands, posteriorly forming three dorsal folds entering the externally distinctly visible pedal groove. The three folds (central being most prominent) extend to level of spawning ducts where only central fold remains; groove ends close behind, i.e. in front of mantle cavity, separated by large mantle bridge. Sole glands along entire groove emptying within foot. Only single pedal fold present in juvenile. Mantle cavity relatively small, anteriorly with openings of hindgut and unpaired outlet of spawning ducts only. Dorsal and posterior portions of 10–13- μm -high epithelium more densely ciliated. Behind the cavity opening are four internal, dorso-ventrally running, frontally directed respiratory folds.

Musculature. Three-layered body wall musculature reinforced ventrally by numerous and spongily arranged longitudinal fibres. Serial dorsoventral bundles large, constricting midgut.

Sensory system. Unpaired cerebral ganglion (120 μm wide, 80 μm high, 60 μm long) gives rise to two pairs of ventrolateral nerves with small basal swelling towards atrial sense organ; a third, ventral pair extends into proboscis. Cerebral connectives separate from their origin. Buccal connectives enter proboscis; presence of buccal ganglia uncertain. First lateral ganglia (120 $\mu\text{m} \times 25 \mu\text{m}$ diam.) extend between cerebral ganglion and body wall. First ventral ganglia (60 μm diam.) above pedal

pit are interconnected by two commissures, each releases a nerve to beginning of foot and a lateroventral connective to one of lateral ganglia. Body nerve cords with ganglia interconnected by ventral commissures and less frequently lateroventral connectives. Starting in region of spawning ducts, lateral cords are medullary, each shows a posterior-most lateroventral connective running between gut and spawning duct. Ganglia posteriora superiora (60 μm diam.), lateral of rectum, interconnected by 100- μm -long medullary supra-rectal commissure (25 μm diam.); releasing at least one pair of dorsocaudal nerves 55 μm apart. Behind above-mentioned terminal connectives, ventral cords curve dorsally to run along dorsal side of the spawning ducts to their ends. Due to protruded proboscis, atrial sense organ is strongly deformed; no ciliary tracts or folds recognizable (see *D. vampyrella*). Ventrally, proboscis epithelium (partly atrial) shows cells 25 μm high that could represent atrial ridges. Frontal and lateral walls of atrium possess blunt papillae filling organ. Dorsoterminal sense organ is a terminal epithelial bulge.

Alimentary tract. Proboscis in both specimens everted, bulb-like. Mouth at tip of proboscis which projects 1 mm from body. Proboscis formed by evagination of posterior roof epithelium of atrial cavity; its musculature formed by ventral portion of dorsoventral musculature and by ventral body wall musculature. Proboscis round in cross-section (160–180 μm) with proximal swelling; epithelium (dorsally 15–20 μm , ventrally 20–25 μm) with gland cells. Central foregut (60–80 μm diam.) lined by weakly folded epithelium (10–15 μm) underlain by musculature.

Space between foregut and proboscis musculature is a mesenchyme rich in lacunae and blood cells. Two tubes with epithelial glands (ventral glandular foregut organs of type C in Salvini-Plawen, 1972, 1978) run through this space, opening at tip of proboscis and extending posteriorly below midgut. Foregut merges dorsoposteriorly into midgut, shortly behind cerebral ganglion; foregut musculature continuous with midgut muscularis. Rostral caecum paired, extending beyond cerebral ganglion. Midgut proper showing mid-dorsal ciliary tract and (due to dorsoventral muscle bundles) lateroventral pouchings. Nematocysts (to 20 µm) and spirocysts (to 30 µm) present throughout gut. Mid-dorsal ciliated tract continuous with more densely and entirely ciliated hindgut, which opens dorsally into mantle cavity above spawning duct outlet.

Circulatory system: Pallial sinus above respiratory folds is antero-dorsally continuous with heart auricles formed by median walls of terminally paired portion of pericardium. An invagination of pericardial roof (beginning with fusion of paired portion) represents the ventricle; both auricles and ventricle are medially lined with muscle fibres. Dorsal sinus runs between gonopericardioducts and over gonads. Blood cells consist of round, pale, homogeneous elements (5–8 µm) with indistinct nucleus and of more irregularly formed cells (to 15 µm diam.) with granules; the latter resemble the inclusions of the epidermal papillae.

Gonopericardial system: Bigger specimen showed beginning of sexual maturity with oocytes in paired gonad. Gonad posteriorly continuous with gonopericardioducts, which open dorsofrontally into pericardium. This organ is terminally paired, giving rise to the ventrolateral, ciliated pericardioducts surrounded by musculature. Neither seminal vesicles nor receptacles are present. Pericardioducts open laterally into anterior spawning ducts, still lined by simple (not yet glandular) epithelium. Along their posterior course the spawning ducts fuse, opening into anterior-most ventral mantle cavity.

Remarks: All known *Drepanomenia* species represent a well-defined group based on the structure of their mantle (strong hollow spicules in radial arrangement, slender epidermal papillae), the ventral foregut glandular organs (type C), the respiratory folds, and the lack of receptacula seminis (Salvini-Plawen, 1978). These characters separate this monogeneric family from others; due to the lack of the radula, no relationships with other cavibelonian families can be indicated.

Up to now, three species of *Drepanomenia* have been described (Table 1). *Drepanomenia vampyrella* (Heath, 1905) from off Hawaii differs from the new specimens by its thick cuticle (200–280 µm), which is extended mid-dorsally to form a 70 µm-high keel, and by the single rostral caecum of its midgut (Heath, 1911: 77–82). *Drepanomenia incrustata* (Koren & Danlielsen, 1877) from the Arctic Sea likewise possesses a thick cuticle (200–270 µm; personal observation of holotype) and a foot of five to three true folds extending throughout the groove. It is not known whether its foregut (with ventral pouch and special musculature) can be protruded as a proboscis (see Odhner, 1921: 19–22). The lateral walls of the midgut in *D. incrustata* form strong irregular folds, being serially constricted by the strong dorsoventral muscle bundles (60–80 µm diam.; holotype, SMNH no.4732). According to Odhner (1921: 21) the spawning ducts in *D. incrustata* are subdivided into an anterior portion ('bladder') with thin walls and a thick-walled posterior portion (shell gland) which subsequently fuses to become an unpaired organ. Finally, *Drepanomenia perticata* Salvini-Plawen, 1978, from the Antarctic Ross Sea is characterized by its thick cuticle (450–500 µm), by the presence of abdominal spicules and by a special bundle of pre-pedal spines. In comparison (Table 1), the present specimens from off New Zealand, with their thin cuticle, represent a well-defined new species.

***Drepanomenia pontisquamata* new species**
(Figures 3, 4, 16)

Types: Holotype (USNM 1016983), 6 mm length (Fig. 16), serial cross-sections on slides; southeastern Canada (44°31'–44°32' N, 56°48'–57°57' W), Station 2–10 of US Antarctic Research Program (USARP), 19 March 1962, 403 m.

Etymology: Latin *pons*, *pontis*, bridge; *squama*, scale; referring to the special character of the large scales at the mantle bridge between atriobuccal opening and pedal pit.

Diagnosis: Body 6 × 1.5 mm with rounded ends; cuticle thick, terminally with one or three longitudinal thickenings; hollow spicules radially arranged, mantle bridge between atriobuccal opening and pedal pit with large scales; pedal groove distinctly visible, with three folds, not in pallial cavity; pallial cavity with ventrorostral pouch and with ten respiratory folds. Cerebral connectives with common trunk. Foregut long and protrusible, ventral foregut glandular organs opening via paired papilla,

Table 1. Specific characters of *Drepanomenia* species (see Heath, 1911; Odhner, 1921, Salvini-Plawen, 1978, and herein).

| Character | <i>D. vampyrella</i> | <i>D. incrustata</i> | <i>D. perticata</i> | <i>D. tenuitecta</i> | <i>D. pontisquamata</i> |
|----------------------|----------------------|-------------------------------------|---------------------|-----------------------------------|--|
| Body size (mm) | 9 | 30 | 7 | 4 | 6 |
| Cuticle (µm) | 200–280 | 200–270 | 400–450 | 50–75 | 150–180 |
| Keel | Cuticular (70 µm) | None | None | Crest of spicules | 1 or 3 terminal cuticular thickenings, crest of spicules |
| Prepedal mantle | ? | Normal | With spines | Normal | With large scales |
| Abdominal spicules | ? | ? | Present | Not present | Not present |
| Pedal folds | 1 | 3–5 | 1 | 3 | 3 |
| Cerebral connectives | Separate (?) | ? | Separate | Separate | Common |
| Atrial ridges | No cilia | ? | Ciliated | No cilia | Ciliated |
| Midgut caecum | Single | Paired | Paired | Paired | Paired |
| Spawning ducts | Almost fused? | Terminally fused | Terminally fused | In part fused | Separate with single papillose outlet |
| Distribution | Oahu, Hawaii | Arctic Ocean off Finmark, Norway | Ross Sea, Antarctic | Tasman Sea west of New Zealand | Off southeastern Canada |
| Depth (m) | 550–575 | 365–550 | 1883–1890 | 531–659 | 403 |

?, No information.

midgut with a paired rostral caecum. Spawning ducts paired with fused opening; no abdominal spicules.

Mantle: Epithelium (20 μm high) producing 150–180 μm thick cuticle interlaced by densely arranged spicules. Terminally, the

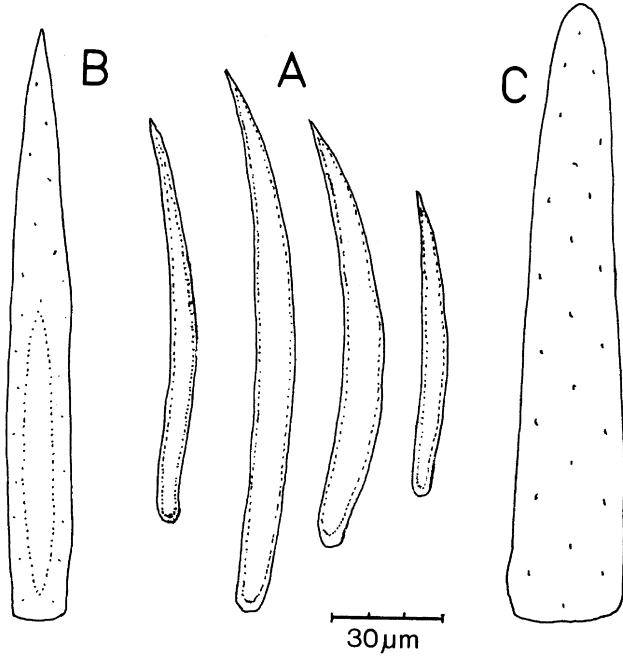


Figure 3. *Drepanomenia pontisquamata* new species: mantle sclerites. A. General spicules. B. Interspersed straight spicules. C. Pre-pedal scales.

cuticle strengthened to one, then three longitudinal thickenings. Epidermal papillae with club-shaped to globular distal swellings with funnel-shaped openings on cuticle surface. Spicules hollow, mostly needle-shaped and somewhat curved, 60–150 μm (mostly 100–130 μm) in length, very thin-walled with internal space up to tip (Fig. 3A). Second spicule type (up to 200 \times 20 μm) interspersed, strong and thick-walled, with long distal solid portion (Fig. 3B), often sunk into the musculature. All arranged in a single layer in obliquely-posterior to radial orientation, mid-dorsally forming a crest. Pre-pedal mantle portion adjacent to atriobuccal opening with some large scales (200 μm long, basally 30–40 μm wide; Fig. 3C). Terminal sense organ surrounded by small, slender scales.

Foot and pallial cavity: Pedal pit sickle-shaped, with ciliated epithelium (20–25 μm high) throughout; follicles of pedal gland open laterally and frontally. Roof of pit forming three folds (excluding mantle folds) which pass the externally visible pedal groove until region of spawning ducts; here, only middle fold continues, ending in front of pallial cavity. Paired sole glands open all along groove lateral of and within folds. Pallial cavity with short, unpaired ventrorostral pouch with apparently mostly cuticularized (i.e. probably microvillized) epithelium (12–15 μm), replaced by 25 μm high ciliated cells mid-dorsally and on pair of lateral folds. Pouch receives spawning ducts frontally (fused in opening only). Hindgut opens dorsally behind, ciliated epithelium continuing into mid-dorsal pouch. Mantle cavity enlarged dorsally and posteriorly, likewise lined by 'cuticularized' cells (12–15 μm). Ten longitudinal plicae (including the two lateral folds of the pouch) arranged radially; only distal two-thirds of plicae with higher ciliated cells. Pallial cavity extends posteriorly above its purely ventral opening and forming proximal, 'cuticularized' portions of respiratory folds.

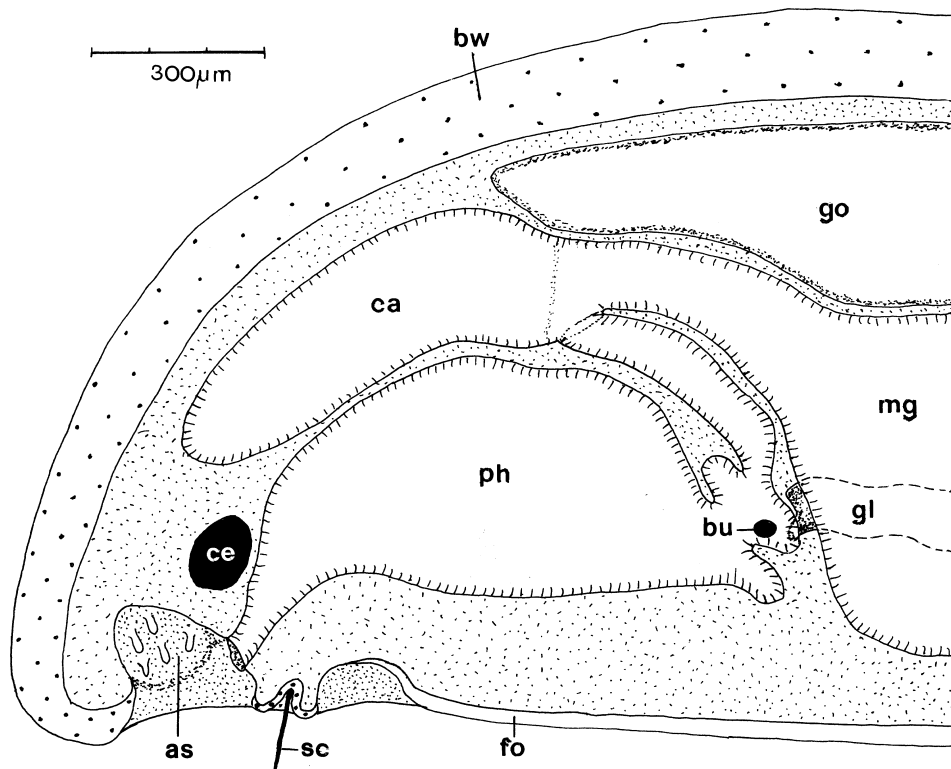


Figure 4. *Drepanomenia pontisquamata* new species: schematic organization of the anterior body, reconstructed from serial transverse sections. Abbreviations: as, atrial sense organ; bw, body wall (mantle and musculature); bu, buccal ganglion; ca, midgut caecum; ce, cerebral ganglion; fo, pedal folds (foot); gl, ventral foregut glandular organ; go, gonad; mg, midgut; ph, pharynx; sc, pre-pedal scales.

Musculature: Three-partite body wall musculature; inner longitudinal layer reinforced ventrally at both sides of pedal groove. Dorsoventral muscle bundles prominent, lower/outer ones 25–40 μm across, upper/inner bundles 40–50 μm in diameter.

Nervous system: Cerebral ganglion unpaired and relatively small (200 μm wide, 150 μm high, 100 μm long), giving rise to two pairs of lateroventral nerves to atrium, one ventral pair to oral region. Cerebral connectives at each side with common trunk. Buccal connectives separate first, running dorsolaterally along the foregut, buccal ganglia (35–40 μm diam.) at bend of foregut, buccal commissure behind bend ventral to foregut glands. Common base of lateral and ventral connectives gives rise to some nerves before separation. Both pairs of connectives show an intermediate swelling with a latero-ventral connective before typical (first) lateral and ventral ganglia; lateral ganglia (40–45 μm diam.) adjacent to body wall. Intermediate swelling of ventral connectives give rise to a more prominent nerve to pedal pit; ventral ganglia (70 μm diam.) above pedal pit with strong commissure. Longitudinal cords consist of fibrous material with fairly regularly differentiated ganglionic swellings; ventral commissures, latero-ventral connectives and dorsal nerves. Posterior-most ventral ganglia (50 μm diam.) with commissure and at each side with latero-ventral connective medially of spawnings duct, this connective being connected to third posterior-most lateral ganglia. Ganglia posterior superiora (100 μm \times 75 μm diam.) above terminal portion of spawning ducts and interconnected by a 350- μm -long, medullary suprarectal commissure (25 μm diam.), giving rise to a paired nerve (gap 150 μm) which innervates terminal sense organ. Lateral cords continue and end by splitting between gill folds.

Sense organs: Atrial sense organ (atrium) spacious, posteriorly paired, with relatively few, elongate papillae intruding into cavity. Half length of atrium roof with wide tract of scarcely ciliated cells; tract divided by mouth opening into paired ciliated ridges which enter medially the lateral extensions of atrium (until beside and behind mouth) and unite with horseshoe-shaped, scarcely ciliated border of atrium. Dorsoterminal sense organ in exactly terminal position, formed by 10–12 μm high 'cuticularized' cells (with microvillous border?) arranged in a bowl and surrounded by small, slender scales; paired innervation from suprarectal commissure.

Alimentary tract: Mouth opening between ciliary tracts at the posterior roof of atrium; buccal cavity with folded, cuticularized epithelium (30–40 μm high). Anterior foregut (about 270 μm diam.) weakly cuticularized, epithelium 15–20 μm high with numerous long and slender papillae. Subsequent foregut continuing by means of a curve in dorsofrontally running upper leg, a narrow tube (about 100 μm diam.) opening above pedal ciliary pit into midgut (Fig. 4). Entire foregut surrounded by strong musculature (30 μm at lower foregut leg, 35 μm at upper tube) of an inner circular layer and a thicker outer longitudinal layer. Buccal cavity and anterior foregut probably protrusible ('proboscis'). Foregut with intercellularly opening, small glandular cells (5–10 μm diam.) between periphery and musculature, containing coarsely granular secretion. Lower leg of foregut posteriorly with short sac; proximal portion of upper leg (i.e. in the turn) with short anterior and short posterior pouch. Into the latter the two ventral glandular organs open ventro-rostrally side by side upon a slightly protruding double papilla. Glandular organs multiply wound (due to retracted foregut), 110 μm wide with 40–50 μm high glandular epithelium (type C organs in Salvini-Plawen, 1972, 1978). They include big granules and drops of secretion; a weak muscularis surrounds the

glandular organs. Upper leg of foregut opens at low angle dorso-rostrally into midgut; midgut with paired, spacious anterior caecum. Caeca and midgut proper show lateral constrictions due to strong dorsoventral muscle bundles. Mid-dorsal ciliary tract of midgut continuous with the entirely ciliated hindgut, which opens dorsally into pallial cavity.

Circulatory system: Heart auricle (atrium) beginning as a dorso-medial invagination of posterior pericardium, covered and internally lined by muscle fibres with connective tissue. Along half of pericardium the auricle is paired; it opens ventrally into ventricle. The ventricle throughout is a dorsally open invagination, internally lined by musculature, and continuous with dorsal sinus still within pericardium. Free dorsal sinus between gonopericardi ducts, mid-dorsally over gonads and between the two midgut caeca. Ventral sinus below midgut delimited by portions of intercrossing dorsoventral musculature. Haemolymph cells of homogeneous, small round bodies (5 μm), and of granulated, mostly oval elements (10 μm \times 7 μm).

Gonopericardial system: Mid-dorsal gonads paired throughout, medially with developing ova (50 μm diam.), lateroventrally with sperm; gonads terminally continuous with two ciliated gonopericardi ducts (100 μm diam.) which are encircled by weak musculature and open frontally into pericardium. Gonads below dorsal sinus with ciliation which lines (as a pair of tracts) the dorsolateral pericardium and proceeds into pericardi ducts. Pericardium spacious (enclosing some genital products) with paired extension continuous with pericardi ducts. Pericardi ducts wide with flat cellular lining, medial epithelium prominently invaginated like a typhlosole; only this is ciliated. Ducts open anteriorly from lateral into the respective spawning duct. Spawning ducts separated throughout until their common opening via short muscular outlet or papilla, and possessing a high epithelium of glandular cells as well as slender ciliated cells; part of this epithelium is protruded into stout folds. Neither seminal receptacles, seminal vesicles, copulatory stylets nor abdominal spicules are present.

Remarks: The present organization clearly fits into the frame of the genus *Drepanomenia*. The configuration of the posterior bend of the foregut suggests its protrusibility. In this connection, the opening of the foregut glands into the posterior portion (pouch) of the upper foregut leg and the buccal ganglia with their commissure located below this, argue against the axial blind sac of the lower foregut leg representing a vestigial radular sheath (the radular sheath being presented always above the gland openings and buccal commissure).

Compared with known representatives of *Drepanomenia* (Table 1), note that the large scales at the mantle bridge between atriobuccal opening and pedal pit in *D. pontisquamata* are paralleled in *D. perticata* by strong spines (see Salvini-Plawen, 1978: 227–230); note also the common trunk of the cerebral connectives (separate in *D. perticata*, *D. tenuitecta* and probably also in *D. vampyrella*; no information for *D. incrustata*). Other differences include the paired midgut caecum and the lack of a distinct mid-dorsal keel in contrast to *D. vampyrella*, the thick mantle cuticle and the lack of abdominal spicules in contrast to *D. perticata*, the specially elaborated spawning ducts as well as the configuration of the posterior pharynx in contrast to *D. incrustata*. The latter region in *D. incrustata* is characterized by a 'thin sub-oesophageal pocket' (Odhner, 1921: 19), which may simply point to some protrusibility, whereas the 'thin' (thin-walled) differentiation appears to be a true character not found in *D. pontisquamata*.

Simrothiellidae Salvini-Plawen, 1978

Diagnosis: Solenogastres with thick cuticle, sclerites as hollow needles (Cavibelonia); radula biserial (or vestigial), ventral foregut glandular organs epithelial.

Remarks: See Remarks on *Aploradoherpia insolita* below.

Genus *Simrothiella* Pilsbry, 1898

Diagnosis: Cavibelonia with hollow spicules intercrossing in several layers; with common atrio-buccal opening; radula biserial, plates according to age of different shape according to developmental stage, with strongly heterogeneous denticles, older plates all retained in place in paired, ventrally curved and terminally coiled radular sac; ventral foregut glandular organs as epithelial ampullae, midgut with regular constrictions; secondary genital opening single, with copulatory stylets; terminal sense organ present; with respiratory organs.

Type species: *Solenopus margaritaceus* Koren & Danielssen, 1877 (Salvini-Plawen, 1975; ICZN Opinion 1185, International Commission on Zoological Nomenclature, 1981)

***Simrothiella margaritacea* (Koren & Danielssen, 1877)**

Solenopus margaritaceus Koren & Danielssen, 1877: 128. Koren & Danielssen, 1879: 328.

Simrothiella margaritacea—Odhner, 1921: 12–19, figs 1–16.

(Figures 5–7A, 19, 20)

Types: 'Prototype' in Odhner (1921), 'lectotypes' in Scheltema & Schander (2000) (ZMUB 2075 and 66806), 12 mm in length, incomplete specimens in alcohol; Boknfjord off Kvitingssog/Stavanger (Norway), 75–115 m.

Remarks: Koren & Danielssen's original material of *Solenopus margaritaceus* (ZMUB 2075 and 66806) remains organizationally undescribed as the only diagnostic species description by Odhner (1921), as well as the present re-examination, refers to specimens from off Kopervik (Boknfjord) at 75–95 m (ZMUB 2078 and SMNH 4731). The latter animals show a 'body rounded at both ends' (Odhner, 1921: 12; Salvini-Plawen, 1968: figs 24–25; Scheltema & Schander, 2000: fig. 20A), whereas the type individuals are 'almost transversely cut off at the hinder end' (Koren & Danielssen, 1879: 328). It is therefore questionable whether Odhner's material and description of *Simrothiella margaritacea* (based on SMNH 4731, see below) is actually conspecific with *Solenopus margaritaceus* Koren & Danielssen. In any case, Odhner's section series on slides (SMNH 4731) should be considered as crucial para(lecto)types of *S. margaritacea*, or (together with ZMUB 2078) as syntypes of a separate species, rather than declared as representatives outside the type material (Scheltema & Schander, 2000).

Diagnosis: Body up to 12 mm long (type material) or 10 mm, respectively (Kopervik material), mantle with epidermal papillae, hollow spicules thick-walled; no distinct dorsal foregut gland; radular plates up to 120 × 60 μm, in adults with very strong lateral denticle up to 180 μm in length and with other small heterogeneous denticles at distal border of posterior portion, these denticles eventually being reduced; radular apparatus without bolster; midgut with short, single rostral caecum, regular constrictions weak; seminal receptacles as pouches of widened spawning ducts only; one long and one much shorter copulatory stylet per sheath; with a pair of strong, short pallial spicules above rostral border of mantle cavity opening; large specimens with suprapallial glands.

Material examined: Four specimens from Boknfjord off Kopervik at 75–95 m, sectioned by N. Odhner: SMNH 4731:2 (transverse sections at 10 μm); 4731:1 (ts 5 μm anterior end), 4731:3 (ts 5 μm posterior body); 4731:4a (longitudinal sections at 5 μm); 4731:4b (ls 10 μm). Odhner's (1921) figures 9, 10, 16 refer to the series 4731:2 and figures 11–14 to 4731:3; the respective sections are marked each on the slides by an encirclement. Three additional specimens from off Kopervik (ZMUB 2078, see Odhner, 1921: 12; Salvini-Plawen, 1968: figs 24–25): two animals serially sectioned (ts 10 μm; one not yet mature) and stained with azan, third individual (9 mm long) used for *in situ* preparation of radular apparatus.

Description: Odhner (1921: 11–19) described the organization in detail except for the not quite understood radular apparatus (see Salvini-Plawen, 1978: 215). In some points this description can be supplemented:

Cuticle about 25 μm thick; hollow spicules generally 120–160 μm (up to 200 μm) long, thick-walled and intercrossing in two or three layers. Epidermal papillae present, but scattered. Single pedal fold to opening of mantle cavity; Odhner's pre-pallial pit (1921: 14) is part of the mantle cavity that is irregularly outlined by contraction (and only present in SMNH 4731:2a). Longitudinal musculature of body wall ventrally reinforced. Atrial sense organ with up to 10 bundled papillae. Foregut surrounded by circular and distinct longitudinal musculature; along the second quarter of its course (from mouth to opening into midgut) with subepithelial pharyngeal glands grouped dorsally and dorsolaterally (no compact gland). Close to transition into midgut, an additional, differently stained cluster of subepithelial pharyngeal glands opens dorsolaterally at each side into pharynx; Odhner (1921: 17, fig. 1) probably mistook these as a distinct dorsal foregut gland (not present in either Odhner's or in the new specimens at hand). Except for some musculature, without special radular support (bolster of

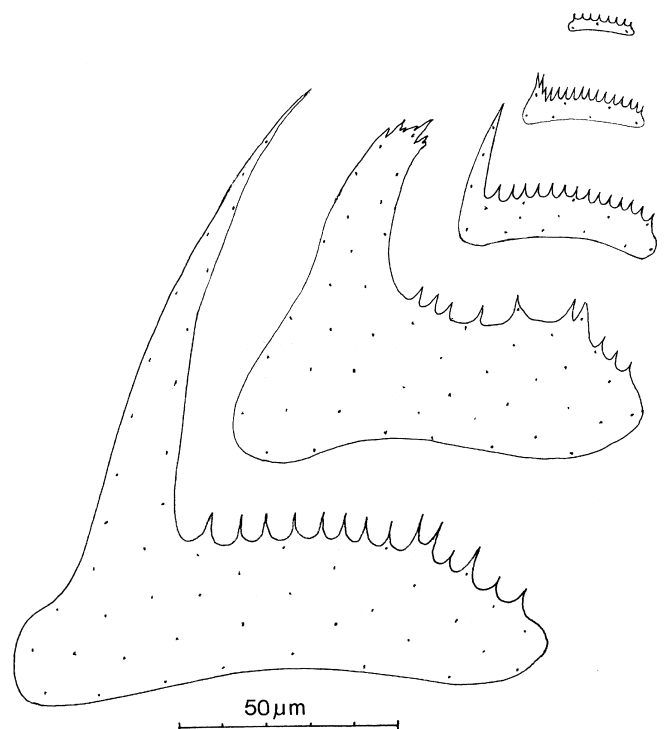


Figure 5. *Simrothiella margaritacea*: developmental sequence (above to below; cf. Fig. 6A) of stages of left radular plates according to serial sections, views of posterior face.

vesicle or chondroid cells). Ventral foregut glandular organs epithelial (type C in Salvini-Plawen, 1972, 1978), forming a pair of ampullae; they are embedded dorsolaterally of radular sheath (see Odhner, 1921: fig. 10), opening at both sides of front end of radula. Rostral midgut caecum single and short, but distinct; midgut more or less distant to body wall, dorsoventral muscles bundles in most individuals not constricting midgut ('only slightly developed' diverticula in Odhner, 1921: 17). Midgut without nematocysts, but SMNH 4731:4a and another specimen each containing one or to worm-like fragments of prey (tentacles of polychaetes or holothurians?) occupying most of length of midgut.

Odhner's specimens (SMNH 4731:2, 4731:3) appear to be protandrous, because the sperm is well elaborated in voluminous lateral sacculations of the gonads, whereas the median eggs are still small (up to 75 μm diam. in 4731:2); in other specimens examined, eggs are even smaller or the gonad is not yet differentiated. Heart extends freely through pericardium, with a single auricle. Pericardioducts emerge laterally at the rear of pericardium and open from dorsal into most anterior portion of the spawning ducts. In Odhner's material (SMNH 4731:2a, 4731:3a) spawning ducts at this position with wide lumen (epithelium about 15 μm high) and posteriorly form 2–3 pouches ('three small vesiculae' in Odhner, 1921: 18, fig. 2), which represent the (not separated) seminal receptacles. Following spawning ducts typically lined (25–30 μm high with slender glandular cells) and continue as somewhat narrowed, lateral portions fusing in their posterior half to a single, bulbous

organ. In histological sections, the pair of long copulatory stylets (over 600 μm long) appear to be solid anteriorly (25 \times 30 μm diam.); adjacent second stylet fairly short and entirely within the sheath. Anterior border of mantle cavity below distal-most stylet sheaths. What Odhner describes as 'a pair of vesiculae or sac-formed glands' (1921: 19, fig. 2v) is not clear. On the one hand, in larger specimens (SMNH 4731:2a, 4731:4a, 4731:4b) there are pouchings of the mantle cavity, and all the anterior as well as dorsal wall (as far as to fig. 16 in Odhner, 1921) is underlain by an extensive mass of suprapallial glands; on the other hand, at both sides above the border of the beginning mantle cavity opening, a strong, short pallial spicule is present within its laterally invaginated sheath, not noticed by Odhner ('accessory copulatory spicules' in Scheltema & Schander 2000: 146). Odhner (1921) counted 20 gill organs, in the new specimens up to about 10 respiratory folds are present; due to distinct lateral folds in larger respiratory organs, these superficially resemble ctenidia. Suprarental commissure above anal opening long (new material 80–110 μm , Odhner's material 250 μm) and medullary (new = 12 μm , Odhner = 22 μm diam.). Terminal sense organ located dorsally behind mantle cavity.

Radular apparatus: Biserial radula as usual formed in sheath and subsequently freely exposed within pharynx. Already in juveniles it continues into two separate, ventrally curved sacs which extend posteriorly and recurve or coil medially at their end (Fig. 6A). During development, the shape of the radular plates or bars changes; plates in adult specimens thus of different outlines,

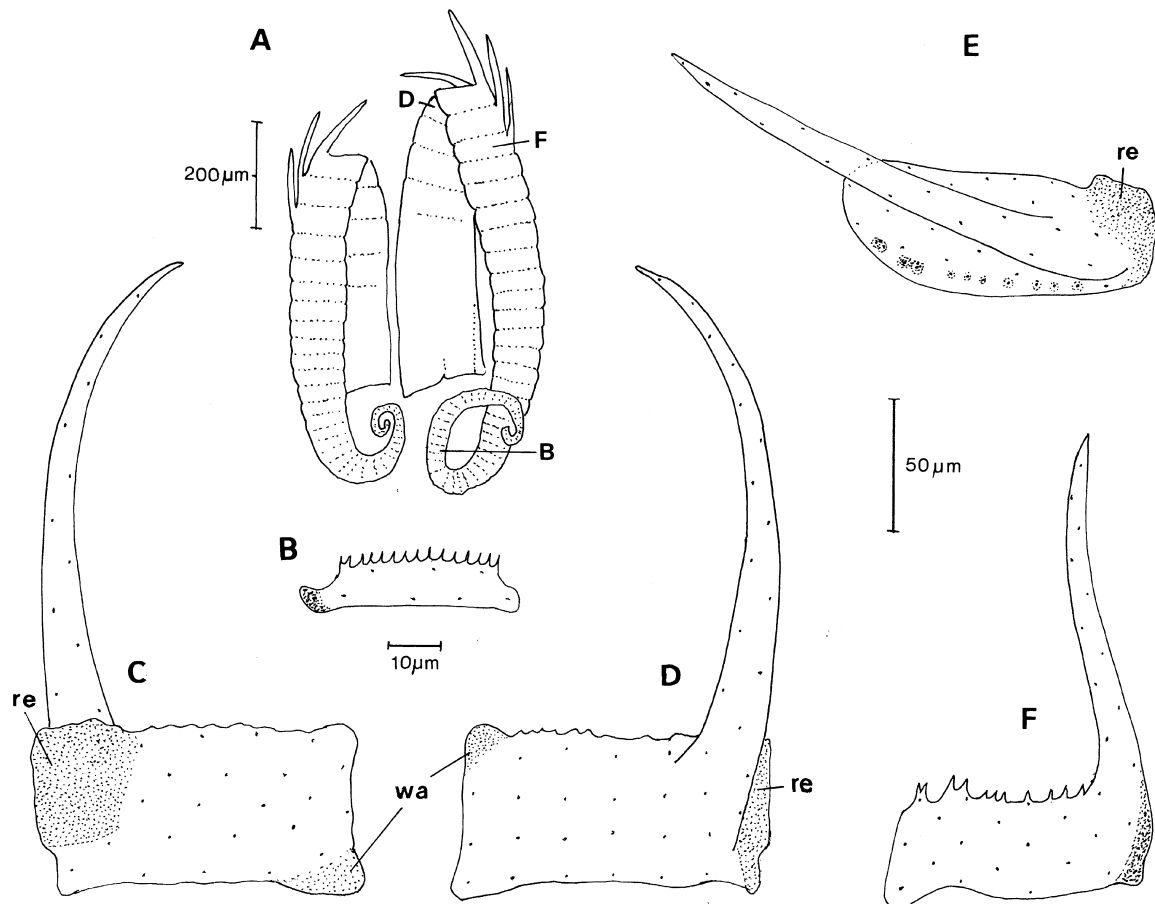


Figure 6. *Simrothiella margaritacea*, radula. **A.** Sketch of isolated radula, ventral view. **B.** Early radular plate, from ventral coil of **A** (between first and second stage in Fig. 5), posterior portion with median border at right. **C.** Pharyngeal radular plate, anterior face (see Fig. 20). **D.** Same pharyngeal plate as **A**, posterior face. **E.** Plate in anteriormost ventral sac, view from above (anterior portion is above). **F.** Plate in anterior ventral sac, posterior portion. Abbreviations: re, cap-like reinforcement; wa, weak portion of plate.

with the earliest form at the tip of the coils (Fig. 5) and Odhner's drawing (1921: fig. 5) refers to a plate (about 60 μm wide) in the posterior portion of the ventral sac. The *in situ* prepared specimen (9 mm long) with a 700 μm long radular apparatus (Fig. 6A) showed a 'coil' of 540° (360° + 180°) and was therefore older (at left about 50 plates, at right about 55 plates in total). Smallest (i.e. earliest juvenile) plates are about 12 μm wide and bear 5–6 equally sized, tiny distal denticles (Fig. 5); subsequent plates have increased size and denticle number. In addition, the denticles become heterogeneous and a strong lateral denticle is added, dominating the outline (Figs 5, 6B, E, F, 7A). Thus in SMNH 4731:4b, the plates exposed to the pharynx (90 μm \times 35 μm , denticle 110 μm long) are prominently provided with heterogeneous denticles (Figs 7A, 20). Other material (SMNH 4731:4a) shows plates of 100 μm \times 40 μm with an up to 180 μm long denticle. In the new material, the three anterior-most ventral plates measured 120 μm \times 40–60 μm and show a 120–160- μm -long denticle; the small heterogeneous denticles, however, are vestigial. The largest pair of plates, exposed to the pharynx (new series sections as well as *in situ* preparation), were 120 μm wide and 60 μm high; each very strong lateral denticle was 180 μm long (basally 28 μm diam.), whereas the small heterogeneous denticles were not elaborated in these most advanced plates (Figs 6C, D, 20).

Within the sheath (slightly bifid proximally in one specimen), the radular material mostly forms two continuous bands (140–170 μm wide), being subdivided only distally into prospective plates (Fig. 6A), 160 μm (new specimens) and 150 μm wide (Odhner) in sections. Within the distal sheath, the free, denticulated rim of each plate is medially directed and points dorso-posteriorly; all denticles emerge from the posterior (!) portion of the about 45- μm -thick plates, whereas the anterior portion lacks special structures except a reinforcement (Figs 6C, 20):

the strong denticle emerges postero-laterally at the plate with a basal thickening (Fig. 6D–F), which therefore embraces the lateral border of the plate and forms a lateral, cap-like reinforcement at the anterior face of the radular plate (Figs 6C–E, 20); on the other hand, the plates are less thick at the medio-basal area of their anterior portion as well as at the medio-distal area of their posterior portion (Figs 6C, D, 20). Within the pharynx, the plates become erect, with the strong denticle pointing into the lumen (Figs 7A, 19). Passing into the ventral sacs, the plates curve down with the heterogeneously denticulated rim pointing ventro-anteriorly and the originally posterior portion of the plates now facing obliquely upwards. This condition elucidates the different aspects of the radular plates: only the posterior portion bears both the strong and the small, heterogeneous denticles distally (well visible in histological sections, see Fig. 5); the anterior portion and face have lateral thickening only (Figs 6C, 20).

Remarks: The specimens at hand belong to the original material collected by G. O. Sars and described by Odhner (1921). Odhner's (1921) unsatisfactory representation of the radular apparatus in *S. margaritacea* has already been unravelled in an earlier investigation; its basic configuration is identical to that in *Kruppomenia*, showing a 'saccoglossan' condition (as also present also in several Amphimeniidae), although the ventral radular sac is bifurcate. Therefore, *Kruppomenia* was put into synonymy (Salvini-Plawen, 1972: 222–223, 1975), although restored by Scheltema & Schander (2000).

Scheltema & Schander (2000) also referred specimens from the West European Basin (southwest of Ireland) to the sole known *Simrothiella* species *S. margaritacea*. This new material (also referred to in Ivanov, 1990), however, actually represents a distinct species, characterized below.

Simrothiella abysseuropaea new species
(Figure 7B)

Simrothiella margaritacea—Scheltema & Schander, 2000: 143–146, figs 20D–J, 21, 22A–G (in part, not *Solenopus margaritaceus* Koren & Danielssen, 1877).

Types: Syntypes (USNM 894261–894266) up to 9.5 mm in length; northeastern part of the West European Basin southwest of Ireland (50°58.7' N, 13°01.6' W), Station 316 of RV Chain Cruise 106, 2173 m.

Ethymology: Greek *abyssos*, abyss; *europa*, mythical Greek princess representing Europe; referring to the provenance of the species.

Diagnosis: Body up to 9.5 \times 0.8 mm. Radular plates with strong lateral denticle (up to 280 μm in length), small denticles scattered at the posterior face (rather than at distal border); reinforcement (buttress) at plates restricted to the anterior face only. Hollow spicules heavy-walled; two copulatory stylets per sheath, one long and a much shorter, S-shaped one; with a pair of strong and short, hooked pallial spicules.

Remarks: 26 specimens from the RV Chain Cruise referred to *Simrothiella margaritacea* by Scheltema & Schander (2000: 143–146, figs 20D–J, 21, 22A–G) are defined by the hard parts only. Among these, the diagnostic characters of the radular apparatus including its size (about 1200 μm long in figs 11B and 21A; 450 μm in fig. 21B, wrong scale?), with larger plates, and the arrangement of denticles and reinforcements, clearly contradict conspecificity with *S. margaritacea* (Fig. 7). Compared with information gained from *S. digitoradulata* (below), these differences exceed mere variations and appear to represent specific

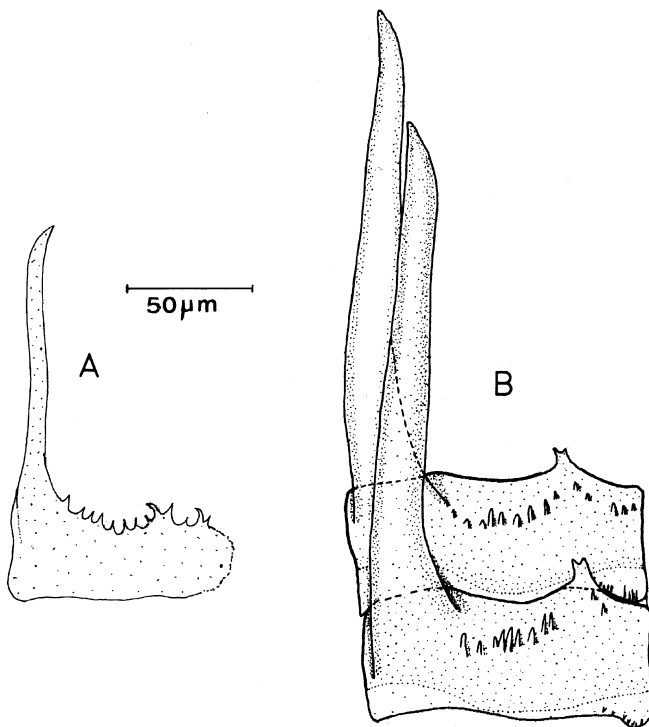


Figure 7. *Simrothiella* spp., posterior face of radular plates. **A.** *S. margaritacea*, one pharyngeal radular plate from Odhner's section series 4731:4b (redrawn from Fig. 19). **B.** *S. abysseuropaea* new species, two radular plates from the West European Basin after Scheltema & Schander (2000: fig. 21F). **A, B** to same scale.

characters. In addition, there is a different distribution. This distribution calls attention to unexpected biodiversity even within a close geographic range. The 'Armauer Hansen' material (62°01' N, 0°08' E; at 1400 m), likewise referred to *S. margaritacea* (Odhner, 1921; Scheltema & Schander, 2000), has not been examined and may possibly belong to another species. The features of *S. abyseuropaea* distinguishing it from *S. margaritacea* are summarized in Table 2.

***Simrothiella digitoradulata* new species**
(Figures 8, 9, 17)

Types: Holotype (USNM 1016984), 3 mm length, serial cross-sections on slides; Atacama Trench off northern Peru (08°13' S, 81°09' W), Anton Bruun Station 11–101 of South-East Pacific Biological Oceanographic Program (SEPBOB), 16 Oct. 1965, 1927–1997 m.

Ethymology: Latin *digitus*, finger; *radere*, to rasp, hence *radula*; radular plates reminiscent of a pointing forefinger.

Diagnosis: Body about 3 × 0.5 mm; no distinct dorsal foregut gland, radular apparatus with paired supportive bolster (vesicle), radular plates with long para-lateral, slender denticle and 5 + 3 small denticles at the face; midgut with short paired rostral caecum. Copulatory stylets of a long and a short element per sheath, posteriorly running within a pouch of mantle cavity. About 20 respiratory folds.

Description: Mantle cuticle depressed with tangential holes of spicules in several layers; no spicules retained, no epidermal papillae discernible. One simple pedal fold until the mantle cavity; cavity extends rostrally of its opening and provided with about 20 radially arranged respiratory folds.

Mouth opening in direct continuation of dorso-posterior atrial cavity, separated merely by a dorsomedial to paired lateral

ciliated tract (Fig. 8); atrial papillae few and blunt, some being basally bundled into three.

Foregut with distinct circular and longitudinal musculature; dorsolaterally, pharyngeal glands are concentrated (doubtfully forming a 'dorsal gland'). Radular apparatus at least 270 µm long; supportive apparatus with a paired, distinct bolster, each of a voluminous lateral vesicle (160 µm long, 70 µm diam.) of few turgid cells and surrounded by musculature, bolsters at their beginning with a strong interconnecting transverse bundle. Radula extending into paired lateroventral sac, distally curving below and medially of beginning vesicle ('coil' of 270°). Ventral foregut glandular organs as a pair of epithelial ampullae (type C in Salvini-Plawen, 1972, 1978) dorso-frontally of each bolster vesicle and opening laterally at the beginning of radula. Free radular plates in pharynx (Fig. 9) about 50 µm wide and 15 µm high, with a 65–80 µm long, distally curved main denticle and 5 + 3 small denticles emerging from the face of the plate (rather than from the distal rim). Largest radular plates (in distal portion of sheath) 85 × 25 µm, diameter of long denticle 8 µm (fragment of 35 µm length). Within ventral radular sac, just behind curve, radular plates 40 × 9 µm with about six denticles, the second outer one being largest (Fig. 9). Radular sheath with a dorsomedian fold throughout, not causing bipartition; long denticles clearly formed by dorsal cells of proximal-most portion.

Midgut with short, paired rostral caecum. Dorsoventral musculature not very prominent, bundles running close to body wall, scarcely constricting midgut. Ventral longitudinal musculature only slightly reinforced.

Unpaired cerebral ganglion 125 µm wide, 35 µm high, 40 µm long. Ganglia posteriora superiora interconnected by a short and medullary suprarectal commissure (35 µm diam.). Suprapallial sense organ in terminal position.

Gonads form scarcely enlarged tubes with developing eggs and continue posteriorly in two ciliated gonopericardioducts. Heart extends freely through pericardium. Spawning duct unpaired throughout, opening ventrally into mantle cavity;

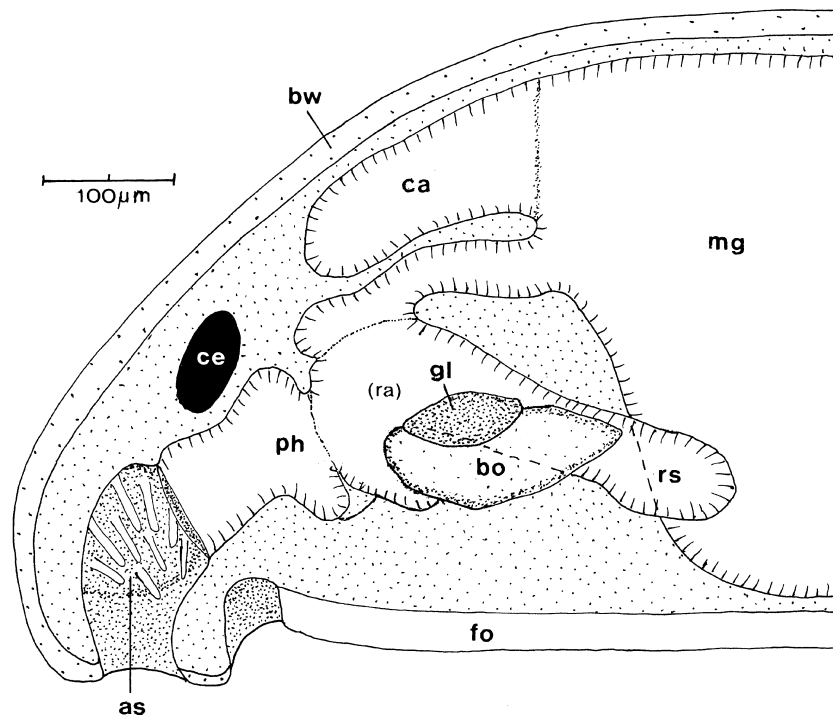


Figure 8. *Simrothiella digitoradulata* new species: schematic organization of the anterior body, reconstructed from serial transverse sections. Abbreviations: as, atrial sense organ; bw, body wall (mantle and musculature); bo, radular bolster; ca, midgut caecum; ce, cerebral ganglion; fo, pedal fold (foot); gl, foregut glandular organ; mg, midgut; ph, pharynx; (ra), space with pharyngeal radula; rs, radular sheath.

seminal receptacles not (not yet?) visible. One pair of copulatory stylets, each proximally accompanied within the sheath by a short second one. Stylets extend far anteriorly; posteriorly they run, adhered medially by a 'mesenterium', each within a pouch of the bottom of the mantle cavity. Pallial spicules or hooks not discernible (not yet developed?).

Remarks: The organization of this not yet fully mature animal identifies it as a member of the genus *Simrothiella*. Up to now, three species of *Simrothiella* are known: *S. margaritacea*, *S. comoren-*

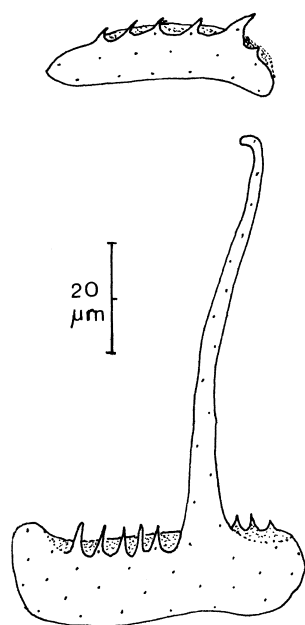


Figure 9. *Simrothiella digitoradulata* new species, radular plates (median border at left): above, radular plate within ventral radular sac; below, radular plate within pharynx (see Figs 21, 22).

sis Todt & Salvini-Plawen, 2003 and the new *S. abyseuropaea*. The shape and structure of the radular plates of the present specimen come close to those of *S. abyseuropaea* (see discussion above). It differs from this species, however, at least by the more detailed shape of the radular plates and by the geographical distribution. The differences from *S. margaritacea* refer to the radula, the presence of a paired radular bolster, the paired midgut caecum and the copulatory stylet apparatus at each side running within a pouch of the mantle cavity. The smaller *S. comorensis* likewise possesses such pouches of the mantle cavity as well as a paired radular bolster (pers. obs.; not mentioned in Todt & Salvini-Plawen, 2003), but differs at least in the structure of the radula, the 'coil' of the ribbon (about 450°; pers. obs.) and the number of copulatory stylets (Table 2). The present specimen thus clearly defines a new species and enlarges the known geographical distribution of *Simrothiella* to the Atacama Trench.

Genus *Aploradoherpia* new genus

Diagnosis: Cavibelonia with hollow spicules arranged oblique-radially in one layer. With common atrio-buccal opening, biserial radula, foregut glandular organs as short epithelial ampullae, no regular midgut constrictions. Secondary genital opening single, no copulatory stylets; with respiratory organs; terminal sense organ present.

Type species: *Aploradoherpia insolita* new species

Etymology: Greek *aploos*, simple; *herpein*, to move slowly and *herpeton*, a slowly moving animal; Latin *radere* to rasp, hence *radula*; referring to the simple radular plates: Feminine gender.

Aploradoherpia insolita new species

(Figures 10–12, 18, 21, 22)

Types: Holotype (USNM 1016985), 3 mm length, serial cross-sections on slides; Atacama Trench off northern Chile (25°43'–25°44' S, 70°58' W), Menzies-trawl at Station 3-62 of US Antarctic Research Program, 21 June 1962, 1863–1965 m.

Etymology: Latin *insolitus*, unusual, strange, odd.

Table 2. Specific characters of known *Simrothiella* species (and treated herein).

| Character | <i>S. margaritacea</i> | <i>S. abyseuropaea</i> | <i>S. digitoradulata</i> | <i>S. comorensis</i> |
|--------------------------------------|-------------------------|--------------------------|-------------------------------|-------------------------------|
| Body length (mm) | 9–12 | 9.5 | >3 | 1.9 |
| Epidermal papillae | Present | ? | ? | Not present |
| Dimension of radular apparatus (μm) | 700 | 1200 | >270 | 200 |
| Ventral 'coil' of radular ribbon (°) | 540 | 270 | 270 | 450 |
| Number of radular plates | 50–55 | 40–45 | ? | 20 |
| Dimensions of largest plates (μm) | 119 × 60 | 130 × 90 | >85 × 25 | 90 × 25 |
| Length of strong denticle (μm) | 180 | 280 | 80 | 40 |
| Arrangement of small denticles | At distal border | At posterior face | At posterior face | At distal border |
| Reinforcement at plate | Cap-like with 'nose' | Limited to anterior face | ? | At posterior face |
| Radular bolster | None | ? | Present, paired | Present, paired |
| Midgut caecum | Single, short | ? | Paired | No |
| Seminal receptacle | Pouch of Spawning duct | ? | ? | ? |
| Spawning ducts | Posterior half fused | ? | Fused throughout | Posterior half fused |
| Copulatory stylet apparatus | Embedded | ? | Within pouch of mantle cavity | Within pouch of mantle cavity |
| No. of stylets | Two pairs | Two pairs | Two pairs | One pair |
| Pallial spicules | One pair: short, strong | ? | ? | ? |
| Suprarectal commissure | Long | ? | Short | ? |
| Provenance, depth (m) | Coastal, 75–115 | Deep sea, 2173 | Deep sea, 1827–1897 | Deep sea, 3716 |
| Geographical distribution | Norwegian shelf region | W European abyssal | Trench off N Peru | Near Comoro Islands |

?, No information.

Diagnosis. Body 3 mm (immature), somewhat tapered posteriorly. Cuticle moderately thick, without epidermal papillae, hollow spicules thin-walled, up to 350 μm in length; pedal groove not continuous with mantle cavity. Radular plates low and curved, with four median denticles; squamous pharyngeal cuticle entering radular sheath; radula support consisting of several muscle bundles; midgut with unpaired rostral caecum. Ganglia posteriora superiora close together; mantle cavity with ventro-rostral pouch; four pairs of pre-pallial spines, the two inner ones with musculature; respiratory organs present as papillae.

Mantle. Epidermis (7–10 μm) with voluminous vacuolized glands, yet no papillae. Mantle spicules needle-shaped and hollow with thin wall, up to 350 μm long, all arranged in one layer oblique-tangentially in posterior direction, causing a net-like perforation of the cuticle (30–50 μm). At each side in front of mantle cavity opening four strong, solid calcareous spines, fairly radially invaginated (Fig. 12) and grouped as two outer ones (about 100 μm \times 10–13 μm diam.) and two inner ones (about 160–200 μm \times 25 μm diam.); inner spines terminally curved, and their simply invaginated epithelium is basally and laterally provided with musculature (absent in the two outer ones).

Foot and mantle cavity: Ciliated pedal pit shallow, anteriorly with outlets of pedal gland. Posterior portion forming a single, weak mid-dorsal fold continuous into the externally well visible pedal groove; groove ending far in front of mantle cavity opening. Paired sole glands emptying laterally into groove as well as into pedal fold (see *Drepanomenia pontisquamata*).

Mantle cavity generally non-ciliated with a spacious, ventro-rostral pouch with dorsal opening of single outlet of spawning ducts. Rectum opens dorsally into mantle cavity; adjacent dorsal and lateral walls forming a total of 10–12 papilla-like respiratory organs (up to 225 μm in length). These are locally ciliated and form lateral bulges or weak folds, thus somewhat resembling ctenidia (see also *Simrothiella margaritacea* and *Kruppomenia minima* in Nierstrasz, 1905: 655–666; Nierstrasz & Stork, 1940:

26–32); cross-sections show two internal lacunae and a pair of weak lateral muscle bundles; ciliation restricted to 1–2 cells laterally (Fig. 10A).

Musculature: Ventral muscles of three-layered body wall musculature reinforced on both sides above pedal groove; in posterior body, these separate and form musculature of the two pairs of inner abdominal spines. Dorsoventral bundles in usual arrangement. Additional musculature: strong foregut coat.

Sensory system: Unpaired cerebral ganglion (150 μm wide, 75 μm high, 70 μm long) gives rise dorso-laterally to three pairs of separate connectives. First lateral ganglia (50 μm \times 25 μm diam.) close to cerebral ganglion, oriented towards body wall. First ventral ganglia (50 μm \times 25 μm diam.) with one commissure above pedal pit. Buccal system with commissure dorsorostrally of bucco-pharyngeal sphincter; buccal connectives continue posteriorly, running dorsally adjacent to bolster apparatus and forming ganglion (30 μm \times 20 μm diam.) at both sides of foregut opening into midgut; commissure of ganglia between radular sheath and midgut.

Longitudinal body cords (15–20 μm diam.) with fairly regularly spaced swellings (ventrally 40 \times 20 μm) interconnected by

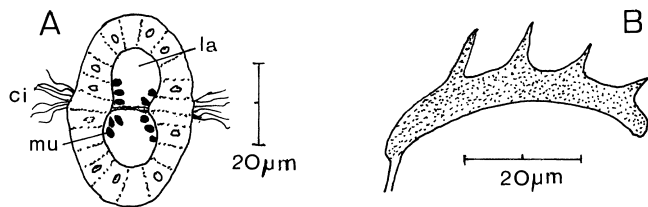


Figure 10. *Aploradoherpia insolita* new genus, new species: **A.** Cross-section through respiratory papilla. **B.** One radular plate (median border at left). Abbreviations: ci, cilia; la, lacuna; mu, muscle.

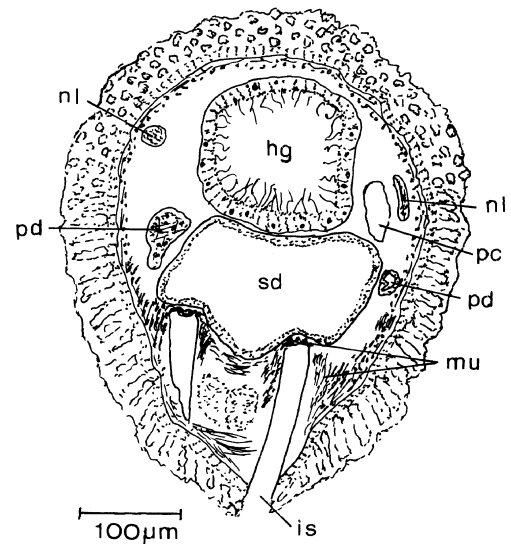


Figure 12. *Aploradoherpia insolita* new genus, new species: cross-section through posterior body in the region of (inner) pre-pallial spines. Abbreviations: hg, hindgut; is, inner pre-pallial spine; mu, musculature; nl, lateral nerve cord; pc, (extension of) pericardium; pd, pericardioduct (at left solid distal end); sd, spawning duct.

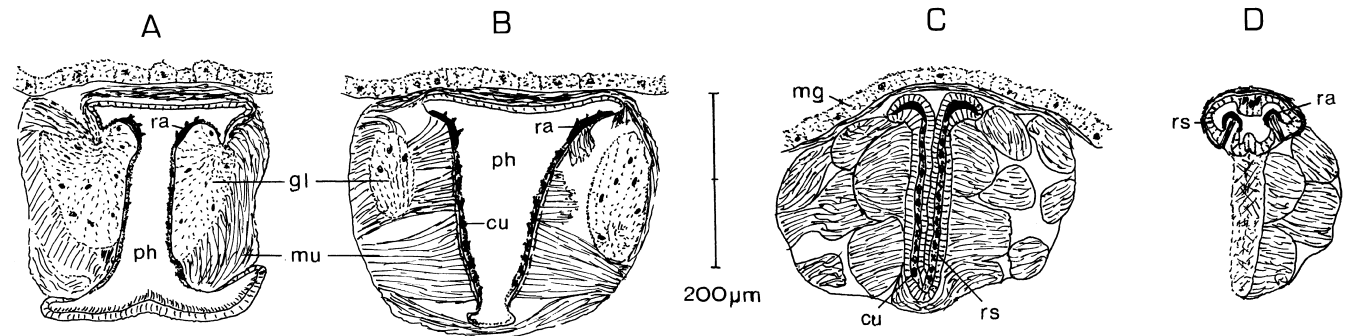


Figure 11. *Aploradoherpia insolita* new genus, new species: diagrammatic cross-sections through radular apparatus (see Figs 21, 22). **A, B.** Sections within pharynx. **C, D.** Sections through radular sheath. Abbreviations: cu, scaly cuticle; gl, foregut gland; mg, midgut epithelium; mu, musculature; ph, pharynx; ra, radular plate; rs, radular sheath.

ventral commissures and less often by latero-ventral connectives. Ganglia posteriora inferiora ($50\ \mu\text{m} \times 25\ \mu\text{m}$ diam.) below spawning ducts and medially of pre-pallial spines, very close together, but not fused. Ganglia posteriora superiora ($70\ \mu\text{m} \times 25\ \mu\text{m}$ diam.) next to anus with a strong, medullary commissure ($15\ \mu\text{m}$ diam.).

Atrial sense organ with papillae mostly united into twos. Roof forming two narrow tracts of ciliary cells, with similar tracts present ventrolaterally. These tracts are elevated neither in ridges nor folds, and in contrast to the usual configuration they do not curve to fuse posteriorly. Three strong muscle bundles (retractors) insert on atrial roof.

Terminal sense organ very big (in relation to body size) and terminally located, protruded and with intruding muscle fibres; distally delimited by a plate of cells $5\ \mu\text{m}$ high. The innervation could not be traced.

Alimentary tract. Mouth opening dorso-posteriorly in the atrium and opening into spacious buccal cavity of high cells with gland cells between, surrounded by dorso-posteriorly strengthened musculature forming a sphincter against pharynx with radular apparatus. The anteriorly high pharyngeal epithelium appears to be ciliated with gland cells, but becomes flat without gland cells and ciliation becomes scarce near radula.

Radular apparatus intrudes into this spacious pharyngeal region ($250 \times 190\ \mu\text{m}$, in cross-section initially nearly rectangular) (Fig. 11A); laterally, bulges ($150\ \mu\text{m}$ high) support radula on both sides; anteriorly, each bulge includes a foregut gland representing compact ampullae with club-shaped, $70\text{--}130\text{-}\mu\text{m}$ -high epithelial cells (type C in Salvini-Plawen, 1972, 1978). More posteriorly, the pharynx closes the ventral transverse space (thus becoming V-shaped in cross-section) and the lateral bulges are underlain by a bolster of three muscle bundles (Fig. 11B). Foregut opens dorsally into midgut.

Biserial radula covers dorsomedian surface of lateral bulges and also curves a short distance rostro-ventrally. Radular sheath begins between bulges behind foregut opening into midgut (Fig. 11C, D). Roof of sheath intrudes a fold, which represents a septum separating the two radular rows. Entire apparatus $250\ \mu\text{m}$ in height, rear of sheath diminishes to $80\ \mu\text{m} \times 100\ \mu\text{m}$ across (Fig. 11D). Within lateral bulges the three-parted musculature of the bolster posteriorly splits further to become several compact bundles (Fig. 11). No large turgid cells or vesicles are associated with the radular support. Anterior, older plates of biserial radula $50 \times 8\ \mu\text{m}$ in size, curved, forming four median denticles at $10\ \mu\text{m}$ intervals (Fig. 10B); their simple form resembles that of *Cyclomenia holoserica* (Nierstrasz, 1902, 1905). Plates cover dorso-medial surface of bulges and are medio-ventrally continuous with a squamous cuticle of $6\text{--}8\ \mu\text{m}$ height built of rods ($4\text{--}5\ \mu\text{m}$ wide), as are underlying cells (Fig. 11B). This cuticle is very similar to the radula itself, which thus appears to cover the entire lateral bulge (Figs 11B, 21, 22). Subsequent condition highly unusual: the median squamous cuticle enters posterior sheath together with radular plates (Figs 11C, 21, 22) and is likewise covered by epithelium of the dorsal septum. Only in the sheath's final $30\ \mu\text{m}$ is the sheath diminished (see above), restricted to radula-forming area (but not the area of the squamous cuticle; Fig. 11D); odontoblasts are about $20\ \mu\text{m}$ high.

Midgut with spacious rostral caecum extending to cerebral ganglion and with a narrow, mid-dorsal ciliary tract; latero-ventral pouchings only weak and irregularly shaped. Hindgut with tall epithelium bearing long cilia; it opens dorsally above beginning of mantle cavity opening.

Present animal with swallowed prey occupying rostral caecum, two-thirds of midgut and posterior pharyngeal space between radular plates. This elongate prey (about $1.2 \times 0.3\ \text{mm}$) covered by a cuticle(?), shows a strongly ciliated gut embedded in dense cell material and muscle fibres (mesenchyme); its body wall

musculature cannot be ascertained, but there are scattered eggs (diam. $15\text{--}20\ \mu\text{m}$) and numerous balls of bundled cilia (sperm?) in the tissues.

Gonopericardial system. Spacious pericardium with mid-dorsally invaginated heart shows a paired rostral extension lateral of the hindgut (primordia of gonads). Terminally, the two pericardioducts emerge laterally, curve anteriorly and end blindly as solid cords (Fig. 12). Without any connection to the latter, the spawning ducts extend below them; they are voluminous but with a simple epithelium. Spawning ducts fuse in their posterior portion and open by a single outlet from dorsal into ventro-rostral pouch of mantle cavity.

Remarks. From the juvenile state of the animal it is unclear whether seminal receptacles are not or not yet present. Although the inner pre-pallial spines show musculature, their fairly radial orientation (Fig. 12) and size are not comparable to growing copulatory stylets (see *Syngenoherpia intermedia* in Salvini-Plawen, 1978). The immature state does underline the heterochronic development of the pericardium and (primordia of) gonadal spaces. In addition, it again demonstrates the independent derivation of the pericardioducts (from the mesodermal pericardium) and the spawnings ducts (from the ectodermal mantle cavity; see also Baba, 1938).

The organization of the present animal clearly places it in Simrothiellidae, but the structure of the radular plates and respiratory papillae are unique within this taxon.

At the supraspecific level, new findings have resulted in recent reclassification of the Simrothiellidae. Based on an earlier re-examination of *Simrothiella margaritacea* and the particular organization of the radular apparatus in *Simrothiella* and *Kruppomenia*, Salvini-Plawen (1972, 1978) synonymized both genera. Recently, Scheltema & Schander (2000) restored *Kruppomenia*, basing separation from *Simrothiella* on details of the radula (simple multi-serrate plates vs. heterogeneously denticulated plates with lateral reinforced thickening or 'buttress'). Further, they removed *S. schizoradulata* S.-Plawen to a new genus *Plawenia*, because of the arrangement of tangential spicules in one layer only (versus diagonal-intercrossingly multilayered or 'skeletal' spicules in *Simrothiella* and *Kruppomenia*). Recently, Arnofsky (2000) erected a new genus *Spiomenia* for a species similar to *Plawenia* having hollow spicules with an asymmetrical axe-shaped ('capitate') tip; the special character of the radular plates in *Spiomenia* (additional denticles lateral of the 'buttress'), however, appears to be relevant only at the specific rather than generic level. The genera *Uncimenia* Nierstrasz and *Sialoherpia* S.-Plawen, previously classified with some doubt among Simrothiellidae (Salvini-Plawen, 1978), are now placed in the Pararrhopaliidae within the subfamily Unciherpiinae (Garcia-Alvarez, Salvini-Plawen & Urgorri, 2001).

Among recognized genera of the family (Table 3), only *Plawenia* and *Spiomenia* correspond with the present specimen in exhibiting a thick cuticle and hollow acicular spicules arranged obliquely (tangentially) in one layer. However, both these genera are characterized by the presence of complex copulatory stylets. Even if we regard that character as unknown in the new species, the simply denticulated radular plates are in strong contrast to *Plawenia* and *Spiomenia*. The different radular configuration between *Simrothiella* and *Kruppomenia* (as stressed by Scheltema and Schander, 2000) parallel the differences between *Plawenia/Spiomenia* and the new species, whose radula is intermediate between that of *Cyclomenia* and *Kruppomenia*. Thus, if *Kruppomenia* is accepted as being generically different from *Simrothiella*, the new species analogously represents a genus proper (regardless of the condition of copulatory stylets). According to current systematics (Salvini-Plawen, 1978; Scheltema & Schander, 2000; Arnofsky, 2000; Garcia-Alvarez et

Table 3. Generic characters in Simrothiellidae (*Spiomenia* differs from *Plawenia* by the presence of distally axe-like spicules only, which may or may not be accepted as a generic character).

| | Tangential spicules | Epid. pap. | Mouth | Radular plates | Paired radula sac | Foregut glands | Cop. styl. | Go sem. | Rec. | Dts | Gills |
|-------------------------|------------------------|---------------|----------|----------------|----------------------|---------------------|---------------|------------|------|-----|-------|
| <i>Simrothiella</i> | Inter-crossing | ± | Fused | Heterodented | + | Ampullae | + | 1 | ? | + | + |
| <i>Kruppomonia</i> | Inter-crossing | ± | Fused | Serrate | + | Ampullae | + | 1 | + | + | + |
| <i>Cyclomenia</i> | Inter-crossing | – | Separate | Simple, wide | – | Ampullae | + | 1 | – | + | + |
| <i>Aploradoherpia</i> | One layer | – | Fused | Simple | – | Ampullae | – | 1 | ? | + | + |
| <i>Plawenia</i> | One layer | – | Fused | Heterodented | + | Ampullae | + | 1 | + | + | + |
| <i>Spiomenia</i> | One layer and axes | – | Fused | Heterodented | + | Ampullae | + | 1 | + | + | + |
| <i>Birasoherpia</i> | Inter-crossing | + | Fused | Heterodented | + | 3 club-shaped tubes | + | 1 | + | + | + |
| <i>Biserramenia</i> | One layer | – | Separate | Serrate | – | Tubes | – | 1 | + | + | – |
| <i>Hellicoradomenia</i> | Solid, one layer | + | Fused | Heterodented | + | Bunches of cells | + | 1 | + | + | + |

Abbreviations: cop. styl., copulatory stylets; dts, dorsoterminal sense organ; epid. pap., epidermal papillae; go, secondary genital opening; rec. sem., seminal receptacle; +, present; –, not present; ±, in part present; ?, unclear or not known.

al., 2001), nine genera are thus recognized within the Simrothiellidae (Table 3), making it the most diverse family within the Cavibelonia.

Rhipidoherpiidae Salvini-Plawen, 1978

Diagnosis: Cavibelonia with thick cuticle, sclerites generally as hollow needles; radula polystichous, ventral foregut glandular organs with subepithelially arranged glands; seminal receptacles in bundles.

Thieleherpia new genus

Diagnosis: Cavibelonia with hollow spicules intercrossing in several layers; with common atrio-buccal opening; radula polystichous; ventral foregut glandular organs tubular with subepithelial layer of gland cells in compact arrangement; midgut with regular lateroventral constrictions; with paired bundle of seminal receptacles, secondary genital opening single; no copulatory stylets; dorsoterminal sense organ(s) present; no respiratory organs.

Type species: *Proneomenia thulensis* Thiele, 1900.

Ethymology: Greek *herpein*, to move slowly and *herpeton*, a slowly moving animal; dedicated to Johannes Thiele (1860–1935), prominent German malacologist. Female gender.

Thieleherpia thulensis (Thiele, 1900)

(Figures 13, 14)

Proneomenia thulensis Thiele, 1900: 111.

Types: Holotype (ZMB Moll. 105.405 b), 25 mm length, section series on slides; Hinlopen Strait, Spitzbergen (80°08' N, 16°55' E), 480 m.

Diagnosis: 13–25 mm long; cuticle 180–220 µm thick, thick-walled spicules tangential and intercrossing in several layers; epidermal papillae present; foregut (protrusible?) with distinct postradular, anteriodorsal portion; radula with 32–36 equal teeth per transverse row (no particular central teeth); ventral foregut glandular organs with long duct, distal half with subepithelial glands in compact arrangement; hindgut with a dorso-lateral bundle of rectal glands; paired bundle of 5–9 seminal receptacles; 2 dorsoterminal sense organs; abdominal spicules not distinct.

Material examined: Holotype and one specimen 13 × 1.5–2 mm, incomplete section series on slides; off northeastern Iceland (67°19' N, 15°52' W), Station 126 of Ingolf Expedition, 29 July 1896, 552 m (ZMUC).

Mantle: New animal with all epidermal papillae strictly in radial arrangement, with distal swellings nearly without exception at the periphery only. Cuticle 180 µm high (holotype 220 µm), spicules measuring 70–210 µm (100–150 µm), thick-walled and tangentially arranged in several intercrossing layers; with interspersed similar radial spicules. Abdominal spicules solid, distally (not very distinctly) hooked, up to 115 µm × 8 µm diam. (80 µm long in Thiele, 1911: 4).

Foot and pallial cavity: Spacious pedal pit with up to five folds, only the median main fold (100 µm high) passes pedal groove (bordered on both sides by mantle fold) until mantle cavity. Voluminous follicles of pedal gland cells open anteriorly into pit, differently staining glands open laterally; smaller sole glands single, not very numerous, corresponding in structure to anterior pedal gland cells. Epithelium of mantle cavity irregularly folded and ciliated, but without formation of respiratory folds or papillae. No posterior extension of cavity beyond its opening.

Musculature: Body wall musculature strong, inner longitudinal layer reinforced ventrally (*M. longitudinalis ventralis*). Upper/inner bundles of dorsoventral musculature providing fibres also into the mantle folds. Entire foregut with distinct longitudinal and feeble circular musculature; four retractors extend from the subradular sac ventro-posteriorly, and two additional retractors insert at the dorsal radular sheath and run to the body wall.

Sensory system: Nervous system (Fig. 13) fused cerebral ganglia giving rise to frontal nerves to atrial sense organ. Lateral and ventral connectives medullary, emerging side by side; buccal connective beginning termino-laterally. Together with the lateral connective, a strong nerve leaves to the lateroventral body wall. First lateral ganglion not prominent (60 µm diam.), subsequent cord (25 µm diam.) predominantly fibrous with interspersed weak swellings giving rise to a dorsal nerve; anterior portion of cords with several nerves running to lateroventral body wall. Each cerebro-ventral connective gives rise to a strong nerve (at left 15 µm diam., at right divided with 10 µm and 7 µm diam.) running to the pedal pit. First ventral ganglia above pedal pit prominent (100 µm diam.) with one strong commissure and with a ventral nerve to posterior pedal pit. Buccal ganglia (70 µm diam.; in holotype 105 × 80 µm) with one commissure only. Ventral cords with weak swelling at intervals between

60 μm and 85 μm , provided with commissures and lateroventral connectives. Suprarectal commissure dorsally with nuclei, nerve cords continuing behind ganglia posteriora and showing two lateroventral connectives. Both the holotype and new specimen with two dorsoterminal sense organs: one above posterior wall of mantle cavity, second at the rear of body (only this recognized by Thiele, 1900: 112), each forming a pit (120 μm diam.) surrounded by slender lanceolate scales (20–30 μm long) and

enclosing a 25–30 μm high sensory epithelium. Both organs with paired innervation, the anterior one from the supra-rectal commissure, the second from the posterior lateral cords (Fig. 13). Atrial sense organ spacious; horseshoe-shaped ciliary tract delimiting sensory area begins mid-dorsally as a single plate that becomes divided.

Alimentary tract: Mouth dorsocaudally within the atrium posterior to ciliary tract. Sphincter at border between buccal cavity and subsequent foregut weak (in contrast to Thiele, 1900: 113). Foregut with lower leg and upper, anterior-dorsally directed portion; radular apparatus in a blind pouch at bend (see Thiele, 1900). Radular teeth all identical: 40–55 μm long and (basally) 5–7 μm wide with a 25–35 μm free tip (see also Thiele, 1911: fig. 6); 32–40 teeth per transverse row, all inserting upon basal cuticle at intervals of 3 μm ; epithelium 15–20 μm high. Upper leg of foregut short and opening from ventro-posterior into midgut; rostral caecum extends into atrial region. Dorsoventral muscle bundles cause distinct, regular, lateroventral constrictions of caecum and midgut, the latter with intruding clustered epithelium. Mid-dorsal ciliated tract wide and beginning within caecum. Anterior midgut containing a piece of an unidentifiable prey with cuticle; no nematocysts observed. Hindgut thoroughly ciliated and receives several tubular outlets of the voluminous rectal gland. The gland cells (20–50 μm diam.) with finely granulated, mucus-like contents packed into follicles, which extend from just behind the pericardium backwards to above mantle cavity.

Ventral foregut glandular organs of unusual organization: there are long and anteriorly wide ducts of 8–10 μm high, cubic cells with central nuclei (5 μm diam.); this epithelium is covered by a 5–8 μm thick matrix (secretion or cuticle? See also Baba, 1940: 134–135 for *Epimения babai*). These portions of the ducts show an S-loop and extend over half the length of whole organs, then changing abruptly their organization: lumen becomes strongly narrowed and lined by a 10–20 μm high epithelium of cylindrical cells with subcentral nuclei, this lining is surrounded by a proper, mainly longitudinal musculature. Simultaneously, subepithelial gland cells organized in follicles of about 150 μm length open inter-cellularly. Follicles in very compact arrangement (Fig. 14), without common surrounding membrane, although individually delimited by a delicate lamina. The glands thus possess a structure defined as type A (Salvini-Plawen, 1972, 1978).

Circulatory system: Heart auricles begin as paired groove at pericardium/pericardioduct transition and continue anteriorly as a

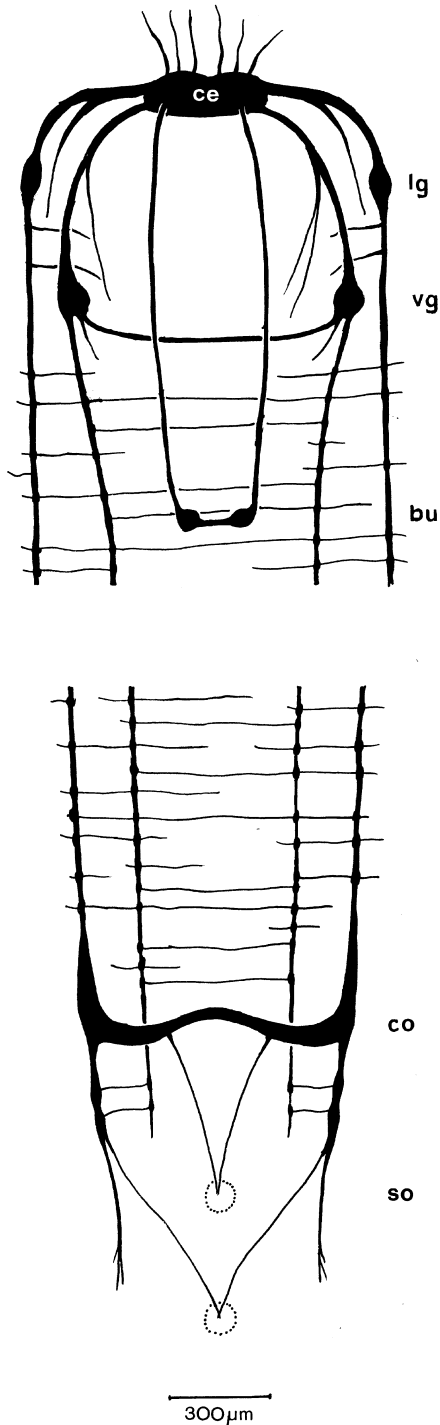


Figure 13. *Thieleherpia thulensis*: nervous system of anterior body (above) and posterior body (below), reconstructed from serial transverse sections (new specimen). Abbreviations: bu, buccal ganglia; co, supra-rectal commissure; lg, (first) lateral ganglia; so, terminal sense organ; vg, (first) ventral ganglia.

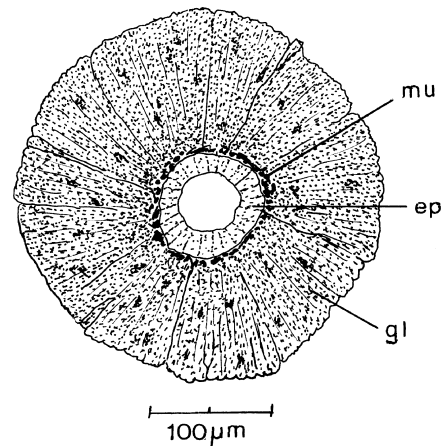


Figure 14. *Thieleherpia thulensis*: transverse section through foregut ventral glandular organ (type A). Abbreviations: ep, epithelial cells of duct; gl, gland cells arranged in follicles; mu, musculature.

short, single dorsal pericardial invagination that closes up below ventricle. Ventricle invaginates above fused atrium and (in contrast to Thiele, 1900: 115) runs freely until anterior end of the pericardium; it continues a certain distance between the gonopericardioducts before passing into the dorsal sinus (rather than aorta), distinct until the middle of the body.

Three types of blood cells: round granulocytes of different size (6–15 μm diam.) with rough granulation and rarely visible nucleus; oval to spindle-shaped erythrocytes (12–18 μm long) with fine granulation and partly with well-visible central rod (cf. Salvini-Plawen, 1997); round and homogeneous to very finely granulated cells with distinct nucleus (2–3 μm diam.).

Gonopericardial system: Gonad paired; stalked eggs (100–160 μm diam.) developing on median walls. Short gonopericardial ducts ciliated throughout, joining the pericardium frontally. Pericardium anteriorly ciliated throughout (except at the ventricle) and laterally provided with several small folds of epithelium. Folds enter pericardioducts; pericardial ciliation subsequently confined to those folded lateral areas. Pericardioducts ciliated throughout, with 5–7 medial, slender epithelial folds attaining a height of 30–60 μm . Distal third of the ducts provided with a strong (19 μm thick) circular musculature. At each junction of pericardioducts with spawning ducts, a bundle of 5–9 tubular seminal receptacles with sperm (70–100 μm long tails) arranged with their heads (6–8 μm long) side by side at the wall. Spawning ducts of new specimen in their anterior third provided with a high glandular epithelium; second third (still paired) and third portion (fused) lined by a flat ciliated epithelium. No copulatory stylet apparatus.

Remarks: The new specimen clearly coincides with the holotype and most of Thiele's (1900) comprehensive description of *Proneomenia thulensis*. The special characters of the curved foregut, the radular apparatus, the ventral foregut glandular organs, the seminal receptacles and the rectal gland are in agreement, and the new specimen also fits the geographical range. Comparative re-examination of both animals, however, revealed some additional information considered above.

With regard to the ventral foregut glandular organs, Thiele (1900: 114) accurately stated that the glandular portion below the midgut must be distinguished from a distinct outleading portion. No description or drawing of the organs themselves with the interconnecting portion, however, was provided. The re-examination of the holotype clearly revealed that the glandular organs proper are simple tubes with subepithelial, elongate gland cells in compact arrangement (Fig. 14), i.e. without surrounding membrane (in contrast to earlier indication: Salvini-Plawen, 1978: 231). This corresponds with the so-called type A (Salvini-Plawen, 1972, 1978) and contrasts to organs with surrounding membrane or musculature (type B; cf. Salvini-Plawen, 1978: Abb. 264 in *Syngonherpia*).

The polystichous radula agrees with that in Rhipidoherpiidae and Proneomeniidae (especially of certain *Dorymenia* species; see Salvini-Plawen, 1978). However, the latter possess purely epithelial foregut glandular organs (type C in Salvini-Plawen, 1972, 1978), whereas Rhipidoherpiidae possess type A glandular organs. Thus, the present species has to be shifted from *Proneomenia* (cf. Salvini-Plawen, 1978: 231) to close to *Rhipidoherpia*. Due to the presence of copulatory stylets in *Rhipidoherpia* (cf. Salvini-Plawen, 1978), however, *P. thulensis* is considered generically separate and is therefore classified in a new genus *Thieleherpia*. The Rhipidoherpiidae, including both genera, are thus confirmed to represent a valid taxon.

Thiele (1900: 115) reported a high number of about 20 seminal receptacles on each side, but the examination of the holotype revealed 7–9 receptacles. Thiele may thus refer to the total number, or he was misled by the multiple cuts of the curved

tubes and somewhat lobulate receptacles, which simulate a much higher number of receptacula than actually exist. From another animal (24 mm long), Thiele (1911) reported only a few, short seminal tubes. With respect to the present new animal with five receptacles at each side, sexual maturity of the species is already attained at a body length of 13 mm.

The original record of *Thieleherpia thulensis* comes from the Hinlopen Strait, Spitzbergen and was firmly coiled around a portion of an alcyonarian colony (Thiele, 1900: 111). Another finding was reported by Thiele (1911) from the Laptew Sea (77°01' N, 114°35' E; 60 m). Derjugin (1915) mentioned the (questionable) occurrence of this species in the Kola Fjord (close to Murmansk; 69°15'19'' N, 33°30'50'' E; 91–128 m), also noted by Thiele (1932). The present new record without any association to Cnidaria comes from off northeastern Iceland at 552 m depth and thus significantly enlarges the known distribution of the species to the southwest.

Proneomeniidae Simroth, 1893

Diagnosis: Solenogastres with thick cuticle, sclerites as hollow needles (Cavibelonia); radula polystichous/polyserial, ventral foregut glandular organs epithelial; seminal receptacles not in bundles.

Remarks: Not *Proneomenidae* Mitchell, 1892. Mitchell (1892: 58) did not introduce a family taxon, elsewhere printed in capitals and centred. Rather he misleadingly used the term as a collective instead of the genus (hence in italics) for the four '*P.*' species treated by Kowalevsky & Marion (1887); in addition, *Proneomenidae* would be a misnomer with respect to a non-existent genus *Proneomena* (rather than *Proneomenia* Hubrecht, 1880).

Genus *Dorymenia* Heath, 1911

Diagnosis: Cavibelonia with hollow spicules intercrossing in several layers; with common atrio-buccal opening; radula polystichous; ventral foregut glandular organs epithelial, midgut with regular constrictions; with copulatory stylets; dorsoterminal sense organ(s) present; no respiratory organs.

Type species: *Dorymenia acuta* Heath, 1911.

Dorymenia quincarinata (Ponder, 1970)

Proneomenia quincarinata Ponder, 1970: 57.

Types: Holotype (DMW M 23193), 31 mm length, intact specimen in alcohol; station 34 of the 1954 Chatham Islands Expedition (44°04' S, 175°23.5' E), 1 February 1954, 237–238 m. Paratype 1 (DMW M 23194), 30 mm length, dissected animal in alcohol; from type locality. Paratype 2 (DMW M 23195), 52 mm length, dissected animal in alcohol; Cook Strait off Lyall Bay, 1962, 14–15 m.

Diagnosis: 30–52 mm long; cuticle thick with five longitudinal ridges along body; foregut with pharyngeal glands and with distinct postradular, antero-dorsal portion; radula with about 40 teeth per transverse row, with two strong central teeth characterized by a single hooked cusp. Spawning ducts with separate outlets (paired secondary genital opening); no sac-like seminal receptacles. Apart from copulatory stylets, with a pair of pallial spines, abdominal spicules present.

Remarks: The disintegrated condition of the re-examined, dissected paratype 2 does not allow more accurate description of the animal's organization. We are thus left with the original description of *Proneomenia quincarinata* by Ponder (1970), and information beyond that needs histological investigation of the

holotype (or new material). Meanwhile, some of the characters in the original description can be re-evaluated, leading to reassignment of the species to the genus *Dorymenia*.

Proneomenia quinquecarinata possesses a pair of copulatory stylets. This is the diagnostic character of the genus *Dorymenia* compared with *Proneomenia* (cf. Thiele, 1913; Odhner, 1921; Salvini-Plawen, 1967, 1978); the present species is thus transferred to *Dorymenia*.

The species is characterized by 'shell gland paired, with separate openings into cloacal chamber' (Ponder, 1970: 47–48). Among Proneomeniidae, including 32 known species, this is the first member with separate outlets of the spawning ducts (paired secondary genital openings). This condition represents a conservative state and is interpreted as a generic character (Salvini-Plawen, 1967, 1978), though exceptions among other families of Solenogastres (e.g. within *Neomenia*) or intermediate conditions occur (e.g. within *Anamenia* or *Wirenia*; Salvini-Plawen, 1972; Handl & Salvini-Plawen, 2001).

Ponder (1970: 51) stated that 'there is no separate seminal receptacle but the shell glands . . . each communicate with a rather diffuse, external strip of (follicular?) tissue'. As all hitherto known Proneomeniidae possess a single, rounded (and mostly stalked) seminal receptacle at the proximal portion of each spawning duct, the reported condition is exceptional and outside the accepted generic definition of either *Proneomenia* or *Dorymenia* (Salvini-Plawen, 1978).

Ponder described (1970: 50–51) a 'pair of thick (glandular?) plates . . . attached dorsally and hang vertically into the chamber behind the cloacal opening', and discussed (1970: 53) 'if these were interpreted as gills it may result in *quinquecarinata* being removed from *Proneomenia*'. According to the drawing (Ponder, 1970: fig. 12), however, these two plates are not respiratory organs, as these are not 'plates' and always elaborated at the posterior (rather than dorsal) wall of the mantle cavity. In addition, the pallial cavity of *Dorymenia harpagata* S.-Plawen shows an anterior tri-partition, as a pair of ventral or frontal vertical walls (plates or septa) intrudes into the cavity (Salvini-Plawen, 1978: 263). This condition corresponds to the 'pair of thick plates' in *D. quinquecarinata*.

Ponder compared his new species with *Dorymenia tricarinata* (Thiele). With respect to the radula, there is even more similarity

to *Dorymenia harpagata*; this species from close to Macquarie Island also shows three longitudinal ridges of the mantle cuticle, with indication of another ridge on one side (Salvini-Plawen, 1978).

These comparisons indicate that the organization of *P. quinquecarinata* more or less fits into the generic framework of *Dorymenia*. Based on the separate outlets of the spawning ducts and the 'certainly unusual' condition of the seminal receptacles (Ponder, 1970: 53), however, a separate taxonomic status (at subgeneric level: *Doryherpia* in Salvini-Plawen, 2003) may prove to be justified when histological investigation of the species is carried out.

Notomeniidae new family

Diagnosis: Cavibelonia with thick cuticle and hollow mantle bodies apparently largely not calcareous and with the internal space filled by matrix. Type of radula unknown (vestigial); ventral foregut glandular organs are subepithelial follicles with outleading duct.

Genus *Notomenia* Thiele, 1897

Diagnosis: Cavibelonia with matrix-filled mantle bodies in one tangential-oblique layer within thick cuticle; mouth opening separated from atrial sense organ; without radula (vestigial); midgut with lateral pouches. One pair of seminal receptacles, secondary genital opening paired, without copulatory stylets. Presence of respiratory organs and dorsoterminal sense organ unknown.

Type species: *Notomenia clavivigera* Thiele, 1897

Notomenia clavivigera Thiele, 1897

(Figure 15A, B)

Notomenia clavivigera Thiele, 1897: 398.

Types: Holotype (ZMB Moll. 105.391), 6 mm length, serial cross-sections on slides; Torres Strait, northeastern Australia, 36 m.

Diagnosis: Body up to 6 mm long and brownish, terminally tapered. Mantle bodies club-shaped (up to 100 μm \times 15 μm

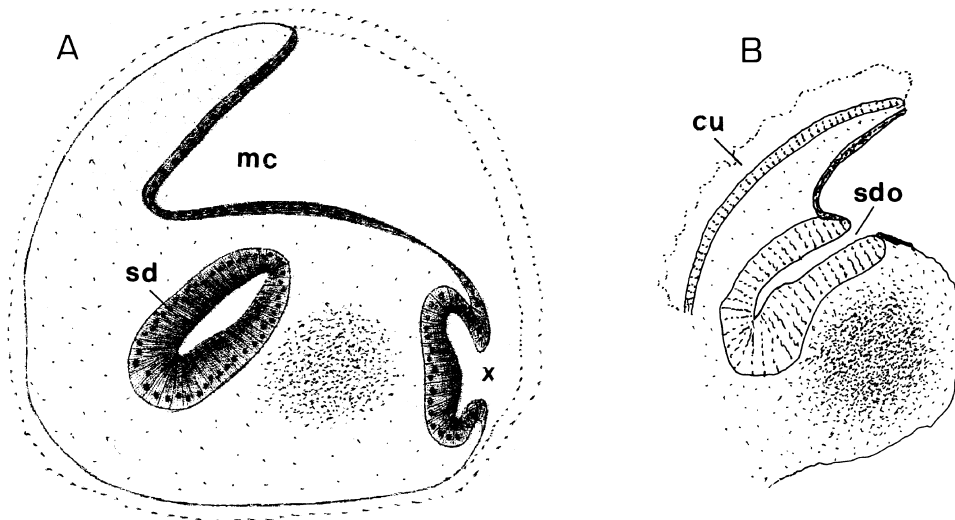


Figure 15. *Notomenia clavivigera*: transverse sections of holotype to demonstrate openings of spawning ducts into mantle cavity. **A.** Section close to body end (after Thiele, 1902: fig. 16, supplemented by original body wall, stippled). **B.** Section further posterior to **A**, through opening of left spawning duct. Abbreviations: cu, mantle cuticle; mc, mantle cavity; sd, spawning duct; sdo, opening of left spawning duct into mantle cavity; x, artificial opening (by rupture) of right spawning duct.

diam.), internal matrix-filled space delimited by a circularly ribbed wall. Epidermal papillae present. Pedal groove with one fold, ending in front of the ventral opening of mantle cavity. Radular sheath present but without teeth, flanked by openings of ventral foregut glandular organs with subepithelial follicles; midgut with single rostral caecum. Spawning ducts at their rostral-most portion curved dorsocaudally, each with a seminal receptacle. Hindgut at transition to mantle cavity with opening into long dorsorostral pouch (brood pouch?).

Remarks: The holotype (about 4 mm long) was damaged terminally before histological treatment; the posterior portion of the mantle cavity (and at right side the entire dorsolateral wall) is missing in the sections. The re-examination of the sections confirmed most of the description by Thiele (1897, 1902), but some details are added below.

In contrast to Thiele (1902), the cuticle measures about 75 μm thick, locally ranging between 50 μm and 119 μm ; the peculiar mantle bodies are embedded obliquely, in the cross-sections thus appearing in several layers. Epidermal papillae fragmentarily visible. Mouth opening distinctly separated from the atrial sense organ. The relationships of the alimentary tract

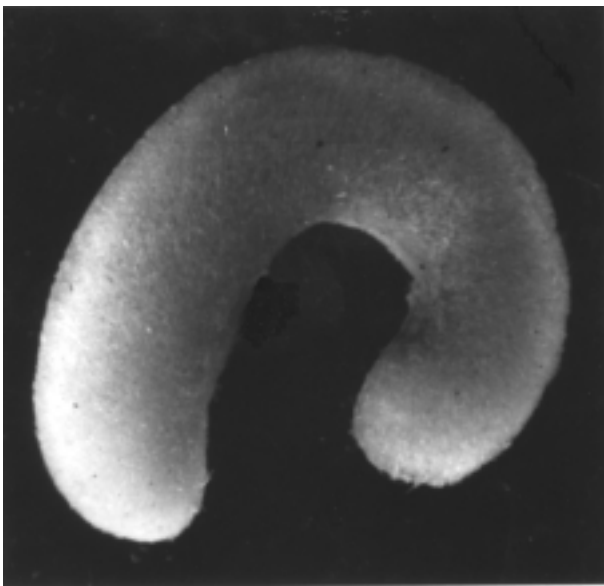


Figure 16. *Drepanomenia pontisquamata* new species: preserved animal (6 mm in size).

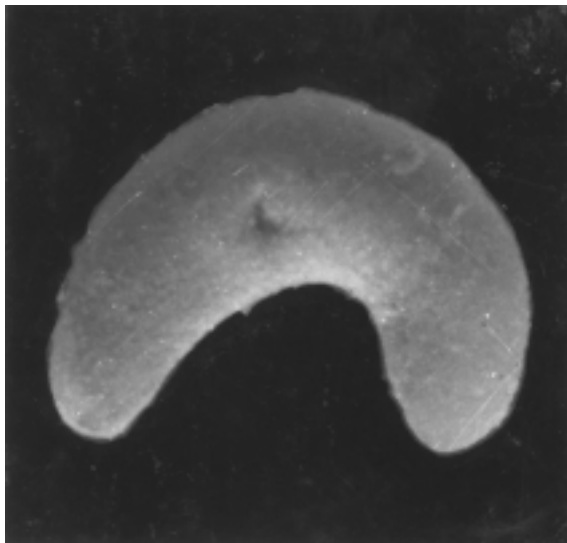


Figure 17. *Simrothiella digitoradulata* new species: preserved animal (3 mm in size, anterior end at right).

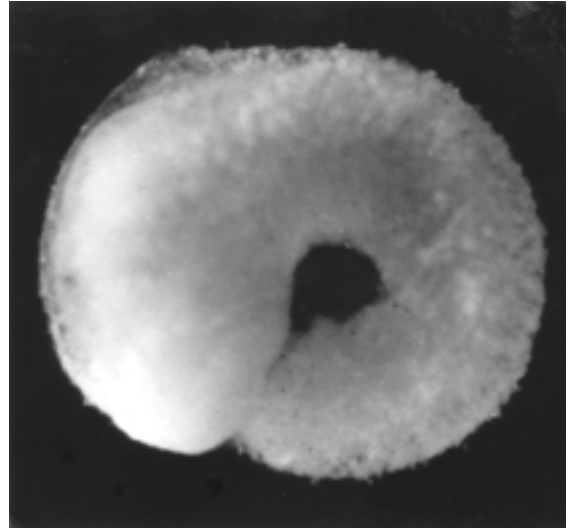


Figure 18. *Aploradoherpia insolita* new genus, new species: preserved animal (3 mm in size).

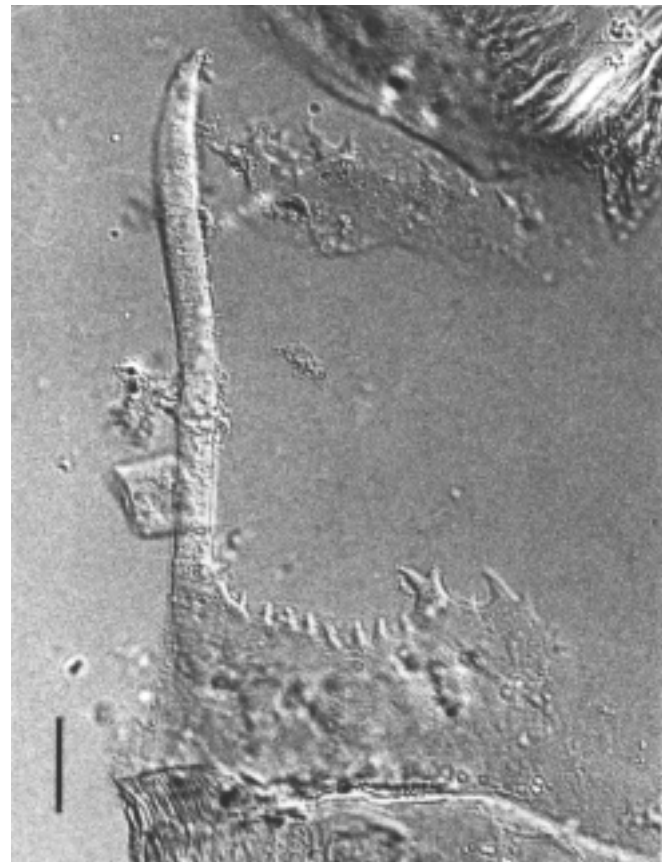


Figure 19. *Simrothiella margaritacea*: cross-section through (posterior portion of) a radular plate exposed to pharynx (from Odhner's series 4731:4b; see Fig. 7A). Scale bar = 20 μm .

with toothless radular sheath, foregut glandular organs (type A in Salvini-Plawen, 1972, 1978) and midgut are clearly presented by Thiele (1902). The heart is an open invagination of the pericardium. Unlike the description by Thiele (1902) the pericardioducts run rostrally and are continuous with the dorsocaudally curved spawning ducts; each seminal receptacle is connected to the transition between the pericardioduct and upper portion of the spawning duct (Thiele, 1902: fig. 14).

The missing rear of the body in the sections of the animal including the posterior mantle cavity with its ventral opening (Haddon in Thiele, 1902: figs 2, 3) prohibits a definitive statement on the respective organs (respiratory organs, dorsoterminal sense organ). Whereas Thiele's fig. 16 shows an artificial opening of the right spawning duct (entire body wall is missing; Fig. 15A), the real (separate) opening of the (left) spawning duct is shown in Fig. 15B. Here, it can be verified that the hindgut/mantle cavity transition (Thiele, 1902: fig. 15) is characterized by an extensive dorsorostral pouch (Thiele, 1902: fig. 14) extending over the pericardium, possibly representing a brood pouch.

Thiele's (1902) neglect of the damaged rear of the body in the sectioned animal led him to somewhat mis-interpret the organization of the mantle cavity. This is repeated by Scheltema (1998: 157) in characterizing the species on the occasion of a new record from the Bass Strait at 40 m.

Due to the lack of some essential organizational information, *Notomenia* was classified among Solenogastres as a genus *incertae sedis* (Salvini-Plawen, 1978; Scheltema, 1998). Based on the present re-examination of the type species, revealing the presence of a thick cuticle, of hollow mantle bodies and of epidermal papillae, the generic diagnosis has been emended and the genus may now be placed among the Cavibelonia. The unique

type of the mantle bodies and the lack of the radula, however, do not allow the genus to be classified within one of the known families (cf. Salvini-Plawen, 1978); therefore, a new family Noto meniidae is proposed.

CONCLUSIONS

The results on new and re-examined species presented here enlarge our information on the organizational diversity of the Cavibelonia and enable more accurate systematic demarcations at the generic and family level. The principal results can be summarized as follows.

The organization of two new species of *Drepanomenia* underlines the isolated status of this genus and thus supports recognition of the monogeneric family Drepanomeniidae. They lack a radula, and other characters do not allow a classification close to any other family of Cavibelonia.

The investigation of *Proneomenia thulensis* (new specimen and holotype) revealed a generic organization close to but distinct from *Rhipidoherpia*, recognized by introduction of the new genus *Thieleherpia*. Both genera are clearly different from other families of Cavibelonia, which confirms the hitherto monogeneric family Rhipidoherpiidae.

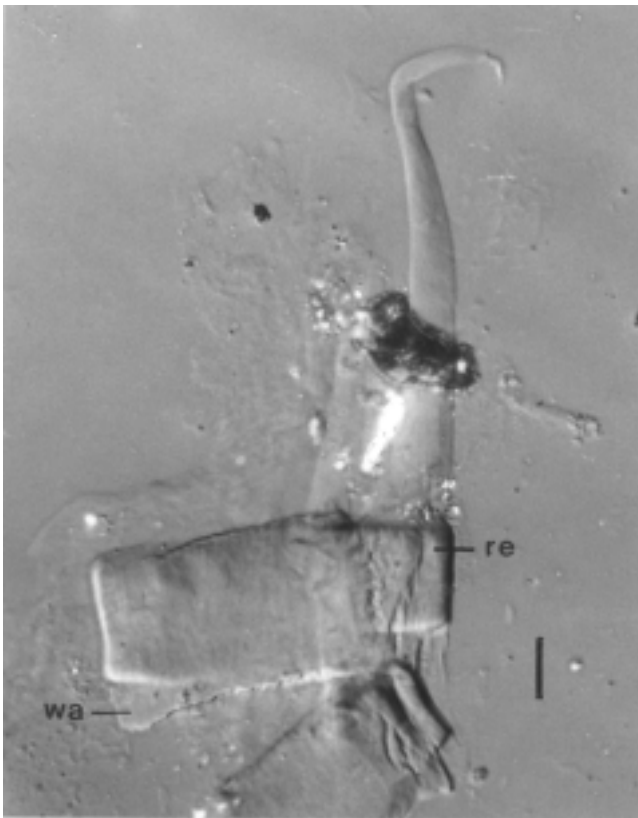


Figure 20. *Simrothiella margaritacea*: radular plate exposed to parynx (*in situ* preparation), view to anterior face with reinforcement (see Fig. 6C). Scale bar = 20 μ m. Abbreviations: re, reinforcement; wa, weak portion.

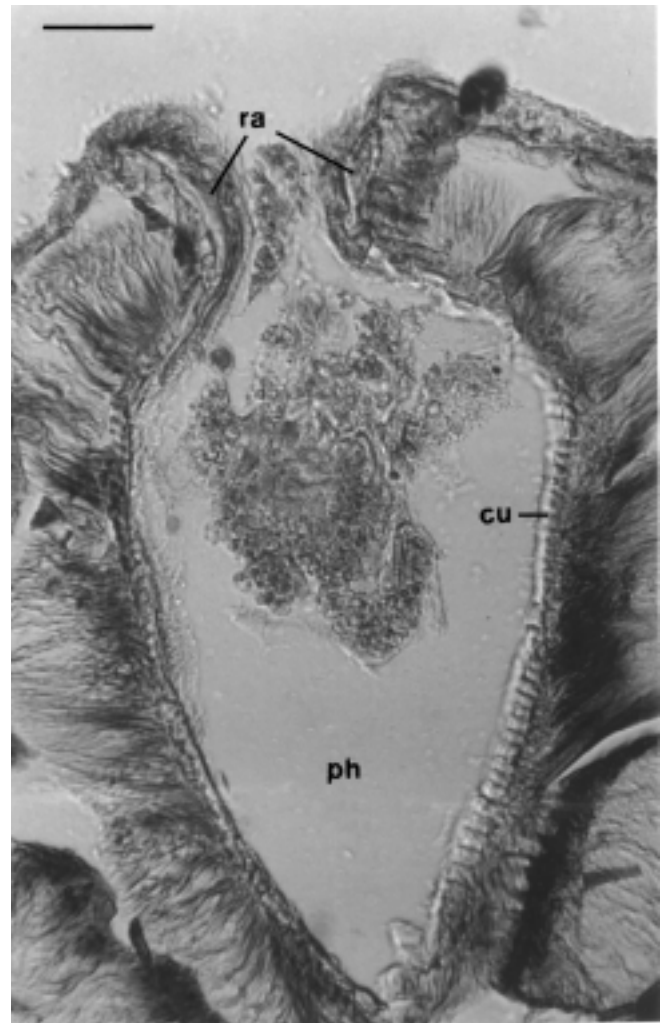


Figure 21. *Aploradoherpia insolita* new genus, new species: cross-section through radular apparatus in the region of pharynx opening into midgut. Scale bar = 30 μ m. Abbreviations: cu, scaly cuticle; ph, pharynx; ra, radular plates.

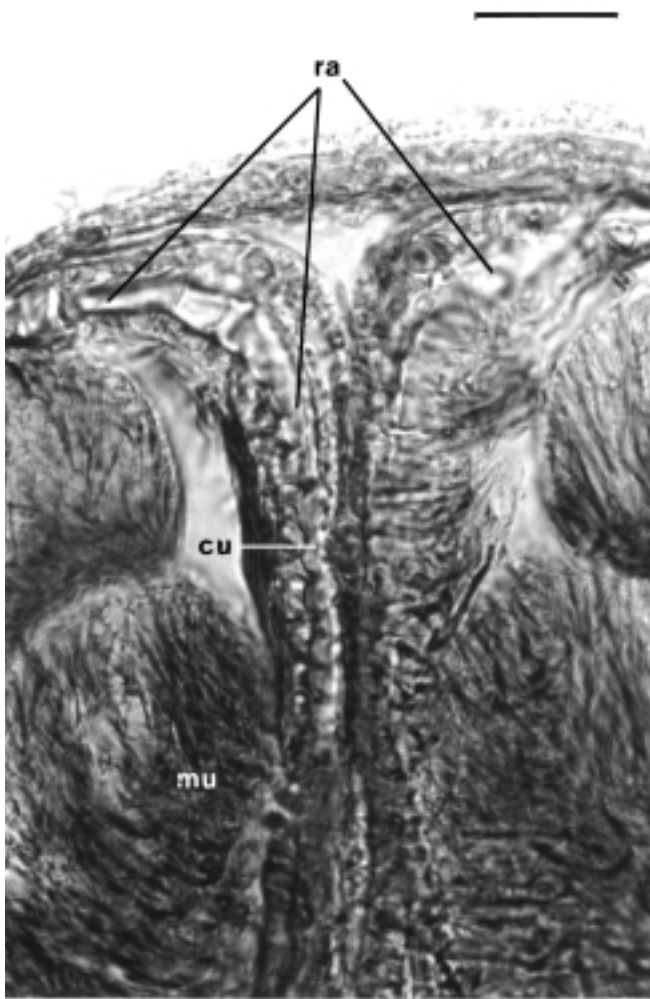


Figure 22. *Aploradoherpia insolita* new genus, new species: cross-section through radular sheath (see Fig. 11C). Scale bar = 20 μ m. Abbreviations: cu, scaly cuticle; mu, musculature; ra, radular plates.

Another *Proneomenia* species, *P. quincarinata*, is transferred within the family Proneomeniidae to *Dorymenia* based on characters already described.

A comparative re-examination of *Simrothiella margaritacea* underlines the high systematic diversity of Simrothiellidae. The detailed configuration of the radula reveals species-level differences between *S. margaritacea* and specimens from the West European Basin leading to the recognition of the new species *S. abyseuropaea*. In contrast, the radula of the new species *S. digitoradulata* from the Atacama Trench is similar to that of *S. abyseuropaea*. Another simrothiellid record from the Atacama Trench represents a new genus and species, *Aploradoherpia insolita*, and thus enlarges the known diversity among Simrothiellidae to nine genera (Table 3).

Notomenia clavigera has been re-examined and its organization places it in the Cavibelonia. However, it cannot be related to any other genus within the framework of the established families, and comparative evaluation leads to its classification within a new family Notomeniidae.

REFERENCES

ARNOVSKY, P. 2000. *Spioomenia spiculata*, gen. et sp. nov. (Aplacophora: Neomeniomorpha) collected from the deep waters of the West European Basin. *Veliger*, **43**: 110–117.

- BABA, K. 1938. The later development of a solenogastre, *Epimonia verrucosa* (Nierstrasz). *Journal of the Department of Agriculture, Kyusyu Imperial University*, **6**: 21–41.
- BABA, K. 1940. The mechanisms of absorption and excretion in a Solenogastre, *Epimonia verrucosa* (NIERSTRASZ), studied by means of injection methods. *Journal of the Department of Agriculture, Kyusyu Imperial University*, **6**: 119–165.
- DERJUGIN, K. 1915. La faune du Golfe de Kola et les conditions de son existence. *Mémoires de l'Académie impériale des Sciences St. Petersbourg*, Série VIII, **34**: 1–929.
- GARCIA-ALVAREZ, O., SALVINI-PLAWEN, L. von & URGORRI, V. 2001. *Unciherpia hirsuta* a new genus and species of Aplacophoran (Mollusca Solenogastres: Pararrhopaliidae) from Galicia, Northwest Spain. *Journal of Molluscan Studies*, **67**: 113–119.
- HANDL, C. & SALVINI-PLAWEN, L. von 2001. New records of Solenogastres-Pholidoskepia (Mollusca) from Norwegian fjords and shelf waters including two new species. *Sarsia*, **86**: 367–381.
- HANDL, C. & SALVINI-PLAWEN, L. von 2002. New records of Solenogastres-Cavibelonia (Mollusca) from Norwegian fjords and shelf waters including three new species. *Sarsia*, **87**: 423–450.
- HASZPRUNAR, G. 2000. Is the Aplacophora monophyletic? A cladistic point of view. *Malacological Bulletin*, **15**: 115–130.
- HEATH, H. 1911. Reports on the scientific results of the expedition to the tropical Pacific. XIV. The Solenogastres. *Memoirs of the Museum of Comparative Zoology at Harvard College*, **45**: 1–182.
- HOFFMAN, S. 1949. Über das Integument der Solenogastren, nebst Bemerkungen über die Verwandtschaft zwischen den Solenogastren und Placophoren. *Zoologische Beiträge von Uppsala*, **27**: 293–427.
- HOFFMANN, H. 1929. Amphineura (I). In: *Bronns Klassen und Ordnungen des Tierreichs*, **3**, Abteilung 1, Suppl.: 1–368. Akademische Verlagsgesellschaft m.b.H., Leipzig.
- HYMAN, L.H. 1967. Mollusca I. In: *The Invertebrates* (L.H. Hyman, ed.), **VI**: 1–792. McGraw-Hill, New York.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE 1981. Opinion 1185, *Simrothiella* Pilsbry, 1898 (Mollusca, Solenogastres): Designation of a type species. *Bulletin of Zoological Nomenclature*, **38**: 185–187.
- IVANOV, D. 1990. The radula of the shell-less molluscan classes (Aplacophora). *Archives of Zoological Museum Moscow State University*, **28**: 159–198 [in Russian].
- KOREN, J. & DANIELSSEN, D.C. 1877. Beskrivelse over nye arter, henhørende til slægten *Solenopus*, samt nogle oplysninger om dens organisation. *Archiv for Mathematik og Naturvidenskab (Christiana)*, **2**: 121–128.
- KOREN, J. & DANIELSSEN, D.C. 1879. Descriptions of new species belonging to the genus *Solenopus*, with some observations on their organization. *Annals and Magazine of Natural History (Series 5)*, **3**: 321–328.
- KOWALEVSKY, A. & MARION, A. 1887. Contributions à l'histoire des Solenogastres ou Aplacophores. *Annales du Musée d'Histoire Naturelle de Marseille*, Zoologie III (Mém. 1): 1–77.
- MITCHELL, P. C. 1892. Mollusca (1890). *Zoological Record*, **27**: 1–71.
- NIERSTRASZ, H. 1902. The Solenogastres of the Siboga-Expedition. *Siboga-Expédition*, **47**: 1–46.
- NIERSTRASZ, H. 1905. *Kruppomenia minima* und die Radula der Solenogastren. *Zoologisches Jahrbuch für Anatomie*, **21**: 655–702.
- NIERSTRASZ, H. & STORK, H. 1940. Monographie der Solenogastren des Golfes von Neapel. *Zoologica (Stuttgart)*, **99**: 1–99.
- ODHNER, N. 1921. Norwegian Solenogastres. *Bergens Museums Aarbok 1918–19, Naturvidenskabelig række*, **3**: 1–86.
- PONDER, W.F. 1970. A new Aplacophoran from New Zealand. *Journal of the Malacological Society of Australia*, **2**: 47–54.
- SALVINI-PLAWEN, L. von 1967. Kritische Bemerkungen zum System der Solenogastres (Mollusca, Aculifera). *Zeitschrift für zoologische Systematik und Evolutionsforschung*, **5**: 398–444.
- SALVINI-PLAWEN, L. von 1968. Über einige Beobachtungen an Solenogastres (Mollusca, Aculifera). *Sarsia*, **31**: 131–142.

CONTRIBUTIONS TO CAVIBELONIA

- SALVINI-PLAWEN, L. von 1972. Revision der monegassischen Solenogastres (Mollusca, Aculifera). *Zeitschrift für zoologische Systematik und Evolutionsforschung*, **10**: 215–240.
- SALVINI-PLAWEN, L. von 1975. *Solenopus margaritaceus* Koren & Danielsen, 1877 (Mollusca, Solenogastres): proposed designation as type-species of the genus *Simrothiella* Pilsbry, 1898. Z.N. (S.) 1983. *Bulletin of Zoological Nomenclature*, **32**: 156–157.
- SALVINI-PLAWEN, L. von 1978. Antarktische und subantarktische Solenogastres – Eine Monographie: 1898–1974. *Zoologica (Stuttgart)*, **128**: 1–315.
- SALVINI-PLAWEN, L. von 1997. Systematic revision of the Epimeniidae (Mollusca: Solenogastres). *Journal of Molluscan Studies*, **63**: 131–155.
- SALVINI-PLAWEN, L. von 2003. On the phylogenetic significance of the aplacophoran Mollusca. *Iberus*, **21**: 67–97.
- SALVINI-PLAWEN, L. von & STEINER, G. 1996. Synapomorphies and symplesiomorphies in higher classification of Mollusca. In: *Origin and evolutionary radiation of the Mollusca* (J. Taylor, ed.): 29–51. Oxford University Press.
- SCHELTEMA, A.H. 1998. Class Aplacophora. In: *Mollusca: The Southern Synthesis* (P.L. Beesley, G.J.B. Ross & A. Wells, eds). *Fauna of Australia*, **5/A**: 145–159. CSIRO Publications, Melbourne.
- SCHELTEMA, A.H. 1999. New eastern Atlantic Neomenioid aplacophoran molluscs (Neomeniomorpha, Aplacophora). *Ophelia*, **51**: 1–28.
- SCHELTEMA, A.H. & KUZIRIAN, A.M. 1991. *Helicoradomenia juani* gen. et sp. nov., a Pacific hydrothermal vent Aplacophora (Mollusca: Neomeniomorpha). *Veliger*, **34**: 195–193.
- SCHELTEMA, A.H. & SCHANDER, C. 2000. Discrimination and phylogeny of solenogaster species through the morphology of hard parts (Mollusca, Aplacophora, Neomeniomorpha). *Biological Bulletin*, **198**: 121–151.
- THIELE, J. 1897. Zwei australische Solenogastres. *Zoologischer Anzeiger*, **19**: 398–400.
- THIELE, J. 1900. *Proneomenia thulensis* n. sp.. In: *Fauna arctica* (F. Römer & F. Schaudinn, eds), **1**: 111–116. G. Fischer, Jena.
- THIELE, J. 1902. Die systematische Stellung der Solenogastren und die Phylogenie der Mollusken. *Zeitschrift für wissenschaftliche Zoologie*, **72**: 249–466.
- THIELE, J. 1911. Die Solenogastres der russischen Polar-Expedition 1900–1903. *Mémoires de l'Académie impériale des Sciences St. Pétersbourg*, Série VIII, Classe physico-mathématique, **29**(5): 1–4.
- THIELE, J. 1913. Solenogastres. *Das Tierreich*, **38**: 1–57.
- THIELE, J. 1932. Die Solenogastren des arktischen Gebietes. In: *Fauna arctica* (F. Römer & F. Schaudinn, eds), **6** (4): 380–382. Frommann Druck (H. Pohle), Jena.
- TODT, C. & SALVINI-PLAWEN, L. von 2003. New Simrothiellidae (Mollusca: Solenogastres) from the Mozambique Channel, western Indian Ocean. *Veliger*, **46**: 263–277.

