



## Contributions to West-Mediterranean Solenogastres (Mollusca) with three new species

### Contribuciones al conocimiento de los Solenogastres (Mollusca) del Mediterráneo occidental, con tres nuevas especies

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#### ABSTRACT

Six species of West-Mediterranean Solenogastres are treated, three of which are described as new to science: *Micromenia subrubra* n.sp. from off Malta, *Macellomenia adenota* n.sp. from off Ceuta, *Urgorria monoplicata* n.sp. from off the Costa Brava. Records of other species (*Nematomenia banyulensis*, *Tegulaherpia* sp. and *Eleutheromenia sierra*) contribute to our knowledge of respective geographical distribution. The re-finding of *E. sierra* also results in the definition of a new genus *Scheltemaia* n.g. for two South-Australian, former *Eleutheromenia* species.

#### RESUMEN

Se estudian seis especies de Solenogastres del Mediterráneo occidental, incluyendo tres nuevas especies: *Micromenia subrubra* n.sp. de Malta, *Macellomenia adenota* n.sp. de Ceuta, *Urgorria monoplicata* n.sp. de la Costa Brava. Se aportan informaciones sobre otras especies, *Nematomenia banyulensis*, *Tegulaherpia* sp. y *Eleutheromenia sierra*, que contribuyen a un mejor conocimiento de sus distribuciones. La redescipción de *E. sierra* justifica la definición de un nuevo género *Scheltemaia* n.g. para dos especies descritas del Estrecho de Bass, Australia meridional.

KEY WORDS: Mollusca, Solenogastres, geographical distribution, new species.

PALABRAS CLAVE: Mollusca, Solenogastres, distribución geográfica, nuevas especies.

#### INTRODUCTION

The Solenogastres are a small class of aplacophoran Mollusca, characterised by the mantle cover of cuticle and unicellularly formed, calcareous mantle bodies or sclerites (scales, spicules, a.o.) and by the laterally rounded body with the foot narrowed to a longitudinal pedal groove. With respect to the mantle cover, to characters of the alimentary tract (no true radula ribbon, midgut without separate

digestive gland) and to the lack of particular excretory organs (no emunctoria), they appear to represent a very conservative off-shoot of Mollusca. Apart from the plesiomorphic, aplacophoran mantle and a few other features, they are by diphyly also clearly different from the Caudofoveata (cf. SALVINI-PLAWEN, 2003).

Solenogastres are generally small (average 3 mm - 3 cm; rarely longer, up

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to 30 cm), and about 230 species are nominally known at present. Their purely marine habitats (mostly below 50 m depth), their organisation based mainly on internal systematic characters, together with the great effort and expense required to collect them have clearly prevented broader assessments and a greater familiarity with this group. Much material from more recent collections (expeditions and individual samplings) awaits elaboration and will no doubt contribute to a still fairly fragmentary knowledge. This is also valid for basic faunistics (biodiversity, biogeography, etc.). Due to such incompleteness, all information - even if frag-

mentary - is of interest. In regard to the revised classification (SALVINI-PLAWEN 1978), systematic problems remain; these also concern several descriptions that are fragmentary compared to the required standard and await supplementation or revision.

The present contribution compiles Solenogastres from different samplings of the western Mediterranean Sea. Apart from enlarging our information on organisational diversity and providing geographical insight, this study also improves our understanding of the biodiversity of Solenogastres even within a fairly well investigated biogeographical region (cf. SALVINI-PLAWEN 1986, 1990).

## SYSTEMATICS

### Ordo PHOLIDOSKEPIA Salvini-Plawen, 1978

Solenogastres with a single layer of adpressed and overlapping solid, scaly mantle sclerites, sometimes

supplemented by other solid sclerites; cuticle thin, no epidermal papillae.

### Family DONDERSIIDAE Simroth, 1893

The family is characterised by two different types of mantle scales, by a monoserial radula provided with paired, long denticles, by the foregut glandular organs as subepithelial folli-

cles (so-called type A in SALVINI-PLAWEN, 1972, 1978), as well as by the lack of respiratory organs. It includes seven genera (cf. SALVINI-PLAWEN 1978).

### Genus *Nematomenia* Simroth, 1893

Type species: *Dondersia flavens* Pruvot, 1890.

*Dondersia* Hubrecht, 1888, partim; *Myzomenia* Simroth, 1893; *Herpomenia* Heath, 1911.

*Definition:* Solenogastres-Dondersiidae with common atrio-buccal opening; radula rudimentary: either monoserial radula with two pairs of distally touching denticles (bifid-monostichous type), or radula sheath without

radula, in part forming the unpaired outlet for the paired foregut glandular organs; midgut without serial constrictions; terminal sense organ present; secondary genital opening single, no copulatory stylets.

### *Nematomenia banyulensis* (Pruvot, 1890)

*Dondersia banyulensis* Pruvot; *Myzomenia banyulensis* (Pruvot) in Simroth 1893;

*Diagnosis:* Body distinctly red, elongate and slender, up to 30 mm, middorsal scales forming a longitudinal crest; main type of scales short and wide, distally pointed, proximally in part notched; mid-foregut forming a protrusible cone, without radula, radula sheath forming the single outlet of paired glandular organs and, by elongation, opening at the tip of the cone, posterior foregut curving anteriorly to open pre-cerebrally into frontal midgut; no papillated dorsal foregut gland; musculus longitudinalis distinctly separated. Spawning ducts fused throughout, axially with one pair of receptacula seminis.

*Remarks:* This well-known species (up to 30 mm in length) is recorded along the European coasts with wide gaps from off Dalmatia/Croatia to the Trondheimsfjord/Norway (PRUVOT 1891, NIERSTRASZ AND STORK 1940, SALVINI-PLAWEN 1997, HANDL AND SALVINI-PLAWEN 2001). There is a recent finding of several 3-5 mm long, red specimens by C. Mifsud (26.8.2002) from off Ras il-Wahx/NW-Malta (ca.35°57'N, 14°19'E) at 120-140 m, and another record (25.6.1994) of two small individu-

als comes from the campaign FAUNA IBERICA III (PB 923-0121), station 186 A, from off Cabo Cros in front of Punta na Foradada/NE-Mallorca (39° 47.64'-39° 49.66' N, 2° 40.78'-2° 38.71' E) at 59-61 m from a bottom also characterised by the presence of Hydrozoa-Sertulariidae. This latter record interbridges the known occurrence from the Gulf of Naples and the Côte Vermeille (Banyuls).

One of the Malta animals (3.6 mm) and the larger individual of the Mallorca specimens (preserved only 3.2 mm long, 0.5 mm high and 0.4 mm wide) were serially cross sectioned (semithin ribbons of 2 µm with glassknife); they show all typical characters of *N. banyulensis* (particularly curved foregut with cone, etc.). Although the Mallorca animal (deposited in the Mus. Nacional Cienc. Nat., Madrid, mol. no. 15.02/15) contained eggs of Ø 80-100 µm and sperm, the receptacula seminis were not yet differentiated. As PRUVOT (1891: 716) indicates that young individuals are pale reddish or orange, the distinct red colour of both the small Mallorca animals (maximum size of only 3.5 mm) is of interest.

### Genus *Micromenia* Leloup, 1948

#### *Rupertomenia* Schwabl, 1955

Type species: *Micromenia simplex* Leloup, 1848.

*Definition:* Solenogastres-Dondersiidae with atrial sense organ (vestibulum) and mouth separate; monoserial radula with one pair of lateral, curved denticles touching each other distally

(bifid-monostichous type); midgut without serial constrictions; terminal sense organ (s) present; secondary genital opening single, no copulatory stylets.

#### *Micromenia subrubra* spec. nov.

**Holotype:** NW-Malta, off Ras il-Wahx, 35°57'N, 14°19'E, yellow mud and sand at 140 m (Sept. 1996); spicules and section series (cs 2 µm) on slides: Naturhist. Mus. Wien (NHMW), Moll. IVN 1002446.

**Paratype 1:** NW-Malta, off Ras il-Pellegrin, about 35°55'N, 14°19'E, 120 m (April 1994); spicules and section series (cs 2 µm) on slides: Nat. Hist. Mus. London, Rg.no. 20020531.

**Paratype 2:** NW-Malta, off Delli, grey mud at 140 m (June 1999); whole animal, 5 mm long (Fig. 10), preserved in ethanol: Naturhist. Mus. Wien (NHMW), Moll. IVN 102447.

*Derivatio nominis:* Latin *subrubrus* = not very bright red, reddish.

*Diagnosis:* Body reddish, to 5 mm x 0.5 mm in size (stretched in life up to 7 mm), dorso-posterior body end generally elongated. Calcareous mantle sclerites of two types: slender shovel-like scales and slightly curved solid needles. Anteriorly concentrated subepithelial glands opening into dorsal pharyngeal pouch; paired ventral foregut glandular organs with single opening; midgut with short rostral caecum. With one pair of receptacula seminis and vesiculae seminales. Mantle cavity extending as a ventrally open gutter onto the elongated dorso-posterior body portion, ventro-rostrally with pouch; 2-4 dorsoterminal sense organs (Figs 1-4, 10, 12).

*Material and methods:* Several specimens had been collected by Constantine Mifsud (Malta) in April, June/July 1994, June 1995, August, Sept. and Nov. 1996, June 1999 and May 2001 from muddy bottoms off Western Malta in the area off Ras il-Pellegrin (between the Gnejna and Fomm ir-Rih bays), about 35°55'N, 14°19'E, at 120-160 m (see MIFSUD, 1996), and off cape Ras il-Wahx, about 35°57'N, 14°19'E, at 140 m.

Ribbons of semithin serial sections (cs 2  $\mu\text{m}$ ) of several specimens have been made with glassknives and stained with Richardson's solution.

*External appearance:* The slender animals are generally 2.5-5 mm in length (Fig. 10), but when stretched in life may even reach a length of up to 7 mm. They are fairly susceptible to mechanical effects and easily damaged through sampling treatment. The animals exhibit in life a distinct, not very intensive reddish colour throughout, ranging from pink to red (see Fig. 4 in MIFSUD 1996). The hind end in adults shows a beak-like extension of the dorso-posterior body (Fig. 10); in smaller (juvenile or sub-mature) individuals (up to 3 mm in length) the posterior body in life may be swollen and appear to be still devoid of the dorso-posterior body elongation. The mantle sclerites are generally adjoining and give the body surface a somewhat shiny appearance; the mid-dorsal scales may form a low crest.

*Mantle:* Cuticle 7-15  $\mu\text{m}$ . Calcareous mantle sclerites of two types (Fig. 1): a)

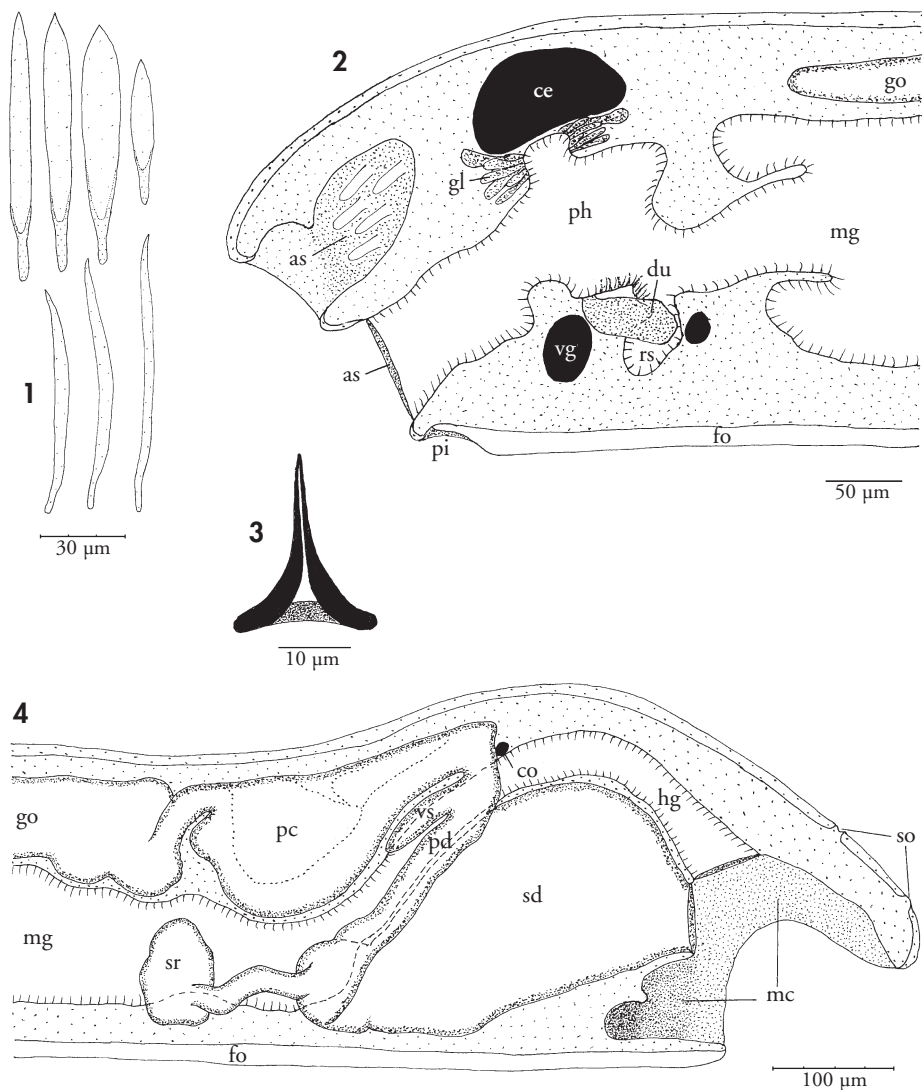
very slender shovel- to trowel-like scales 55-110  $\mu\text{m}$  long (handle 12-20  $\mu\text{m}$  long) and 7-15  $\mu\text{m}$  wide; b) slightly curved solid needles with indistinct handle, 80-110  $\mu\text{m}$  long x 4-6  $\mu\text{m}$  wide; both types may extend beyond the general body contour.

*Foot and mantle cavity:* Pedal ciliary pit flat and wide (125  $\mu\text{m}$ ), densely ciliated, without folds or ridges. Foot formed by posterior narrowing of the ciliated epithelium, changing along its course between a flattened ridge (25  $\mu\text{m}$  wide) with centrally high cells and a real fold. It does not enter the mantle cavity.

Pedal gland voluminous with large follicles at both sides in the anterior body. Sole glands along pedal groove small, scattered, of same histological quality as pedal glands.

Mantle cavity as an elongated, ventrally open gutter extending along entire dorso-posterior beak-like body portion, densely ciliated without respiratory formations. At the beginning of this beak-like portion the ventroterminal body wall including "abdominal" spicules is curved dorso-anteriorly to form a wide dorsally open gutter facing the gutter of the mantle "cavity". This entire internal space is rostrally three-partitioned (Fig. 4): dorsal epithelium closing up as rectal opening (anus); central portion closing up to represent the short outlet of the voluminous spawning duct; the ventral portion becoming a rostral, wide and flattened pouch which - at least dorsally - appears to be lined by mantle epithelium (with cuticle-like substance and embedded small sclerites). More frontally this pouch either (holotype) continues ventrally in a fairly circular blind sack (Figs. 4, 12), or shows a mid-ventral ridge, implying distinct symmetry of the wide pouch; the latter condition (paratype 1) extends anteriorly until just below the end of the pericardium.

*Musculature:* Body wall musculature distinct but not very compact, its fibres showing a loose arrangement enclosing lacunae. No lateroventral reinforcement of longitudinal fibres. The regular dorsoventral bundles are weak and run peripherally, only occasionally causing



Figures 1-4. *Micromenia subrubra* spec.nov. 1: mantle sclerites; 2: organisation of the anterior body; 3: one radula tooth/plate; 4: organisation of the posterior body. Abbreviations, as: atrial sense organ; ce: cerebral ganglion; co: suprarectal commissure; du: outlet of ventral foregut glandular organs (type A); fo: pedal fold (foot); gl: follicles of glands; go: gonad; hg: hindgut (rectum); mc: mantle cavity; mg: midgut; mo: mouth opening; pc: pericardium; pd: pericardioduct; ph: pharynx; pi: pedal pit; rs: radula sheath; sd: spawning duct; so: terminal sense organ; sr: receptaculum seminis; vg: (first) ventral ganglion; vs: vesicula seminalis.

*Figuras 1-4. Micromenia subrubra spec.nov. 1: Escleritas del manto; 2: organización de la parte anterior del cuerpo; 3: diente radular; 4: organización de la parte posterior del cuerpo. Abreviaturas, as: órgano sensorial atrial; ce: ganglio cerebral; co: comisura suprarrectal; du: abertura de los órganos digestivos ventrales anteriores (tipo A); fo: pie; gl: grupos de glándulas; go: gónada; hg: recto; mc: cavidad del manto; mg: tubo digestivo; mo: abertura bucal; pc: pericardio; pd: pericardioducto; ph: faringe; pi: foseta pedal; rs: rádula; sd: conducto de la puesta; so: organo sensorial terminal; sr: receptáculo seminal; vg: (primer) ganglio ventral; vs: vesicula seminal.*

constrictions of the midgut. At the beginning of the pericardium, the inner/upper pair of dorsoventral bundles fuses with the peri-pericardial musculature.

*Sensory system:* Cerebral ganglion (110-125  $\mu\text{m}$  wide, 75-80  $\mu\text{m}$  high, 70  $\mu\text{m}$  long) with separate connectives, the buccal ones first and very close to the ventral connectives. Four laterofrontal pairs of medullary roots of cerebral nerves (holotype), a ventro-lateral, a lateral and two subsequent dorsolateral ones; the lateral and dorsolateral roots connect at each side to an adjacent basal ganglion; this latter gives rise to only two (rather than three) nerves which lead together with the separate ventro-lateral cerebral nerve to the atrial region. All these (six) nerves are medullary.

Lateral ganglia elongate (55  $\mu\text{m}$  x  $\varnothing$  30  $\mu\text{m}$ ) and adjacent to the cerebral ganglia. Ventral ganglia voluminous ( $\varnothing$  60 x 45  $\mu\text{m}$ ), interconnected by two commissures, followed by another pair of ventral ganglia with their commissure, all posterior to the ciliated pedal pit (Fig. 2). Buccal ganglia ( $\varnothing$  up to 45 x 25  $\mu\text{m}$ ) postero-lateral of the radula sheath between the follicles of the foregut glandular organs, interconnected by an exceptionally long commissure dorso-terminally of the sheath (150  $\mu\text{m}$  when relaxed in the here 300  $\mu\text{m}$  wide body, 60  $\mu\text{m}$  when contracted and curved).

Suprarectal commissure overlying rectum just below end of the pericardium (Fig. 4). The lateral cords continue medullarily into the dorsoposterior body extension and form two additional thick commissures.

Atrial sense organ clearly separated from mouth. A distinct pre-atrial, ciliated pit is formed which leads into the voluminous atrium. Atrial ciliary tract running at the periphery of the opening only, frontally continuous with the pre-atrial pit. No dorsal ciliation. Cavity itself with several stoutish papillae, most being elaborated as pairs.

There are two (holotype) to four (paratype 1) subsequent dorso-terminal

sense organs at the posterior elongation of the body (Fig. 4).

*Alimentary tract:* Mouth opening wide, separate from the atrium, leading into a voluminous (or but longitudinally folded) foregut with a dorsal enlargement below the cerebral ganglion. This pouch receives frontally subepithelial follicles of glandular cells (Fig. 2) without forming a papilla. Behind pouch, foregut with some distinct circular musculature.

Radula (Fig. 3) consists of monoserial teeth or plates (20  $\mu\text{m}$  wide), each with a curved denticle laterally (up to 20  $\mu\text{m}$  long), both which are very close medially and touch distally. Ventral foregut glandular organs present as wide ducts or ampullae (Fig. 2) with large subepithelial follicles filling the space to the midgut; wide ducts fuse to open by a single outlet ventral of the anterior radula.

Foregut in radular region with dorsal and lateral coating of small subepithelial foregut glands adjacent to strengthened circular musculature. Postradular foregut opening axially without sphincter into the (surrounding) midgut. Frontal midgut caecum short. Midgut, depending on the individual, at a more or less distinct distance from the body wall. Regionally showing irregular bulges, but no true serial constrictions due to the dorsoventral musculature and not forming regular lateroventral pouches. Middorsal ciliary tract present. In two specimens small nematocysts were embedded in the midgut epithelium.

*Circulatory system:* Atrium of heart forming a spacious invagination of the pericardial roof, being free in its anteriormost portion only and interconnected with the ventricle by one distinct opening. Ventricle for half or two-thirds its entire extension as an invagination of anterior pericardium.

Body spaces (pseudocoel) between the organs in part filled by distinct mesenchyme as well as blood cells. The latter consisting of round cells ( $\varnothing$  2-5  $\mu\text{m}$ ) with in part densely granulated contents and well visible nucleus, and of

more irregular, vacuolised cells ( $\text{\O} 3\text{-}7 \mu\text{m}$ ).

*Gonopericardial system:* The two gonads distinctly separated throughout, containing eggs of at most  $40 \mu\text{m}$  in diameter. Terminal portion of the gonads in fully mature animals serves as a voluminous sperm bag, then being ventrally continuous with the two short and wide gonopericardioducts, which are ciliated throughout. Ducts open dorsally into the pericardium, ciliation continuing as a paired, wide lateral tract throughout pericardium and entering pericardioducts. Pericardioducts emerging termino-laterally, each elaborating in its subsequent curve towards anterior an elongate and wound, anteriorly directed vesicula seminis (Fig. 4). Ciliated pericardioducts open rostrally from laterodorsal into the respective spawning duct.

Both spawning ducts connected anteriorly by a curved duct (stalk) with a voluminous receptaculum seminis (Fig. 4). After a short length, both glandular spawning ducts open antero-laterally into a voluminous continuation showing a rostro-median pouch between the openings and being provided with a distinctly lower, ciliated epithelium. This subsequently single spawning duct soon widens laterally and becomes dorsally as well as ventrally lined by a high glandular epithelium and provided with some musculature. It opens by means of a short and simply-lined, central outlet, surrounded by musculature, into the "mantle cavity" (see above).

*Discussion:* It should be mentioned that two sub-mature animals showed an atrial sense organ without papillae, and it cannot be evaluated whether this refers to the sub-mature status or reflects a teratological condition.

The characteristic radula classifies the present animals within the Dondersiidae in the closer relationship of *Dondersia* Hubrecht, 1888, itself (see SALVINI-PLAWEN, 1978) and of *Micromenia*. As already pointed out earlier (SALVINI-PLAWEN, 1972: 218), the genus *Micromenia* differs from *Dondersia* by the absence of serial midgut constrictions due to the peripheral course of the dorsoventral

muscle bundles. Such a condition, however, could perhaps be correlated with body size and would then not represent a good generic character. Apart from this, note the closer similarities with respect to the shovel- to trowel-like scales in the present species and in *Dondersia festiva* Hubrecht, 1888, as well as in *Heathia porosa* Heath, 1911 (see SCHELETMA, 1998a). There is also a remarkable multiplication of dorsoterminal sense organs in some *Dondersia* species: two in *D. festiva* and *D. indica* Stork, 1941, three in *D. annulata* Nierstrasz, 1902, and eleven in *D. californica* Heath, 1911.

With respect to the mentioned elaboration of the midgut, the species in question belongs to *Micromenia*. At present, two *Micromenia* species are known, i.e. *M. simplex* Leloup and *M. fodiens* (SCHWABL, 1955). Besides the known geographic occurrence off Spitzbergen, *M. simplex* differs from the specimens at hand by several dominant characters, e.g. the lack of the dorsoposterior body elongation, the differentiation of scattered pharyngeal glands, the paired opening of the ventral foregut glandular organs and the unpaired spawning duct (LELOUP, 1948; SALVINI-PLAWEN, 1972). *M. fodiens* is known from SW Sweden and from Norway in the area off Bergen (SALVINI-PLAWEN, 1988); new evidence comes from the Skagerrak (two localities, 70-80 m) and the Trondheimsfjord (several localities, 185-530 m) (pers. comm. C. Handl, Vienna). *M. fodiens* differs from the present animals by the whitish body colour and the lack of the dorsoposterior body elongation as well as of a pedal fold, the shape of the scales, the rudimentary atrial sense organ without papillae, and also by details of the gonopericardial system (SCHWABL 1955, SALVINI-PLAWEN 1972, 1988).

*M. subrubra* spec.nov. is thus well-separated and its finding enlarges the biodiversity of *Micromenia* by a Mediterranean species. With respect to the body colour, together with *Nematomenia banyulensis* (above) and the enigmatic *Nematomenia (?) corallophila* (KOWALEVSKY, 1881) recorded upon *Corallium rubrum*

(L.) off La Calle/Algeria (cf. SALVINI-PLAWEN 1997), *M. subrubra* is the third "red Solenogastre" in the region.

Family MACELLOMENIIDAE Salvini-Plawen, 1978

The family is characterised by the nail-shaped type of mantle sclerites, by a monoserial radula of serrate plates, by the foregut glandular organs as subepithelial follicles (so-

called type A in SALVINI-PLAWEN, 1972, 1978), as well as by the presence of respiratory organs; at present it includes one genus only (cf. SALVINI-PLAWEN, 1978).

Genus *Macellomenia* Simroth, 1893

Type species: *Paramenia palifera* Pruvot, 1890.  
*Paramenia* Pruvot, 1890, partim [non Brauer and Bergenstam, 1889]

*Definition:* Solenogastres-Macellomeniidae with solid acicular sclerites with enlarged basal plate; paired ventral foregut glandular organs (type

A) with distally single outleading duct; terminal sense organ present; secondary genital opening unpaired; no copulatory stylets.

*Macellomenia adenota* spec. nov.

**Material:** A single specimen 1.65 mm long and 0.75 mm across was collected in May 1986 from the Strait of Gibraltar, off Punta Almina (North of Ceuta: 35°54.1'N, 0°16.5'W; 25-40 m). After examination of the mantle cover, ribbons of semithin serial sections (somewhat oblique cs 2 µm) were made with a glassknife and stained with haematoxyline-eosine.

**Holotype:** Mus.Nat.Hist.Nat. (Malacologie), Paris; section series

*Derivatio nominis:* Greek *adén* = gland, Latin *-otus* = provided with; referring to the paired pre-pallial "abdominal gland" in addition to the foregut glands.

*Diagnosis:* Body less than 2 mm long; mantle sclerites with spine slightly curved and up to 125 µm long, not forming a crest; atrial sense organ (vestibulum) and mouth opening separate; radula plates curved with seven denticles, the median one most prominent; midgut with paired rostral caecum, without regular lateral constrictions; with paired "abdominal gland" and paired abdominal spicules, all opening into a pre-pallial mantle invagination (Figs 5, 6, 16).

*Description:* Characteristic solid mantle sclerites (Figs. 5a, b) with a 70-100 µm long, slightly curved spine and an oblique basal plate (20-25 µm x 12-15 µm) reinforced at the free proximal rim. Some sclerites embedded in epidermis which includes several larger gland

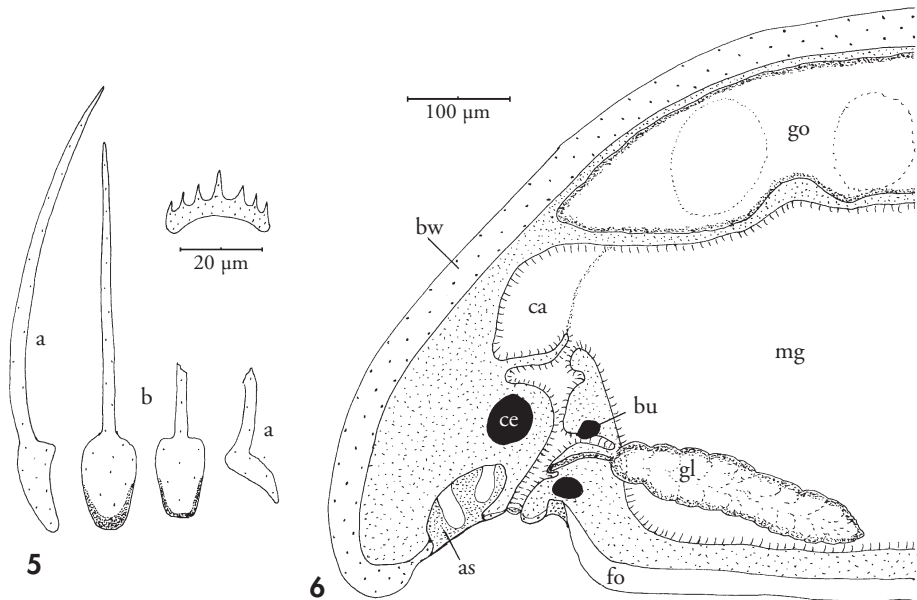
cells. Mantle cuticle thin, about 15 µm (13-20 µm).

Rear of body with mantle cavity not retained. With pre-pallial ventral mantle invagination with opening of a paired, slender pouch, each including a bundle of at least 12 slender spicules or spines (abdominal spicula). In addition, a paired short tube also opens aside the end of the foot lateral in the groove of the mantle invagination; it is elaborated just antero-dorsal of each spicule pouch, provided with an epithelium of well elaborated glandular cells and surrounded by musculature ("abdominal gland", Fig. 16).

Pedal pit of foot simple, receiving the outlets of the pedal gland follicles. The single pedal fold soon flattens to a wide ciliated ridge ending with mantle invagination. Sole glands along groove present.

Body wall musculature without particular ventral reinforcement of the lon-





Figures 5, 6. *Macellomenia adenota* spec.nov. 5: mantle sclerites from lateral (a) and frontal (b), and one radula plate; 6: organisation of the anterior body. Abbreviations, as: atrial sense organ; bu: buccal ganglion; bw: body wall (mantle and musculature); ca: midgut caecum; ce: cerebral ganglion; fo: pedal fold (foot); gl: ventral foregut glandular organ; go: gonad; mg: midgut.

*Figuras 5, 6. Macellomenia adenota spec.nov. 5: escleritas del manto en vista lateral (a) y frontal (b), y diente radular; 6: organización de la parte anterior del cuerpo. Abreviaturas, as: órganos sensorial atrial; bu: ganglio bucal; bw: pared del cuerpo (manto y musculatura); ca: ciego digestivo; ce: ganglio cerebral; fo: pie; gl: órgano glandular digestivo ventral; go: gónada; mg: tubo digestivo.*

gitudinal layer. Serial dorsoventral bundles weak, running fairly close to body wall, not constricting midgut.

Preoral atrial sense organ ending as blind sack (Fig. 6), with few single, stoutish papillae. Alimentary canal with mouth opening separate from atrium, leading into a short foregut. Animal with somewhat protruded radula apparatus, foregut forming a posterior pouch above radula sheath as well as a flat blind sack extending rostrally over the cerebral ganglion. Plates of monoserial radula only 25 µm wide and curved; with seven denticles, the median one distinctly being strongest (Fig. 5). No particular radula support.

Ventral foregut glandular organs, each consisting of a densely packed bunch of subepithelial follicles extending

lateroventrally of the midgut and emptying at each side into short duct; both ducts uniting from lateral to a median outlet with circular musculature. Duct running below radula sheath and then below free radula to open beneath anterior most plate of protruded radula.

Foregut opening into midgut above beginning radula, midgut giving rise from this area to a paired rostral caecum with high epithelium (30-120 µm) equal to that of midgut. Midgut with some nematocysts.

Nervous system with single cerebral ganglion (110 µm wide, 40 µm high, 35 µm long), connectives of body cords emerging separately. Buccal ganglia (Ø 25 µm) aside radula sheath (Fig. 6), their commissure over sheath. Ventral ganglia (Ø 65 x 35 µm) adjacent to pedal pit.

Animal mature, paired gonad with relatively large eggs ( $\emptyset$  up to 110  $\mu\text{m}$ ). Other organs of gonopericardial system (pericardium, spawning ducts, etc.) and mantle cavity not retained.

*Discussion:* Within Macellomeniidae, only two species of *Macellomenia* have been described so far, viz. *M. palifera* (Pruvot, 1890) and *M. aciculata* Scheltema, 1999, both provided with a similar, remarkable mantle cover of solid acicular spicules with enlarged basal plate. The present specimen fits well into that frame, but exhibits specific differences. *M. aciculata* possesses radula plates with five equal denticles, the mouth opens at the back of the atrial sense organ and there is a lack of abdominal spicules (SCHELTEMA 1999). The present specimen coincides with the geographically closer type species *M. palifera* by the radula plates with seven denticles and by the presence of invaginated pouches for abdominal spicules (PRUVOT, 1891: 790-791). There are specific differences however: (a) Curved radula plates with a distinctly prominent median denticle; (b) paired midgut caecum (not present in *M. palifera*; PRUVOT 1891: 790); (c) the paired "abdominal gland" (see below) emptying into the mantle invagination close in front of the abdominal spicules; (d) body length (though mature, less than 2 mm; *M. palifera* = 4-8 mm, Pruvot 1891: 727) and lack of a middorsal crest of spicules (PRUVOT, 1891: 727 and Fig. 4). Most probably (e), also in *M. palifera* the mouth opening is located within the preoral atrium.

Though the gonopericardial system, the mantle cavity and the terminal sense

organ of the present specimen are not known, this animal clearly represents a proper species, *Macellomenia adenota* spec. nov.. An association of abdominal spicula with a paired gland has been reported also in *Squamatoherpia tricuspidata* (BÜCHINGER AND HANDL, 1996), though in different mutual arrangement. The histology of the present "abdominal glands" looks similar to that of spawning ducts; as no characters of the pericardium and mantle cavity are known, the glands could be the anlagen of those organs. If so, however, the spawning ducts would represent fairly unusual, lateral organs with medial opening into a pre-pallial mantle invagination. The presence or absence of a terminal sense organ, as well as the common (*M. aciculata*; *M. palifera*?) or separated atrial and buccal openings (*M. adenota*) are judged to be generic characters (SALVINI-PLAWEN, 1967b, 1978); due to the currently limited insight in species organisation and species diversity of Macellomeniidae, however, no reclassification is proposed herein.

No accurate evaluation is possible with regard to the *Macellomenia* specimens reported by Caudwell et al. (1995) from the Irish Sea at 80 m and 120 m. In view of the present species from the Strait of Gibraltar and of *M. aciculata* from 50° N, 13° W, the geographical distribution of each *Macellomenia* species appears to be limited. This is in contrast to an earlier estimation (Salvini-Plawen, 1997) and speaks against a conspecificity of the Irish specimens with the Mediterranean *M. palifera* from the Côte

Vermeille. However, as already surmised (Salvini-Plawen 1997: 44), only an anatomical investigation of the Irish

animals can clear up the conspecificity issue.

Family LEPIDOMENIIDAE Pruvot,

## 1902

The family is characterised by one type of scaly mantle sclerites, by a distichous radula, by the foregut glandular organs as subepithelial follicles (so-called type A in

SALVINI-PLAWEN, 1972, 1978), as well as by the lack of respiratory organs; it

includes at present three genera (cf. SALVINI-PLAWEN, 1978, 1988).

Genus *Tegulaherpia* Salvini-Plawen,

1983

Type species: *Tegulaherpia stimulosa* Salvini-Plawen, 1983.

*Definition:* Solenogastres-Lepidomeniidae with atrial sense organ (vestibulum) and mouth opening separate; terminal sense organ present; secondary genital opening unpaired; with copulatory stylets; no respiratory organs.

### *Tegulaherpia* (?) spec.

**Material:** A single specimen was collected by Diego Moreno (Cabo de Gata/Almería) from sand below stones at Punta del Esparto nearby Los Escullos, Cabo de Gata (Southeast Spain, » 36°50'N, 02°03'W) at 1 m depth only. After examination of the mantle scales, ribbons of semithin serial sections (cs 2 µm) were made with a glassknife and stained by Richardson's solution. The slides (mantle scales and series section) are deposited in the Mus. Nacional Cienc. Nat., Madrid, mol. no. 15.02/14.

*Description* (Fig. 7): Specimen of 1.25 mm length and 0.35 mm across with an evenly rounded body (Fig. 7 A), not yet mature, though developing eggs visible. Of whitish colour and smooth surface with small, densely adjoining and strongly overlapping, delicate scales measuring 23 x 18 µm (Fig. 7 C) tightly adjacent. Atrial opening with anterior stereocilia ("bristles"), mouth and foot well visible in life (Fig. 7 A).

Unfortunately, the animal was very poorly preserved (partly in histolytic state) and only a few characters can be verified. Mouth opening distinctly separate from the atrial sense organ and leading into a fairly straight foregut surrounded by strong longitudinal musculature. Distichous radula consisting of paired, erect teeth with symphysis, each provided with a distal hook and four median denticles (Fig. 7 B). Foregut glandular organs not traceable. Single cerebral ganglion above the mouth (90 µm wide, 60 µm high, 45 µm long) gives rise to the connectives separately. Apart from the gut, no organ of the posterior body (spawning ducts, etc.) were clearly

traceable. Gut containing several nematocysts, among them stenoteles, of a hydrozoan food.

*Discussion:* The mantle scales, the distinctly separate atrial sense organ and mouth, and the distichous radula fit well within the characters of the genus *Tegulaherpia*. Other characters, however, particularly the foregut glands and the copulatory stylets, could not be verified to confirm the generic classification. The shape and size of the scales (23 x 18 µm), and the radula (with four median denticles per tooth) do not coincide with the two known European *Tegulaherpia* species (cf. SALVINI-PLAWEN, 1988, 1997). No specific relationship can therefore be hypothesised. The Adriatic *T. stimulosa* Salvini-Plawen, 1983 possesses 30-40 µm x 20-25 µm sized scales and 4-5 radula denticles; the geographically overlapping, West-Mediterranean and NE-Atlantic *T. myodoryata* Salvini-Plawen, 1988 (= *T. celtica* Caudwell et al., 1995) shows somewhat larger scales, 30-45 µm x 20-30 µm, and 4-5 radula denticles (SALVINI-PLAWEN, 1988; HANDL AND SALVINI-PLAWEN, 2001). Fig. 7 D shows a scale of *T. myodoryata* from the most eastern record off Malta (see MIFSUD, 1996: Fig. 3) for comparison. Most specific differences between both known species, however, concern the arrangement of the copulatory stylet apparatus and the outlet of the (fused) spawning duct (SALVINI-PLAWEN, 1988); no comparison of the present animal can therefore be made. According to the mantle scales, the specimen appears to represent a species proper.

The habitat (sand) could also point to Meiomeniidae which have mesopsammic species; yet, these are characterised by mantle sclerites of two or three different kinds (SALVINI-PLAWEN,

1985; GARCIA-ÁLVAREZ, URGORRI AND CRISTOBO, 2000b).

Apart from the possible presence of an independent, third *Tegulaherpia* species, this finding is likewise of inter-

est as the shallowest record of a solenogastre (one meter depth only). Due to the need of calmer waters for ciliary gliding, Solenogastres species are generally very rare on substrata shallower than about 50 meters, including *Urgorria monoplicata* (below) or the mesopsammic representatives (cf. GARCÍA-ÁLVAREZ ET AL., 2000b). However, exceptions such as *Epimения arabica* Salvini-Plawen and Benayahu, 1991, a large-sized species (13-21 cm) living hidden in Alcyonaria-colonies at 2-5 meters depth, occur.

Ordo CAVIBELONIA Salvini-Plawen,

or in Simrothiellidae: they are either (1) in a radial or (2) in a tangential alignment (HOFFMAN 1949). The latter may be produced (2a) in a single, obliquely disposed layer, or (2b) they are arranged in two or more fairly rectangularly intercrossing layers of low angle and almost embedded within the cuticle (and also termed "skeletal"; SCHELTEMA, 1999, SCHELTEMA AND SCHANDER, 2000). Another criterion exists with respect to the enclosed cavity: the spicules may be either thick-walled or thin-walled. Spicules may be distally

hooked (or barbed), asymmetrically flattened and serrate, or asymmetrically axelike enlarged (termed "captate" by ARNOVSKY, 2000).

Family PARARRHOPALIIDAE Salvini-

1978

Solenogastres with acicular, generally hollow mantle spicules, cuticle mostly thick, with epidermal papillae.

*Remarks:* As some findings indicate (SALVINI-PLAWEN, 1978; SCHELTEMA AND KUZIRIAN, 1991; HANDL AND SALVINI-PLAWEN, 2002), the main character of this taxon - the hollow acicular spicules - strictly taken may be polyphyletic (not supported, however, by computerised cladograms; cf. SALVINI-PLAWEN, 2003). Investigations have also called attention on differences in the developmental arrangement of the spicules at the generic level, e.g. in Pararrhopaliidae (cf. Table I)

Plawen, 1972

(Parameniidae Simroth, 1893; Parameniidae Pruvot, 1902; Perimeniidae Nierstrasz, 1909\*); Pruvotiniidae Heath, 1911; Pruvotiniidae Scheltema, 1998)

\* As NIERSTRASZ (1909: 291-292) consciously introduced a synonymy (*Perimения* instead of *Pruvotina*), his family "Perimeniidae" cannot be accepted as valid.

The family is characterised by a distichous radula, by the foregut glandular organs generally as subepithelial follicles (so-called type A in SALVINI-PLAWEN 1972, 1978), as well as by the additional presence of hooked mantle spicules and/or of a middorsal

papillous pharyngeal gland and/or of respiratory organs (SALVINI-PLAWEN, 1978, GARCÍA-ÁLVAREZ, SALVINI-PLAWEN AND URGORRI, 2001); it includes 15 genera (Table I).

Genus *Eleutheromenia* Salvini-Plawen, 1967

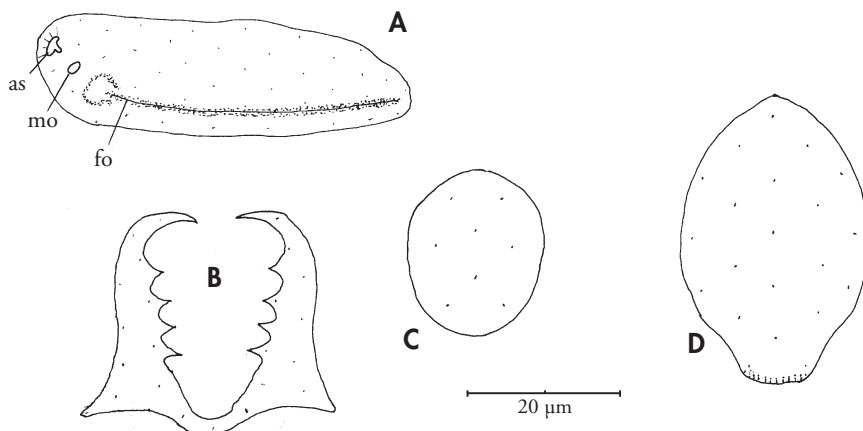


Figure 7. A-C: *Tegulaherpia* (?) sp. A: living animal from ventrolateral (sketch by Diego Moreno, Cabo de Gata); B: one pair of radula teeth with symphysis; C: one mantle scale. D: Mantle scale of *Tegulaherpia myodoryata* from off Malta. Abbreviations, as: atrial sense organ; mo: mouth opening; fo: pedal fold (foot).

Figure 7. A-C: *Tegulaherpia* (?) sp. A: animal vivl en vista ventrolateral (esquema de Diego Moreno, Cabo de Gata); B: par de dientes radulares con sínfisis; C: escala del manto. D: Escala del manto de *Tegulaherpia myodoryata* de Malta. Abreviaturas, as: órgano sensorial atrial; mo: abertura bucal; fo: pie.

(*Paramenia* Pruvot, 1890, partim [non Brauer and Bergenstamm, 1889]; *Pruvotina* Cockerell, 1903, partim; *Perimenia* Nierstrasz, 1909, partim)

Type species: *Paramenia sierra* Pruvot, 1890; Costa Brava.

**Definition (amended):** Solenogastres with hollow spicules in more than one layer, also including hooked ones; with common atrio-buccal opening; radula present, ventral foregut glandular organs subepithelial with paired outlet (type A); no dorsal papillous foregut gland; midgut with serial ventro-lateral constrictions; with dorsoterminal sense organ, with respiratory organs; unpaired secondary genital opening; no receptacula seminis and no copulatory stylets.

*Eleutheromenia sierra* (Pruvot, 1890)

*Paramenia sierra* Pruvot, 1890

**Material:** One specimen (preserved 11,5 mm long, with lobes up to 1,7 mm high) of typical aspect and shape (Fig. 11) comes from the Skjörn Fjord north of Trondheim/Norway at 218 m depth (collected 2.3.1992 by G. Steiner, Vienna). Ribbons of semithin serial sections of this specimen (cs 2 µm) were made with glassknives and stained with toluidine-blue.

Type material no longer existent. The present material (series sections on slides) is deposited in the Naturhist. Mus. Wien (NHMW), Moll. IVN 102448.

**Diagnosis:** Body up to 12 mm x 2 mm with middorsal carina extended to a se-

ries of 15 prominent lobes; cuticle moderately thick, no epidermal papillae; spicules upright, tangential and intercrossed, as well as hooked, all hollow; elongate scales along the pedal groove. Abdominal spicules in a paired bundle, each consisting of numerous hollow straight elements. Radula teeth with distal hook, no median denticles; ventral foregut glandular follicles with paired duct, midgut with rostral caecum. Vesiculae seminales present, no receptacula seminis; up to 28 gill folds. Costa Brava, Bretagne, Irish Sea, Trondheim area; 40-128 m (Figs. 8, 11, 15).

**Body wall:** Body marked by a mid-dorsal carina elaborated into three

smaller and twelve subsequent prominent lobes (Fig. 11). In these bulges, circular musculature splits into a small subepithelial fraction (entering the bulge) and main fibres traversing the base of bulge, thus as usual delimiting body cavity. Space between this split musculature filled by mesenchyme and large vacuole (gland) cells. Regions between the lobes normally structured.

Epidermis covered by a 25-30  $\mu\text{m}$  thick cuticle, locally reaching 50  $\mu\text{m}$ . Especially in the posterior body, big, pluricellular epidermal glands, but no true epidermal papillae; only a few epidermal protrusions scattered ventrally at both sides of the posterior pedal groove (mantle rims).

Mantle with three main types of hollow spicules (Fig. 8) in part extending beyond cuticle and thus resulting in a somewhat rough surface. Spicule types are (a) more or less straight ones (130-350  $\mu\text{m}$ ), (b) similar type with a harpoon-like indentation at the solid distal portion (up to 400  $\mu\text{m}$ ; see "species incerta II" in SALVINI-PLAWEN, 1978: 118-119 and *Unciherpia* in GARCÍA-ÁLVAREZ ET AL., 2001), and (c) somewhat bent spicules (up to 125  $\mu\text{m}$ ) with solid distal portion forming a hook with knob at the turn. In addition, some very slender acicular spicules and, sporadically, ones with distal serration (d) occur; along the pedal groove (e) elongate scales (up to 80 x 13  $\mu\text{m}$ ).

Behind foot, a pair of ventromedially directed invaginations of the body epithelium, each embedded within ventral body wall musculature and housing a bundle of straight, 130  $\mu\text{m}$  (or more) long, hollow abdominal spicules (Fig. 15). Epidermis as usual underlain by circular and longitudinal muscles; only weak lateroventral reinforcement of longitudinal musculature.

*Foot and mantle cavity:* The ciliated pedal pit gives rise to a single longitudinal fold which runs through the pedal groove. The foot ends, however, in front of the abdominal spicules, not entering the mantle cavity. The pedal gland is voluminous, and the sole glands open all over into the pedal fold and groove.

The mantle or pallial cavity holds at its posterior wall blunt gill folds (28 in PRUVOT, 1890, 1891). The hindgut opens frontally and, even more anteriorly, the outlet of the spawnings ducts opens ventrally. Between the end of the foot and the opening of the mantle cavity the invaginated bundles of the abdominal spicula are elaborated (Fig. 15). There are no copulatory stylets.

*Sensory system:* Cerebral ganglion unpaired (240  $\mu\text{m}$  wide, central  $\varnothing$  130  $\mu\text{m}$ ) giving rise to connectives separately; two pairs of small ganglia immediately adjacent to it, innervating the atrial region. Lateral body cords loosely provided, ventral ones more densely provided with nuclei; in the posterior body, cords are clearly medullary. In the ventral system, ganglia with commissures fairly densely elaborated, without correspondance to lateroventral connectives. The (first) ventral ganglia ( $\varnothing$  80  $\mu\text{m}$ ) showing two commissures; without commissural sack. Buccal ganglia likewise prominent ( $\varnothing$  60  $\mu\text{m}$ ).

Suprarectal commissure 150  $\mu\text{m}$  long ( $\varnothing$  40  $\mu\text{m}$ ) and interconnecting the ganglia posteriora superiora medullarily; at least two pairs of posterior nerves originate there.

Atrial sense organ with stoutish single or bifurcated papillae and bordered by a horseshoe-shaped ciliary fold, the dorso-posterior incurvings exclude the buccal groove continuous with the mouth.

Region of the dorsoterminal sense organ (close to the body end, according to PRUVOT, 1891) in present animal destroyed.

*Alimentary tract:* Mouth opening in the dorsoposterior area of the common atrio-buccal cavity, connected with the sensory region by a groove. Buccal space with high folds leading into the pharyngeal foregut; foregut with distinct pre-radular circular musculature and intercellularly opening, subepithelial pharyngeal glands; without compacted dorsal foregut gland (with papilla). Radula typically distichous, each tooth (25-30  $\mu\text{m}$  high) with a distal hook; median denticles could not be dis-

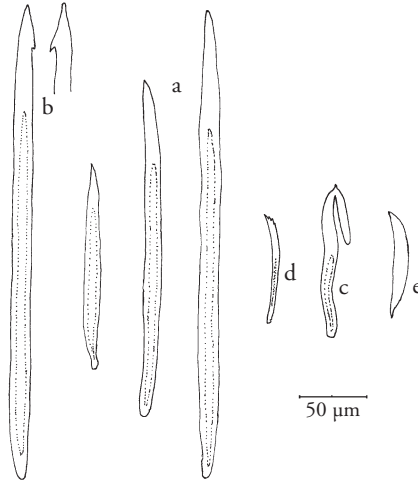


Figure 8. *Eleutheromenia sierra* (Pruvot) from the Trondheim area, types of mantle sclerites.

Figura 8. *Eleutheromenia sierra* (Pruvot) del área de Trondheim, tipos de escleritas del manto.

cerned in the sections. Radula support represented by an assemblage of muscular and connective tissue. Ventral foregut glandular organs as follicles emptying at each side into distinct opening lateroventrally of radula (type A in SALVINI-PLAWEN, 1972, 1978). Midgut with rostral caecum and constricted only ventro-laterally by serial dorsoventral muscle bundles to form pouches. No nematocysts were observed within the gut. Middorsal ciliary tract widens to cover entire hindgut opening into mantle cavity above and behind unpaired spawning duct outlet.

*Gonopericardial system:* Paired gonad showing developing germ cells in the posterior region within lateral sacks, the most posterior pair representing vesiculae seminales. Paired gonopericardial ducts opening dorsofrontally into pericardium with a paired anterior beginning. Pericardium voluminous with paired lateral ciliary tract and containing mature eggs ( $\text{\O} 140 \mu\text{m}$  or  $150 \times 130 \mu\text{m}$ ); probably due to such conditions, PRUVOT (1891) consistently termed the pericardium as "sac ovigère". Heart throughout as mediadorsal invagination, anteriorly very wide, then hanging by a double "mesenterium" into the pericar-

dial lumen. Atrium clearly paired and fusing just before the axial transition into ventricle. Two kinds of blood cells: round, homogeneous ones ( $\text{\O} 10 \mu\text{m}$ ) and oval to round, vacuolated or variously granulated cells ( $10\text{-}20 \mu\text{m}$  long).

Pericardioducts emerging posteriorly, forming in their curve towards anterior short sacculations (vesiculae seminales) and opening laterodorsally into respective spawning duct. No receptacula seminis present. Spawning ducts voluminous, highly glandular, and subdivided into two equal sections: paired portion not axially continuous with unpaired section, the latter extending somewhat below the former, with paired dorsoventral interconnection. Unpaired section opening by means of simple outlet ventrally to exterior; this opening representing the anterior-most area of the mantle cavity opening.

*Discussion:* Though the present specimen comes from Skjörn Fjord (Trondheim region), the type locality of *Parameenia sierra* (Pruvot) is off the Costa Brava (Catalunia/Spain); for comparison with the description by Pruvot (1891), a full descriptive presentation of the new finding was given here. The specimen from Norway exhibits an almost identi-

cal organisation to *E. sierra* which includes, for example, also the dorso-frontal opening of the gonopericardioducts into the pericardium (PRUVOT, 1891: Fig. 17). Some characters are not mentioned by Pruvot (such as, e.g. the posterior-most gonad serving as seminal vesicles, or the subdivision of the spawning ducts); there appear to be, however, just three discrepancies. First, the mantle spicules are not exactly identical. Second, in the region of the posterior body drawn as a cross section by PRUVOT (1891: Fig. 61), Pruvot claims a "glande cloacale" (Fig. 61: y). Here, apart from muscle fibres, numerous sole glands, the medullary ventral nerve cords as well as two connected ganglia innervating the spawning ducts are present in the Norwegian specimen. Some of these structures could represent Pruvot's gland as no real glandular organ is discernible; also the distance to the mantle cavity ("cloaca") is too long in both Pruvot's animal and the present specimen to represent a pallial gland.

A third and more essential point of disagreement of the new specimen with *Paramenia sierra* appears due to PRUVOT's (1891: 790) somewhat misleading description of the "petits caecums" at the end of the pedal groove, which he equalises with "l'appareil spiculaire périal de *Proneomenia vagans*" [= *Pararrhopalia pruvoti* Simroth, 1893]. This equalisation led to the (incorrect) definition of *Paramenia sierra* as possessing copulatory stylets (THIELE, 1913b, SALVINI-PLAWEN, 1967b). As Pruvot, however, describes correctly in detail (PRUVOT, 1891: 790), *P. sierra* possesses "une paire de petits caecums" (plural!)... "plongés dans les muscles longitudinaux ventraux, dans chacun desquels" he recognised "un faisceau de spicules". This is an exact description of a paired bundle of abdominal spicules, such as exists in the present individual (Fig. 15).

The Norwegian specimen described here is thus regarded as conspecific with *Eleutheromenia sierra* (Pruvot).

Apart from the single, no longer existent type specimen (11-12 mm x 2 mm) of the original description by PRUVOT (1890, 1891) from off Portaló Island

(Cap Creus/Costa Brava) at 75-80 m, and a finding from off Roscoff/Bretagne at about 40 m (Pruvot, 1897), several other records have been reported from the Irish Sea (cf. SALVINI-PLAWEN, 1997). Though without closer examination, due to their typical appearance (lobulated keel), however, these latter specimens may likewise belong to *E. sierra*; this is biogeographically supported by Pruvot's record from off Roscoff and by the present specimen (Trondheim area).

*Paramenia sierra* Pruvot was generically transferred by SALVINI-PLAWEN (1967b) to a new genus *Eleutheromenia*. A second species, *Pruvotina impexa* THIELE (1913a), after re-examination was generically separated later as *Labidoherpia impexa* (Salvini-Plawen, 1978). Most recently, SCHELTEMA (1998b) and SCHELTEMA AND SCHANDER (2000) described two *Eleutheromenia* species from the Bass Strait, South of Australia. According to the descriptions and a preliminary re-examination of specimens (*E. minus* from Slope Station 40, *E. bassensis* from BSS-S 202; a full description of the anatomies is in preparation by Cl. Handl, Wien/Vienna, Austria), both these latter species differ markedly in several characters from *Eleutheromenia sierra* (PRUVOT, 1891 and above):

(1) They do possess copulatory stylets, in contrast to *E. sierra* (with abdominal spicules, see above);

(2) The ventral foregut glandular organs are tubular with epithelial gland cells (type C in SALVINI-PLAWEN 1972, 1978);

(3) In both species a "ventral commissure sack" of unknown function is present, similarly as in the gymnomeniids *Genitoconia*, *Wirenia* [= *Aesthoherpia*] and *Gymnomenia* (SALVINI-PLAWEN, 1967a, 1988, HASZPRUNAR, 1986, SCHELTEMA, 1999);

(4) The glandular antero-ventral portion of the pericardium (not in open communication with the mantle cavity) - in connection with the pericardial glands - speculatively might represent part of some kind of excretory system.

With respect to the generic characters among the family Pararrhopaliidae (Table I), at least the above characters (1)



Table I. Generic characters in Pararrhopaliidae (see SALVINI-PLAWEN 1967b, 1978; GARCÍA-ÁLVAREZ *ET AL.*, 2001, GARCÍA-ÁLVAREZ AND URGORRI, 2001). A: ventral foregut glandular organs with subepithelial follicles (type A); C: ventral foregut glandular organs epithelial (type C); dts: dorso-terminal sense organ; pphf: peri-pharyngeal ring of follicular glands; -: absent; +: present.

*Tabla I. Caracteres genéricos en Pararrhopaliidae (ver SALVINI-PLAWEN 1967b, 1978; GARCÍA-ÁLVAREZ ET AL., 2001, GARCÍA-ÁLVAREZ Y URGORRI, 2001). A: órganos glandulares digestivos ventrales con folículos subepiteliales (tipo A); C: órganos glandulares digestivos ventrales epiteliales (tipo C); dts: órgano sensorial dorso-terminal; pphf: anillo perifaringeo de glándulas foliculares; -: ausente; +: presente.*

	hooked spicules	dorsal gland	ventral glands	respiratory folds	mouth separate	copulatory stylets	radula	cuticle	dts
<i>Pruvatina</i>	+	+	A	+	-	-	+	thick	+
<i>Pararrhopalia</i>	+	+	A	-	+	+	+	thick	+
<i>Labidoherpia</i>	+	+	A	+	-	+	+	thick	+
<i>Eleutheromenia</i>	+	-	A	+	-	-	+	thick	+
<i>Gephyroherpia</i>	+	-	A	+	+	-	+	thick	+
<i>Luitfriedia</i>	+	-	A	+	-	-	-	thick	+
<i>Lophomenia</i>	-	+	A	?	+	-	+	thick	+
<i>Metameria</i>	-	+	A	-	+	-	+	thick	+
<i>Hypomenia</i>	-	+	A	-	+	-	+	thick	?
<i>Halomenia</i>	-	-	A	+	+	-	+	thick	+
<i>Forcepimonia</i>	-	-	A	?	+	?	+	thin	-
<i>Scheltemaia</i>	+	-	C	+	-	+	+	thick	+
<i>Unciherpia</i>	+	-	pphf	+	-	-	-	thin	+
<i>Uncimonia</i>	- (?)	-	pphf	+	+	-	-	thin	+
<i>Sialoherpia</i>	-	-	pphf	?	+	?	-	thick	+

and (2) concern the generic level. Apart from the different type of the foregut glandular organs in both Australian species (see also *Unciherpiinae* in GARCÍA-ÁLVAREZ *ET AL.*, 2001), copulatory stylets are only present in *Labidoherpia* Salvini-Plawen (with papillous dorsal pharyngeal gland) and in *Pararrhopalia* Simroth (with papillous gland,

mouth separate). Thus, both these species, *E. mimus* and *E. bassensis*, do not fit into an existing genus and consequently are transferred to a separate genus *Scheltemaia* gen.nov. (see also the cladistic analysis in SALVINI-PLAWEN, 2003).

### *Scheltemaia* gen. nov.

Type species (with respect to the more accurate description): *Eleutheromenia mimus* Scheltema and Schander, 2000; Bass Strait (South Australia).

*Definition:* Solenogastres-Pararrhopaliidae with hollow spicules including hooked ones; with common atrio-buccal opening; radula distichous; paired ventral foregut glandular organs

each as tubes or sacks with epithelial gland cells (type C in SALVINI-PLAWEN 1972, 1978); no dorsal papillous foregut gland; with "commisure sack" between (first) ventral ganglia; with dorsotermi-

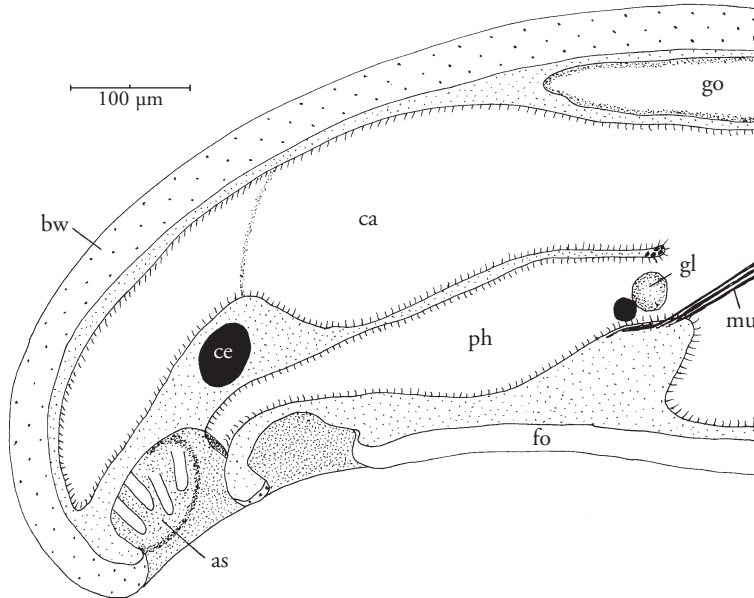


Figure 9. *Urgania monoplicata* spec. nov. Organisation of the anterior body. Abbreviations, as: atrial sense organ; bw: body wall (mantle and musculature); ca: midgut caecum; ce: cerebral ganglion; fo: pedal fold (foot); gl: ventral foregut glandular organ; go: gonad; mu: muscle bundle; ph: pharynx.

Figura 9. *Urgania monoplicata* spec. nov. Organización del cuerpo anterior. Abreviaturas, as: órgano sensorial atrial, bw: pared del cuerpo (manto y musculatura); ca: ciego digestivo; ce: ganglio cerebral; fo: pie; gl: órgano glandular digestivo ventral; go: gónada; mu: unión muscular; ph: faringe.

nal sense organ, with respiratory organs; unpaired secondary genital opening; with copulatory stylets; no receptacula seminis. Two species known.

Family RHOPALOMENIIDAE Salvini-Plawen, 1978

The family is characterised by a thick cuticle and hollow acicular spicules in several layers, without hooked spicules; radula distichous or lacking; no papillate dorsal foregut gland, ventral foregut

glandular organs subepithelial (type A) and/or epithelial (type C; SALVINI-PLAWEN, 1972, 1978); no respiratory organs. It includes five genera (GARCÍA-ÁLVAREZ AND SALVINI-PLAWEN, 2001).

Genus *Urgania* García-Álvarez and Salvini-Plawen, 2001

Type species: *Urgania compostelana* García-Álvarez and Salvini-Plawen, 2001; off northwestern Spain.

*Definition:* Solenogastres-Rhopalomeniidae with epidermal papillae and hollow acicular spicules in several intercrossing layers; mouth opening within the atrium; without radula; paired foregut glandular organs epithelial (type C in SALVINI-PLAWEN 1972, 1978); dorso-terminal sense organ present; secondary genital opening unpaired, no copulatory stylets.

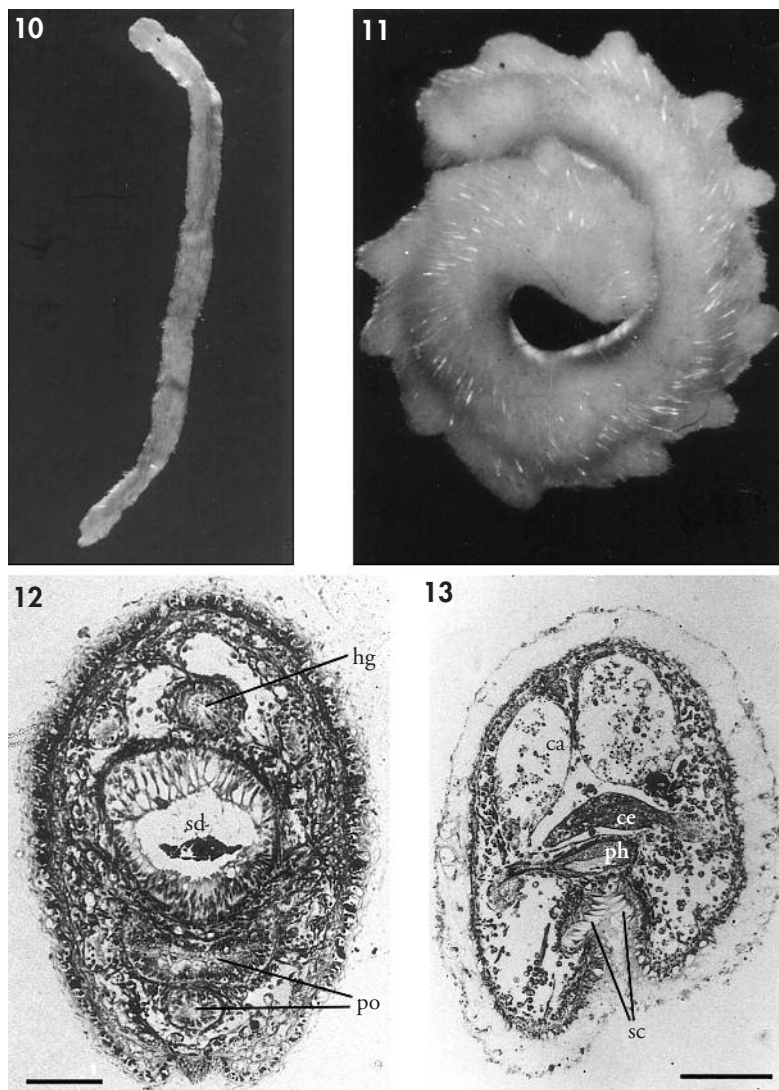


Figure 10. *Micromenia subrubra* spec.nov. (paratype 2), preserved 5 mm specimen; note beak-like extension of dorsal body end (below). Figure 11. *Eleutheromenia sierra* (Pruvot) from Trondheim area, preserved animal (11.5 mm long). Figure 12. *Micromenia subrubra* spec.nov., cross section through posterior body behind pericardium [hg: hindgut; po: anterior pouch of mantle cavity with separated antero-ventral portion; sd: spawning duct] scale bar: 50  $\mu$ m. Figure 13. *Urgorria monoplicata* spec.nov., cross section through mantle bridge (retracted) between atriobuccal opening and pedal pit with pre-pedal scales (sc) [ca: midgut caecum (paired); cc: cerebral ganglion; ph: pharynx] scale bar: 100  $\mu$ m.

Figura 10. *Micromenia subrubra* spec.nov. (paratipo 2), espécimen fijado, 5 mm; nótese la extensión con forma de pico en la parte final (abajo). Figura 11. *Eleutheromenia sierra* (Pruvot) del área de Trondheim, animal fijado (11.5 mm). Figura 12. *Micromenia subrubra* spec.nov., sección del cuerpo posterior tras el pericardio [hg: intestino posterior, po: saco anterior de la cavidad del manto con porción separada antero-ventral, sd: conducto de puesta] escala: 50  $\mu$ m. Figura 13. *Urgorria monoplicata* spec.nov., sección entre la abertura atriobuccal y la foseta pedal con escalas pre-pedales (sc) [ca: ciego digestivo, cc: ganglio cerebral, ph: faringe] escala: 100  $\mu$ m.

*Urgorria monoplicata* spec. nov.

**Material:** A single specimen of 2.2 mm length ( $\varnothing$  0.5 mm) with evenly rounded body end originates from off the Costa Brava (Girona/Spain), from the "Furrió de Tamariu", sandy bottom in 35 m depth (collected 16.9.1990 by Luis Dantart, Barcelona).

After examination of the sclerites, ribbons of semithin serial sections (cs 2  $\mu$ m) were made with a glassknife and stained with RICHARDSON's solution.

The specimen (series sections on slides) is deposited as holotype in the Mus. Nacional Cienc. Nat., Madrid, mol. no.15.02/13.

**Derivatio nominis:** Greek *monos* = one, Latin *plica* = fold; referring to the single pedal fold.

**Diagnosis:** Body 2.2 mm x 0.5 mm, with evenly rounded ends; cuticle fairly thin without keel formation; foot with one single fold only until mantle cavity; no radula or vestige of radula sheath, ventral foregut glandular organs as very small sacks opening ventrolaterally, terminal foregut with two pairs of strong muscle bundles to lateral body wall; midgut with large rostral caecum, rostrally paired, and with regular constrictions. Spawning ducts in their distal half fused, with simple opening; one pair of non-stalked, dorsoposterior receptacula seminis. Figs 9, 13, 14.

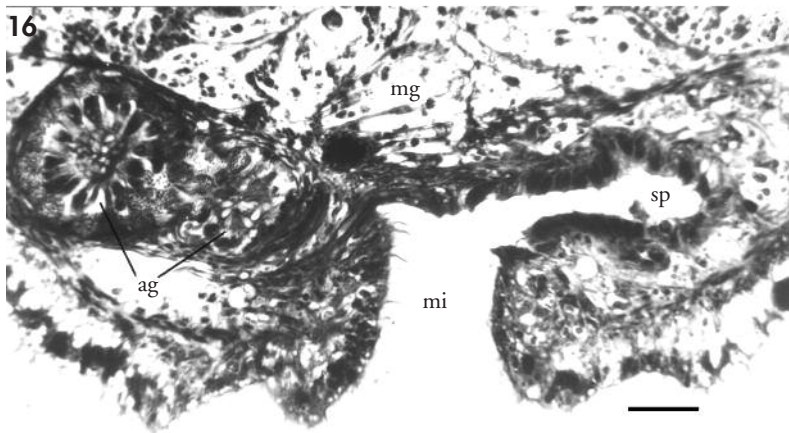
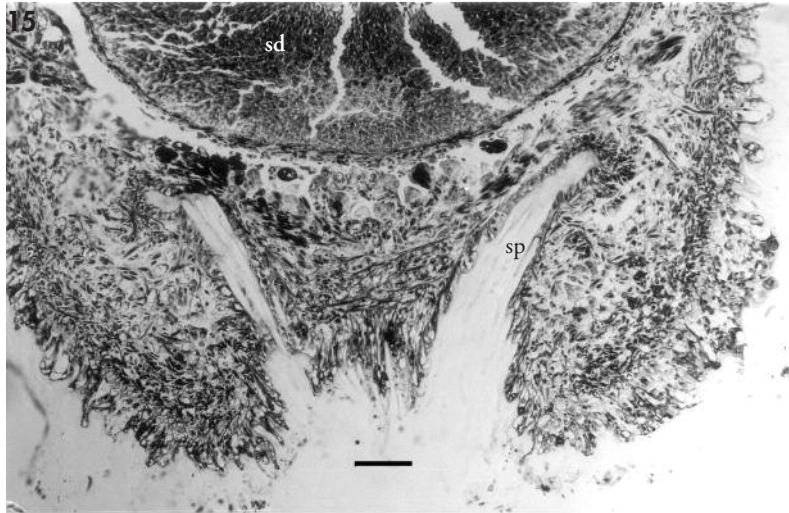
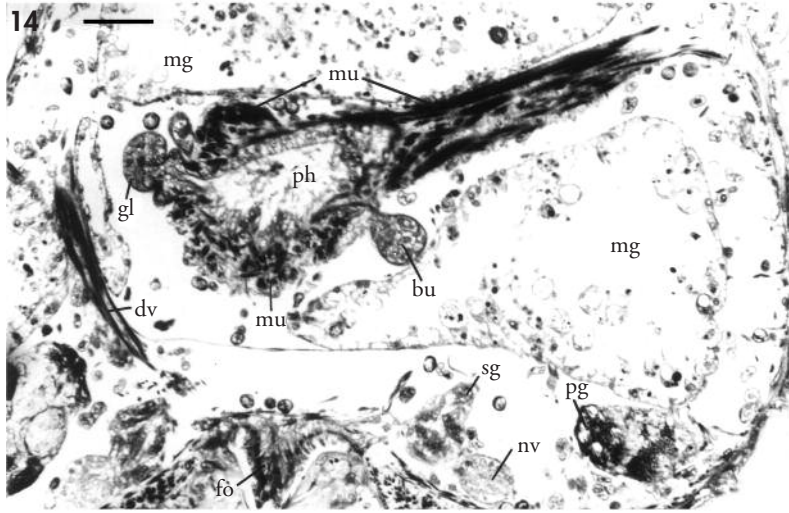
**Mantle:** Mantle producing a moderately thick cuticle only (40-50  $\mu$ m) without marked thickenings; epidermal papillae distally balloon-shaped. Spicules (average 100  $\mu$ m long) acicular and hollow, in tangential and intercrossing layers; no hooked or distally serrate spicules; along foot elongate scales (about 40  $\mu$ m). Mantle bridge between atrio-buccal opening and pedal pit likewise with distinct scales (Fig. 13).

**Foot and mantle cavity:** Pedal pit receiving outlets of the voluminous pedal gland follicles that extend at both sides in the anterior body. Ciliated epithelium of pit not forming folds. At end of pit a single, distinct fold is differentiated, continuing until the pallial cavity. Sole glands parallel internally the foot. Mantle cavity representing a simple ciliated space receiving dorsomedially the rectum and medioventrally the single outlet of the posteriorly fused spawning ducts. There are neither respiratory organs nor accessory genital organs.

**Musculature:** Body wall musculature not very prominent, longitudinal portion showing an only moderately elaborated ventral reinforcement. Similarly, the dorsoventral bundles are typically differentiated, but not very strong. Their fairly medial course serially in dis-

(Right page) Figure 14. *Urgorria monoplicata* spec. nov., somewhat oblique cross section through region of terminal foregut [bu: right buccal ganglion; dv: dorsoventral muscle bundle; fo: pedal fold (foot); gl: left foregut gland; mg: midgut; mu: musculature forming bundles; nv: medullary ventral nerve cord; pg: (portion of) pedal gland; ph: pharynx; sg: sole gland], scale bar: 30  $\mu$ m. Figure 15. *Eleutheromenia sierra* (Pruvot) from Trondheim area, cross section through pre-pallial (post-pedal) region with abdominal spicules (sp) [sd: spawning duct], scale bar: 50  $\mu$ m. Figure 16. *Macellomena adenota* spec. nov., somewhat oblique cross section through pre-pallial (post-pedal) mantle invagination (mi) with "abdominal gland" (ag) just before opening, and with opening of pouch of abdominal spicules (sp) [mg: midgut], scale bar: 30  $\mu$ m.

(Página derecha) Figura 14. *Urgorria monoplicata* spec. nov. Sección oblicua a la altura de la región terminal del digestivo anterior [bu: ganglio bucal derecho; dv: musculatura dorsoventral; fo: pie; gl: glándula digestiva izquierda; mg: intestino medio; mu: unión muscular terminofaringeal; nv: cordón nervioso ventral; pg: (parte de) glándula pedal; ph: faringe; sg: glándula de la suela], escala: 30  $\mu$ m. Figura 15. *Eleutheromenia sierra* (Pruvot) del área de Trondheim, sección de la región prepaleal (post-pedal) con espículas abdominales (sp) [sd: conducto de la puesta], escala: 50  $\mu$ m. Figura 16. *Macellomena adenota* spec. nov., sección a la altura de la invaginación prepaleal (post-pedal) del manto (mi) con "glándula abdominal" (ag) justo antes de la abertura y con la abertura de la bolsa de espículas abdominales (sp) [mg: intestino medio], escala: 30  $\mu$ m.



tances of 50-80  $\mu\text{m}$  causes deep constrictions of the midgut, forming respective lateral pouches. Special musculature is elaborated in connexion with the posterior foregut.

*Sensory system:* Fused cerebral ganglion above the mouth exhibiting a triangular outline in cross section (ventrally 125  $\mu\text{m}$  wide, 60  $\mu\text{m}$  high, 50  $\mu\text{m}$  long). Laterofrontal pairs of small ganglionic formations innervate the atrial sense organ and the mouth opening. The connectives emerge laterally, the very short (20  $\mu\text{m}$ ) ventral and lateral ones in close contact. The (first) lateral ganglion at each side is latero-posteriorly elongated. The first "ventral" swelling, due to the short connective, is located lateroventrally of the cerebral ganglion; the true ventral ganglia ( $\varnothing$  60  $\mu\text{m}$  x 30  $\mu\text{m}$ ) are formed above the beginning pedal fold. The remaining nervous system exhibits no unusual configuration. The 125  $\mu\text{m}$  long suprarectal commissure is medullary ( $\varnothing$  20  $\mu\text{m}$ ).

The atrial sense organ is bordered by the horseshoe-shaped ciliary tract, the dorsal limbs running parallel in distinct distance. The papillae are single and blunt ( $\varnothing$  12-15  $\mu\text{m}$ ). A single dorsoterminal sense organ is elaborated middorsally above the posterior rectum.

*Alimentary tract:* Mouth opening dorsally at the rear end of the atrium, behind the curved ciliary tracts. Foregut representing an elongate tube, coated throughout its course by a delicate circular and a distinct longitudinal pharyngeal musculature. The epithelium consists in the anterior third of cubical cells (about 6  $\mu\text{m}$  high), further on of irregularly club-shaped cells (8-12  $\mu\text{m}$  high). It is intruded (partly in the anterior third, all along posterior third) and forms up to 12 distinct longitudinal folds.

A short distance in front of the ventral opening of the foregut into the midgut, the dorsal and lateral longitudinal pharyngeal muscles are concentrated to a pair of dorsolateral bundles which run transversely to the lateral body wall (Figs 9, 14). In that narrow

area, the ventral pharyngeal muscles also become concentrated to a pair of ventral bundles; both extend (in the present specimen) asymmetrically at the same body side far posteriorly to join the musculature of the body wall (not before the middle of the body).

In this terminal portion of the foregut (formation of muscle bundles) the buccal ganglia ( $\varnothing$  25  $\mu\text{m}$ ) are elaborated laterally (Fig. 14). The ventral glandular organs are separated by the buccal commissure ventral to the foregut; they open ventrolaterally into the foregut (Fig. 14). The organs are very small (40-50  $\mu\text{m}$  long,  $\varnothing$  30  $\mu\text{m}$ ), somewhat irregular sacks with glandular epithelium and a narrow outleading lumen (type C in SALVINI-PLAWEN 1972, 1978).

Midgut possessing a voluminous rostral caecum extending to body tip (Fig. 9), splitting frontally in the region of the mouth to a paired organ. Due to the serial muscle bundles, there are regular, deep lateral constrictions of the midgut. The midgut and its caecum include, among dissolved food material, also nettle capsules of Cnidaria.

*Gonopericardial system:* Paired, hermaphroditic gonad. Eggs at the connecting median walls measure maximally  $\varnothing$  50  $\mu\text{m}$ , indicating that full maturity has not been reached. The single heart auricle is an invagination of the pericardial roof, and the ventricle represents a largely free organ. There are two kinds of blood cells: a) small and coarsely structured granulocytes ( $\varnothing$  5  $\mu\text{m}$ ); b) finely granulated, round haemocytes ( $\varnothing$  10  $\mu\text{m}$ ).

The pericardiodycts emerge laterotermally. They open from dorsal into the respective spawning duct, the latter bending dorso-posteriorly into a scarcely separated, wide tube: receptaculum seminis. The spawning ducts are paired in their anterior portion; single opening into the central mantle cavity represents a simple, narrowed and short outlet (pore). There are neither vesiculae seminales nor accessory genital organs (copulatory stylets, abdominal spicula).

*Discussion:* Among the five genera of the family Rhopalomeniidae (GARCÍA-ÁLVAREZ AND SALVINI-PLAWEN, 2001), the present specimen coincides on the generic level with *Urgorria* based on the mantle elaboration, the atrio-buccal cavity, the lack of the radula and the configuration of the genital apparatus. The conformity with the hitherto sole species *U. compostelana* even includes such characters as the special scales at the mantle bridge between the atrio-buccal opening and the pedal pit, the similar musculature of the foregut, the unpaired to paired midgut caecum, and the receptacula seminis. Only few characters actually differ from those in *U. compostelana*: the body cuticle forms no middorsal reinforcement (in *U. compostelana* the 40-100  $\mu\text{m}$  thick cuticle with spicules locally forms a middorsal crest up to 150  $\mu\text{m}$ ); only a single pedal fold is elaborated, which continues to the mantle cavity (in *U. compostelana* there are two pedal folds which fuse into a single one in the region of the anterior spawning ducts and flatten to a mere ridge close to the mantle cavity to a mere ridge); the position of the dorso-terminal sense organ differs (above the anterior mantle cavity; in *U. compostelana* at the rear of the body); the heart ventricle represents a free tube (in

*U. compostelana* it remains an invagination throughout); the different relation of the foregut musculature (the muscle layer around the foregut in *U. compostelana* is weaker than the bundles at the terminal foregut, which are also much stronger than those in the present specimen 1). The present specimen thus represents a proper species *Urgorria monoplicata* spec.nov.

The common atrio-buccal opening in *Urgorria* separates this genus from all other Rhopalomeniidae, and *Urgorria* is thus well-defined (GARCÍA-ÁLVAREZ AND SALVINI-PLAWEN, 2001). At the same time, the condition of the ventral foregut glandular organs (type C in SALVINI-PLAWEN, 1972, 1978) required somewhat altering the definition of the family itself (see GARCÍA-ÁLVAREZ AND SALVINI-PLAWEN, 2001 versus SALVINI-PLAWEN, 1978). The type species *Rhopalomenia aglaopheniae* (Kowalevsky and Marion, 1887) exhibits two pairs of ventral foregut glandular organs (cf. PRUVOT, 1891, NIERSTRASZ AND STORK, 1940, SALVINI-PLAWEN, 1972, GARCÍA-ÁLVAREZ ET AL., 2000a): one pair forming subepithelial follicles around short ducts (type A) and one globular pair of epithelial glands (type C). All other *Rhopalomenia* species (representing *Entonomenia* Leloup to be restored cf.

SALVINI-PLAWEN 1972) as well as all other Rhopalomeniidae except *Urgorria* (no information for *Pruvotia*) possess type A foregut glandular organs only; thus, *Urgorria* (uniquely type C organs) is well-contrasted also in this respect. Accordingly, we may accept that within Rhopalomeniidae the ventral foregut glandular organs became differently elaborated at the generic level as "subepithelial (type A) and/or epithelial (type C)" organs (see family characters above).

Apart from the presentation of a new species which establishes the occurrence of *Urgorria* also in the Western Mediterranean Sea, the finding of *U.*

*monoplicata* at a fairly shallow depth of only 35 meters is worthy of note.

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