

**New Species of *Synagoga* (Crustacea: Ascothoracida) from Plankton
off Okinawa, Japan, with a SEM Study of the Carapace**

MARK J. GRYGIER¹⁾

and

SUSUMU OHTSUKA

Fisheries Laboratory, Hiroshima University, 1294
Takehara-cho, Takehara, Hiroshima 725, Japan

With Text-figures 1-10 and Table 1

Abstract A free-swimming adult male of the ascothoracidan crustacean *Synagoga millipalus* sp. nov. is described from plankton in the East China Sea off Okinawa, Japan. This is the first Pacific record of the genus. The new species is distinguished at length from its most similar congener, *S. paucisetosa* Grygier from the bathyal equatorial Atlantic. The ornamentation of the carapace is described by scanning electron microscopy. The inner surface has a continuous but regionally differentiated, submarginal palisade of partly fused spines as well as lanceolate guard setae with distally pointing barbs, a deep anterior pit, concentric zones of pores, and a cluster of minute pores at the posterior angle. The external surface has rimmed pores and hair sensilla, but most of the diverse outer integumental organs reported from another morphologically generalized ascothoracidan, *Waginella metacrinicola* (Okada), are absent. Two of the five pairs of lattice organs (=cardic organs) along the hinge line have anterior rather than posterior pores. This orientation differs from that of other ascothoracidan and tends to weaken a recent analysis, using Ascothoracida as the outgroup, of lattice organ variation among the cyprid larvae of Cirripedia.

The Ascothoracida comprise more than 90 described species of parasitic maxillopodan crustaceans related to the Cirripedia within the Thecostraca. Their hosts include anthozoans and echinoderms. Unlike nearly all other ascothoracidan, species of the genus *Synagoga* are not attached to or enclosed within their hosts as adults, but remain free-swimming and are occasionally caught in plankton. Their nauplius larvae and any subsequent ascothoracid-larvae (bivalved, cypridiform stages) have not yet been described; only a post-larval juvenile form and adult males and females of different degrees of sexual maturity are known.

Synagoga has a wide distribution in the Atlantic, Indian, and (present report) Pacific Oceans, but is known from very few specimens. *Synagoga mira* Norman (1888), several males of which were found on the antipatharian black coral *Antipathes larix* Esper in the Bay of Naples, was one of the first known species of the Ascothoracida (for illustrated descriptions see: Norman, 1913; Grygier, 1983a). Grygier (1983a) described *S. normani* based on a female found on an alcyonacean soft coral, *Dendronephthya* sp., near Mombasa, Kenya. Grygier (1990) also described *S.*

1) Mailing address: 14804 Notley Rd., Silver Spring, MD, 20905, U.S.A.

paucisetosa and *S. bisetosa* (the latter only provisionally included in this genus) based on a mature male and an immature possible female, respectively, from the bathyal Atlantic, hosts unknown, as well as an unnamed, mid-oceanic, planktonic juvenile from the eastern Indian Ocean (Grygier, 1988). Grygier (1983a) transferred two other species, *S. metacrinicola* Okada, 1926, and *S. sandersi* Newman, 1974, to a separate new genus, *Waginella*.

This paper presents the description of a new species of *Synagoga* caught in plankton near Okinawa, Japan. A scanning electron microscopical (SEM) study of the the cuticular ornamentation of the carapace is included for comparison with that of *Waginella metacrinicola* (see Grygier & Itô, in press).

A single adult male was collected aboard TRV "Toyoshio-maru" in the East China Sea off Okinawa between Ie-shima and Aguni-shima (11 May 1991, 26°42.90'N, 127°28.11'E-26°42.17'N, 127°30.40'E, 19:26-20:15, oblique tow from 575 m to surface with ORI net, 0.33 mm mesh). The specimen was originally fixed and preserved in neutralized sea-water formalin. After the removal of the left carapace valve, the specimen was observed with a Nikon Optiphot differential interference microscope in a glycerine whole mount and drawings were prepared using a camera lucida. The left thoracopods and frontal filament complex were mounted on a glass slide in glycerine jelly for detailed examination. The left carapace valve was dehydrated through an ethanol series, transferred to isoamyl acetate, critical point dried using liquid CO₂, mounted on a brass stub, and photographed with a JEOL JSM-T20 scanning electron microscope operating at an acceleration voltage of 20 kV.

Ascothoracida

Synagogidae Gruvel, 1905

***Synagoga* Norman, 1888**

***Synagoga millipalus*, sp. nov.**

(Figs 1-10, Table 1)

Diagnosis

Anterior pit of carapace more than 10 times deeper than inner diameter. Segment 4 of antennule with small spine and two large, densely setulose setae; segment 6 longer than segment 5, with more or less parallel margins. Oral cone reaching only to level of ends of thoracopodal protopods. Proximal exopodal segment of legs 2-5 with one strong, subapical, lateral seta instead of numerous weak ones. No medial seta on basis of thoracopod 4. Three setae on exopod of thoracopod 6. Epaulets of thoracomere 6 with numerous round spots with thin cuticle. Rami of penis each ending in four long setae. Row of 12-13 ventral spines on furcal rami; posteroventral telsonic setae longer than this spine row.

Type specimen

The adult male holotype has been deposited in the Los Angeles County Museum of Natural History (Cat. no. LACM 94-19).

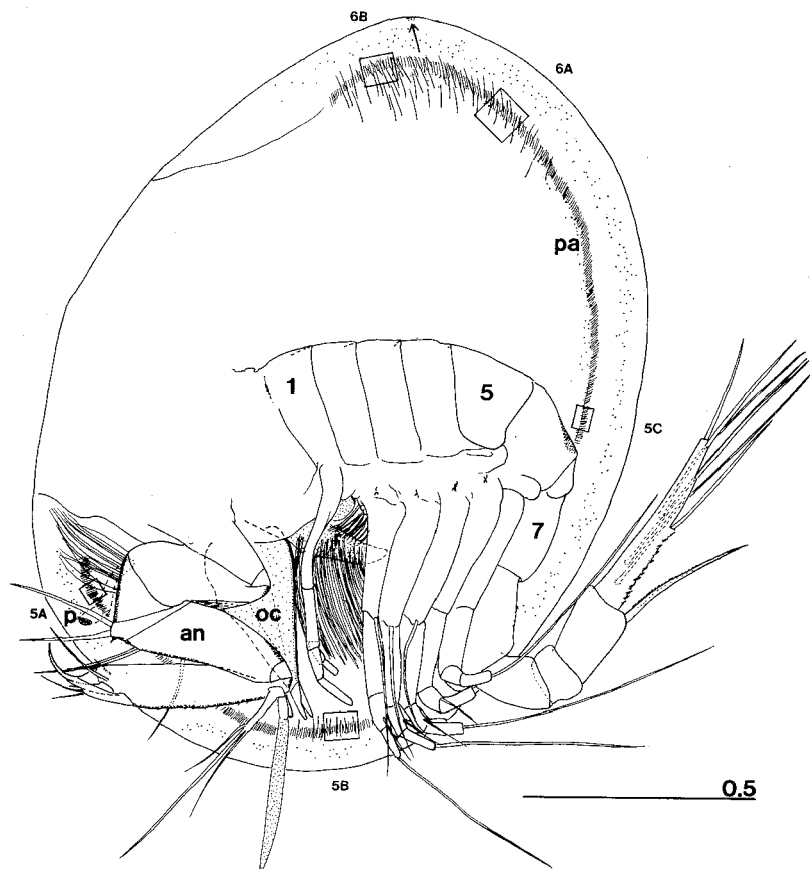


Fig. 1. *Synagoga millipalus*, sp. nov., male holotype, lateral view with left carapace valve removed and most thoracopodal setae omitted, some trunk somites numbered, arrow pointing to patch of minute pores at posterior end of valve (enlarged in Fig. 4A). Five labelled squares locate approximately the parts of the palisade enlarged in Figs 5A-C and 6A-B. an, antennule; oc, oral cone; p, pit; pa, palisade. Scale in mm.

Etymology

Noun in apposition, from Latin *mille* (thousand) and *palus* (stake), referring to the fused spines that form a submarginal palisade on the inner surface of each carapace valve.

Description

Carapace (Figs 1-6, 7A). The carapace is bivalved and lenticular, 1.66 mm long, 1.25 mm high (Fig. 1). The valve outline is oval with a slight anterodorsal bulge and slightly projecting but rounded posterior angle.

At high magnification, a fingerprint-like pattern of fine cuticular ridges spaced about $0.15\ \mu\text{m}$ apart is evident on the outer surface of the valves (Figs 2C-D, 3B-D). By

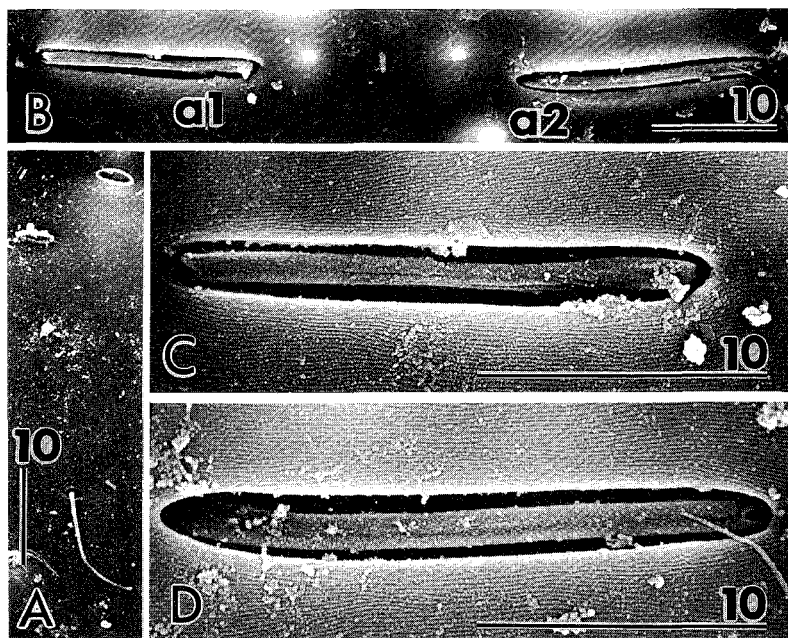


Fig. 2. *Synagoga millipalus*, sp. nov., male holotype, external features of left carapace valve. A. Pore and hair-like seta near anterior margin; B. General view of first (a1) and second (a2) lattice organs near dorsal margin; C. First lattice organ; D. Second lattice organ. Scales in μm .

light microscopy, the entire outer cuticle is seen to be uniformly and densely porose, with approximately equal numbers of narrow pore canals and much larger, conical pores that narrow towards the exterior. The mouths of the conical pores are rimmed ovals with a major diameter of 1.4–3.4 μm ; a few hair-like sensilla 12–16 μm long are found among them (Fig. 2A). Five lattice organs (sensu Jensen et al. 1994) or cardiac organs (sensu Itô & Grygier 1990) lie alongside the dorsal margin, two near the front of the hinge, three near the rear, and all in line with each other (Figs 2B–D, 3). Their precise situation relative to the ends of the hinge could not be determined. In the rear group, the two anterior organs lie closer together, the same distance apart as the two organs in the anterior group. Each lattice organ consists of a trough 15–21 μm long and 2.0 μm wide, with a narrow rim. A sessile tube 0.9–1.3 μm thick occupies the whole length of the trough. The tube has a minutely granular surface texture. There is a pore at the anterior end of the tube in the front lattice organ of each of the two groups, but at the posterior end in the others.

On the inner surface, there are three sets of pores: an immediately submarginal band (Figs 1, 7A), another band farther away from the margin and just within the palisade as defined below (Figs 1, 7A), and scattered pores over the rest of the interior, especially anteriorly (Fig. 4C). These pores are similar to the external ones, but each is situated on a round platform 2.8–3.4 μm in diameter (Figs 5B, 6A–B). About a dozen, much smaller, closely spaced pores are found just inside the

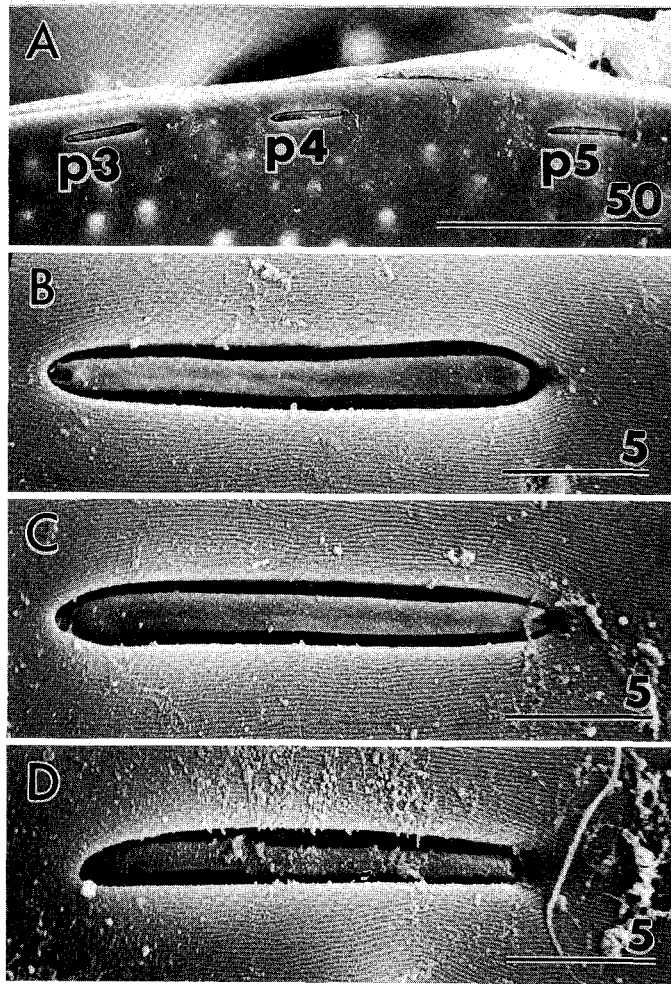


Fig. 3. *Synagoga millipalus*, sp. nov., male holotype, posterior lattice organs of left valve. A. General view of third (p3), fourth (p4), and fifth (p5) lattice organs near dorsal margin; B. Third lattice organ; C. Fourth lattice organ; D. Fifth lattice organ. Scales in μm .

posterior angle of the carapace (Fig. 4A). Short, villus-like processes $2.7\ \mu\text{m}$ in length fringe the entire free margin of the valve (Fig. 4B).

The palisade (new term) comprises a single, regionally differentiated row of radially pointing, basally fused spines arising $100\text{--}130\ \mu\text{m}$ inward from the free margin of the valve (Figs 1, 5, 6, 7A, pa). The palisade spines are $14.3\text{--}42\ \mu\text{m}$ long, being shortest anterodorsally and midventrally and longest posteroventrally; the fused zone accounts for $10.3\text{--}13.8\ \mu\text{m}$ everywhere. The longer spines are also more robust; the posteroventral spines are $2.9\ \mu\text{m}$ thick but the midventral ones a mere $0.7\ \mu\text{m}$. In the anterodorsal and midventral regions (Figs 5A, C, 7A), the $14.3\text{--}15.2\ \mu\text{m}$ long spines are completely fused in groups of 16–20 and 20–26, respectively, for 75–80%

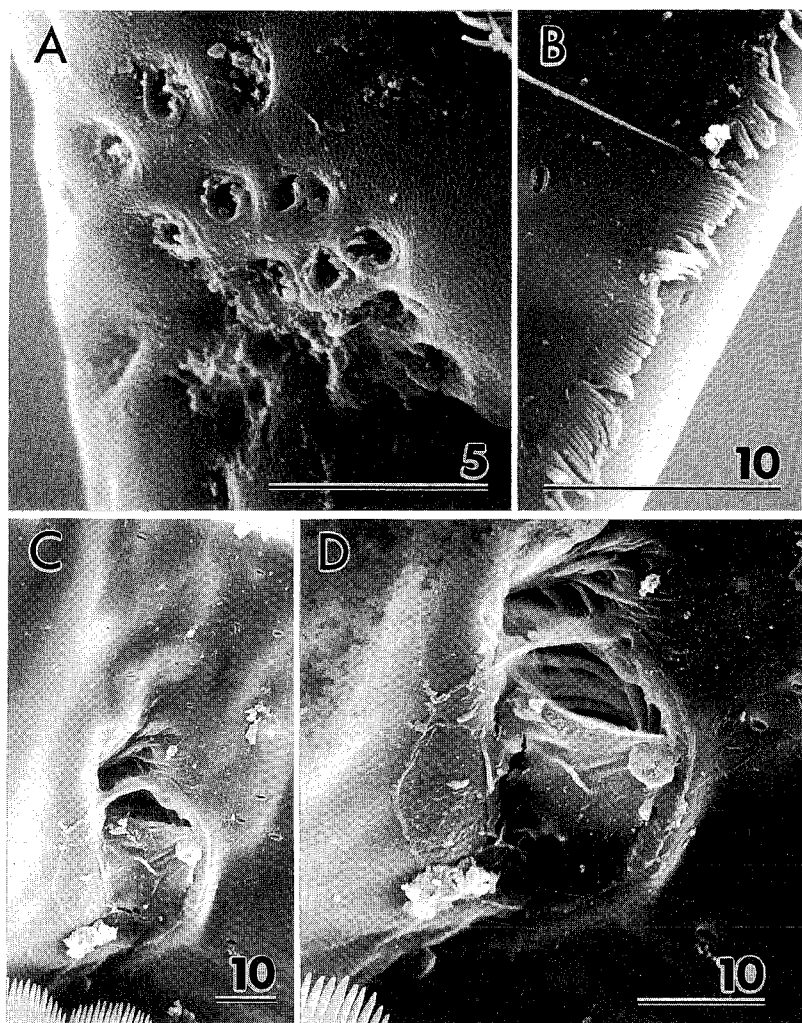


Fig. 4. *Synagoga millipalus*, sp. nov., male holotype, internal ornamentation of left carapace valve. A. Patch of pores inside posterior angle, valve margin on left; B. Villus-like fringe at posterodorsal valve margin; C. Anterior pit between valve margin (above right) and palisade (below left); D. Pit orifice, showing a few of the parallel ridges in two sets within. Scales in μm .

and 80–90% of their length, respectively, to form toothed scales that are 15–16 μm wide and only weakly connected to each other by easily torn membranous zones. The anteroventral spines (Fig. 5B) are 17.9–21.3 μm long and fused for 60–73% of their length. Similarly, the posterior spines (Fig. 6B) are 15.8–20 μm long and fused for 52–63% of their length. The individual spines are 1.2–1.5 μm thick in the anteroventral and posterior regions. In the posteroventral region (Fig. 6A), the spines are considerably longer, less than 40% of their length is fused, and there are deep indentations between the spines.

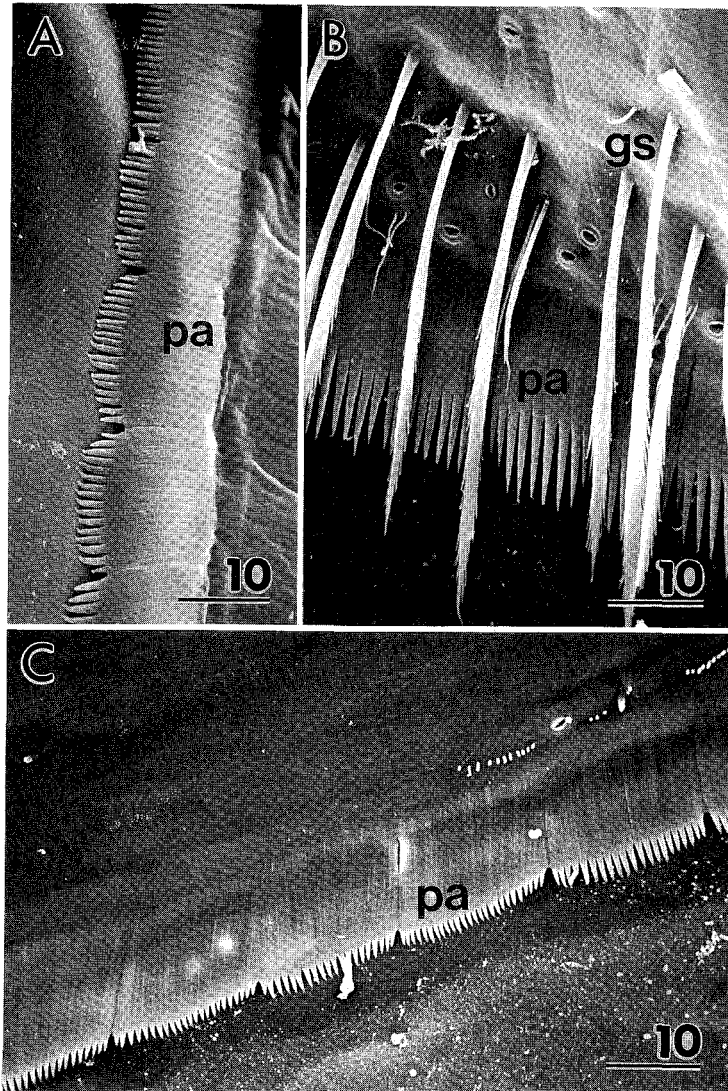


Fig. 5. *Synagoga millipalus*, sp. nov., male holotype, palisade (pa) of left carapace valve. A. Anterodorsal region; B. Anteroventral region, also showing guard setae (gs); C. Ventral region. Scales in μm .

Setae are present inwards from the palisade in the anterior, anteroventral, posteroventral, and posterior sectors. The most prominent of these are lanceolate guard setae of various lengths that are provided with double row of distally pointing barbs and reach farther outward than the palisade spines except posteroventrally (Figs 5B, 6A-B, gs). Especially posteriorly, rows of long, simple, fine hairs are found among the guard setae and inwards from them (Fig. 6A-B). Posteriorly, a few fine hairs not in rows are found between the palisade and the margin.

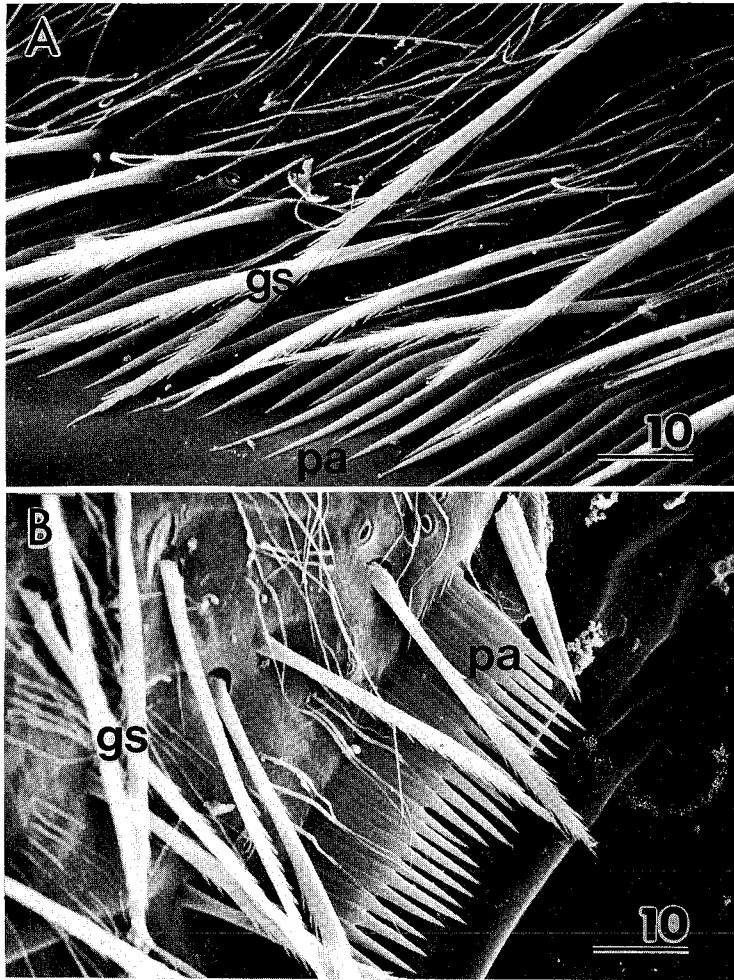


Fig. 6. *Synagoga millipalus*, sp. nov., male holotype, palisade (pa) and guard setae (gs) of left carapace valve. A. Posteroventral region; B. Posterior region. Scales in μm .

An elongate, cylindrical pit opens anterodorsally on the inner surface between the palisade and margin (Figs 1, 4C-D, 7A). It is $175\ \mu\text{m}$ deep, $8\text{--}19\ \mu\text{m}$ in interior diameter (narrowest at midlength), and lined with thick cuticle. The orifice is partly blocked by a membrane, possibly representing a secretion (Fig. 4C-D). Inside the orifice are two opposing sets of curved, parallel, diagonal ridges (Fig. 4D); with the light microscope, these sets can be seen along the outer two-thirds of the pit's length (Fig. 7A, s). In the innermost third, the hypodermis side of the cuticle is produced into blebs (Fig. 7A, bl). The entire pit sits within a tissue capsule, and the wide space between the two is now empty (Fig. 7A, cp).

No gut diverticula were observed within the valves, but droplets of a clear, sticky substance were expressed from the body and valve when the valve was dissected

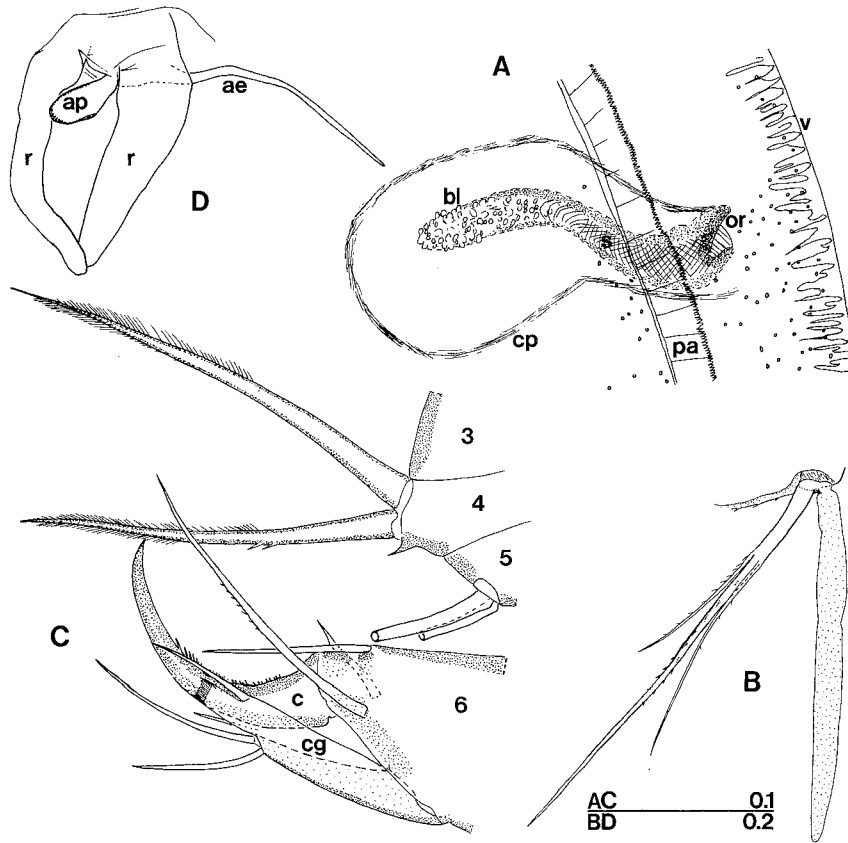


Fig. 7. *Synagoga millipalus*, sp. nov., male holotype. A. Anterior carapace pit; B. Proximal sensory process of left antennule; C. Distal armament of left antennule, outer view, segments numbered; D. Left frontal filament complex, medial view, all filament-like processes removed (cf. Fig. 1). ae, proximal aesthetasc; ap, basal appendix; bl, blebby region of pit; c, claw; cg, claw guard; cp, tissue capsule around pit; or, pit orifice; pa, palisade; r, ramus; s, striated region of pit; v, valve margin. Scales in mm.

away. Masses of spermatids were found within the central part of the valve and also within the cephalic part of the main body.

Cephalon (Figs 1, 7B-D). The cephalon bears a pair of large antennules, a pair of plumose frontal filament complexes, and an oral cone. The antennules are 6-segmented and when retracted are W-shaped (Fig. 1, an). The triangular first segment and parallelogram-shaped second segment are unarmed. The anterior margin of the triangular third segment is lined with long, hair-like setae. The very short fourth segment has a small spine and two long, normal rather than spiniform setae, each bearing two crowded rows of short setules (Fig. 7C). The tapered fifth segment has two basal setae and another at midlength that passes medial to the sixth segment; all three setae are spinulose. The sixth segment is longer than the

fifth and its margins are nearly parallel except proximally. The proximal sensory process bears a basal aesthetasc and three non-articulated, spinulose, setiform elements at the end of a cylindrical shaft (Fig. 7B). The claw bears a row of denticles along a part of its inner margin, the more distal denticles being larger (Fig. 7C, c). Of the three setae at the base of the claw, the longest, lateral one is also spinulose. The claw guard bears four setae and its apical hood has a striated margin (Fig. 7C, cg).

The pair of frontal filament complexes is actually attached to the inside of the carapace valves rather than to the cephalon proper. There are two plumose rami, each about 260 μm long and the posterior one somewhat thinner than the ventral one (Fig. 7D, r). Both rami bear vast numbers of c. 260–320 μm long filaments along their whole length, and these give the entire organ a plumose appearance (Fig. 1). The thickly chitinized basal appendix at the base of the anterior ramus extends posteroventrally from a constricted base and is 82 μm long and maximally 39 μm thick (Fig. 7D, ap); the proximal aesthetasc (Fig. 7D, ae) extends forward nearby and is 260 μm long and about three times thicker at the base than the filaments of the rami.

The oral cone is about 450 μm long and 200 μm deep, reaching the same level as the distal ends of the thoracopodal protopods (Fig. 1, oc). It is from the labrum ensheathing the other mouthparts. Since only one specimen was available, the oral cone was not dissected and no detailed description of the mouthparts is offered. The maxillules and medial languette, at least, are similar to those of other species of *Synagoga*. The tips of the mandibles and maxillae protrude from the tip of the cone but are appressed to each other and thus obscured.

Trunk (Figs 1, 8A, 10A). There are seven well-defined thoracic somites if the male genital somite is included, in conformance with Grygier's (1983b) 5–7–4 tagmosis scheme. The first six each bear a pair of thoracopods and the seventh bears the biramous medial penis. The first four somites are rectangular in side view and similar in height and length, but the next two are longer dorsally than ventrally, and the seventh, with its anteroposterior axis directed ventrally, is longer than high. The next three limbless somites together with the telson form a U-shaped abdomen; the first of these somites is the longest and the third the shortest. The telson bears a pair of spine-like posteroventral setae and the furcal rami. There is little trunk ornamentation aside from sparse spinules (ctenae?) dorsally on all the somites and the telson.

The ventrolateral margins of the tergites are reasonably well defined in the first six thoracic somites, and those of the fifth somite are especially strongly sclerotized (Fig. 8A). The margin of the tergite of the sixth somite is produced posteriorly into a rounded swelling, the epaulet, which has many tiny, circular spots of thinner cuticle (Fig. 8A, ep). A rectangular zone of rather soft cuticle occupies the pleural area between the tergite margins and the thoracopods in thoracic somites 2–5 (Fig. 8A).

Thoracopods (Figs 1, 8, 9). The six pairs of natatory legs are long and unusually slender (Fig. 1). The rod-like first pair (Fig. 8B) is somewhat separated from the others, which overlap each other considerably. There is no filamentary appendage

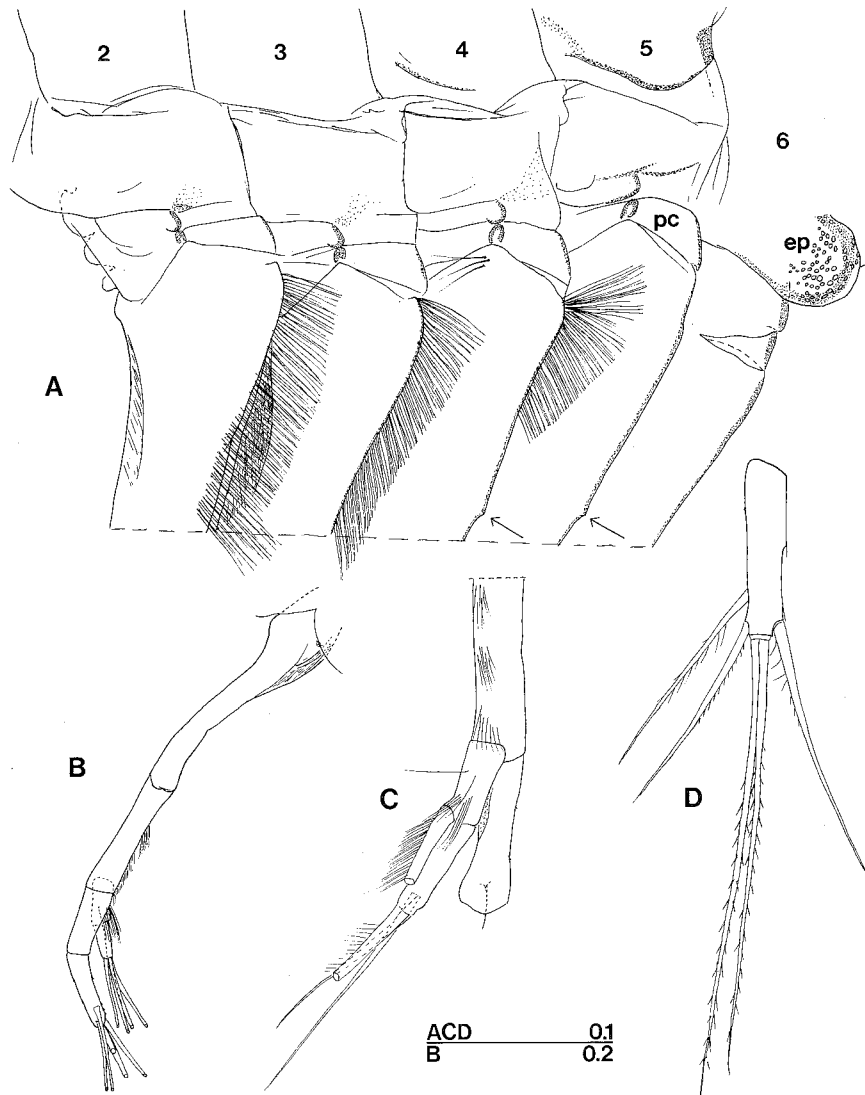


Fig. 8. *Synagoga millipalus*, sp. nov., male holotype. A. lateral view of limb bases of left legs 2-6, arrows marking angular protrusions of coxae in legs 4 and 5; B. Left leg 1, in situ, lateral view; C. Leg 1, medial view, showing distal part of basis, endopod, and first exopodal segment; D. Leg 1, second exopodal segment. ep, epaulet; pc, precoxa. Scales in mm.

at the base of the first leg. The legs of pairs 2-5 closely adjoin each other medially. Their baso-lateral pivot points are formed by two opposing condyles, the proximal one hook-shaped and the distal one an inverted U belonging to the band-like precoxa (Fig. 8A, pc). A wedge-shaped sclerite interrupts the protopodal shaft of leg 6 posteriorly near its base (Fig. 8A). The legs are otherwise divided into a coxa, basis, 2-segmented exopod, and 2- (legs 1 and 6) or 3- segmented (legs

Table 1. Setation of thoracopods in male holotype of *Synagoga millipalus*, sp. nov. Positions 1–9 are shown in Fig. 9A. In position 4, a + b + c differentiates the medial, apical, and lateral setae, respectively. In position 5, d + e differentiates the major apical setae from a minor medial one, respectively.

Position	1	2	3	4	5	6	7	8	9
				a + b + c	d + e				
Leg 1	0	0	0	1+2+2	3	(1)		0	0
Leg 2	1	0	1	0+3+2	2+1	1	0	1	0
Leg 3	1	0	1	0+3+2	2+?	1	0	1	0
Leg 4	1	0	1	0+3+2	2+0	1	0	0	0
Leg 5	0	0	1	0+3+2	2+0	1	0	0	0
Leg 6	0	0	0	0+3+0	2+0	(0)		0	0

2–5) endopod (Figs 8B–D, 9); the proximal two endopodal segments of leg 2 are not fully separated (Fig. 9A). The distal exopodal segment is nearly equal in length to the proximal segment, or, in more posterior legs, distinctly shorter than it. Legs 4 and 5 have a tiny, angular projection at about midlength of the outer coxal margin (Fig. 8A, arrowed).

The limb setation is outlined in Table 1. In addition, there are a hair-like seta on the first exopodal segment (position 3) in leg 1 (Fig. 8C), a short, blunt, socketed spine medially on the second segment (position 4a) in at least left legs 4 and 5 (Fig. 9C–D), and a medial endopodal pore (position 5e) in both legs 4 (Fig. 9C). The seta on the first exopodal segment (position 3) in legs 2–5 is situated markedly subapically, especially in the more posterior legs (Fig 9A–D). Most of the thoracopodal setae bear two rows of long setules. However, most of the setae of leg 1 are simpler, and the two longest exopodal setae have a double row of spiniform rather than fine setules (Fig. 8C–D).

Leg 1 has fine hairs (actually extremely fine setae, but quite distinct from the natatory setae of Table 1) along the lateral side of the basis and part of the first endopodal segment, five clumps of hairs along the medial side of the basis, and two clumps on the medial side of the first endopodal segment (shown in part in Fig. 8B, C). In legs 2 and 3, both margins of the coxa are lined with long, fine hairs; in leg 4, only the proximal part of the outer margin is so lined (Fig. 9A–C). Legs 2 and 3 additionally have fine hairs along the inner margins of the basis and the third endopodal segment (Fig. 9B–C). Leg 5 has some hairs on the inner margin of its second endopodal segment (Fig. 9E). Laterally on the exopod, fine hairs occur abundantly along the first segment proximal to the lateral seta in legs 2–5 and sparsely on the second segment in legs 2–6 (Fig. 9).

Penis (Fig. 10A). The penis is relatively enormous and has about the same bulk as the somite that bears it plus the following somite. The rigid, proximal part of

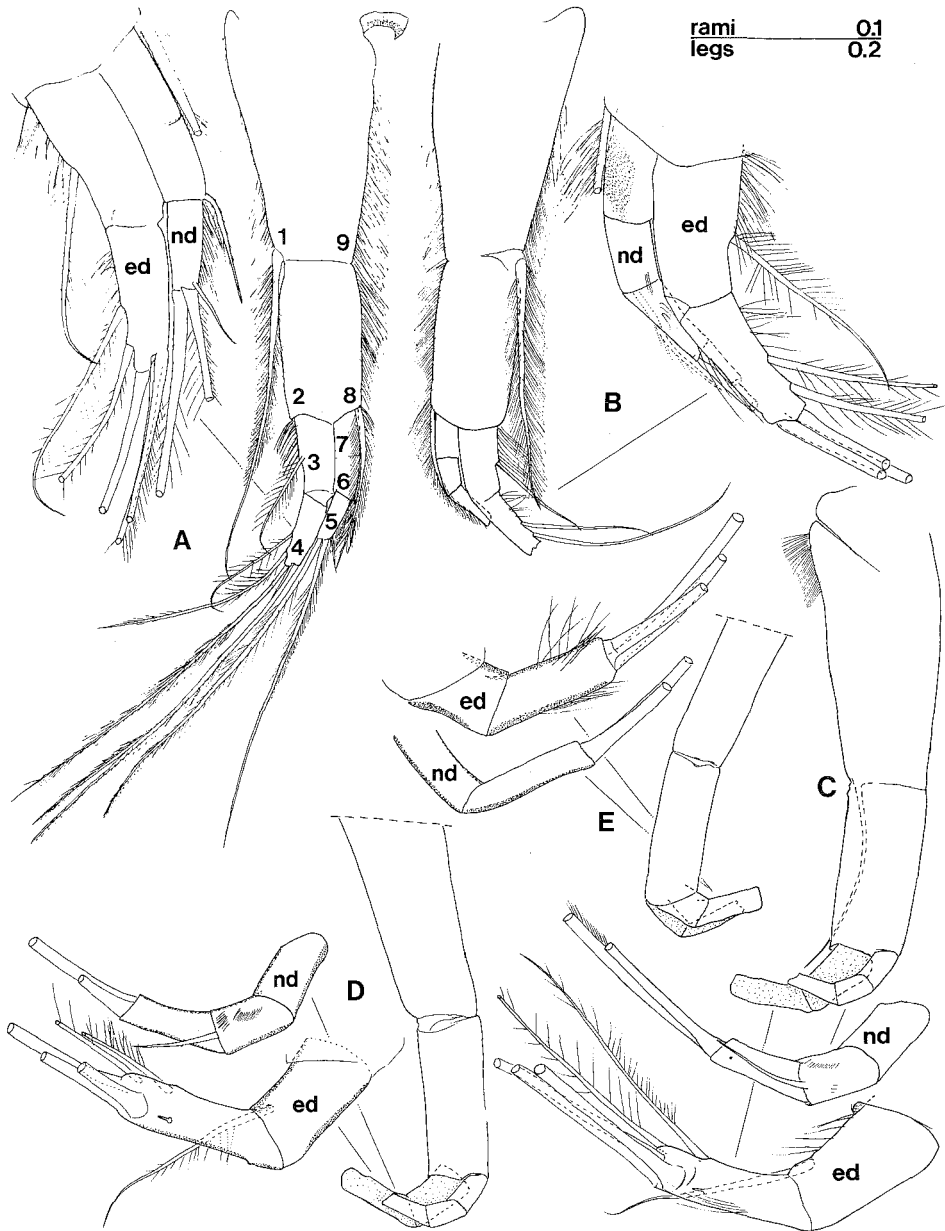


Fig. 9. *Synagoga millipalus*, sp. nov., male holotype, left legs 2-6, with details of their rami (ed, exopod; nd, endopod); see text for full account of setulation of setae. A. leg 2, numbers 1-9 referring to sites in Table 1; B. Leg 3; C. Leg 4; D. Leg 5; E. Leg 6. Scales in mm.

the shaft is supported anteriorly by a massive thickening, the distal third of which is bent 90° forward and ends in a short, soft, spiniform process at the apex of a large, knobby spine. There is a cup-shaped, tendinous attachment for the intrinsic muscles

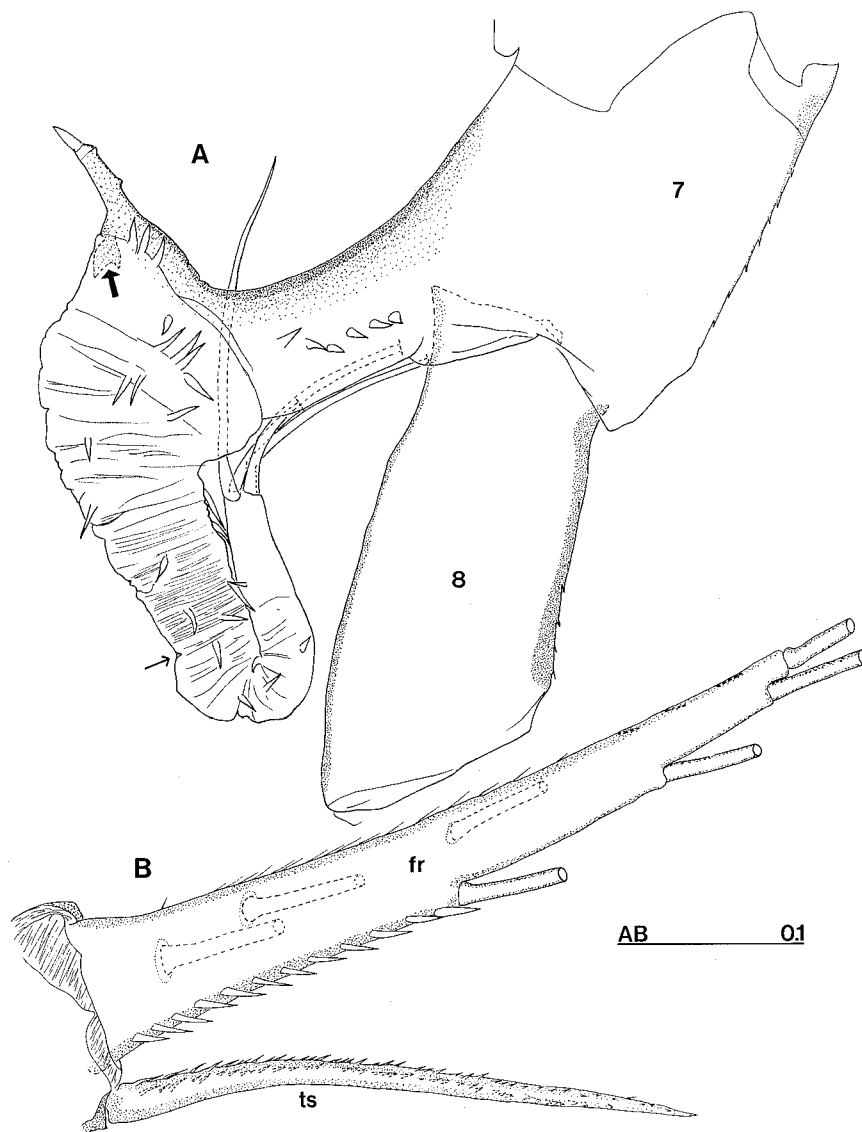


Fig. 10. *Synagoga millipalus*, sp. nov., male holotype. A. Trunk somites 7 and 8 with penis on seventh, large arrow indicating internal tendinous element on which intrinsic muscles insert, small arrow marking bases of rami (only left ramus shown, hiding right ramus); B. Left furcal ramus (fr) and spine-like seta (ts). Scale in mm.

at the base of the spine. A very broad-based but tapering, flexible, wrinkled part of the shaft follows, bearing many short, soft spiniform processes. The two vermiform rami are folded back against this part of the shaft, bear additional spiniform processes, and each ends in four setae that are considerably longer than the retracted rami themselves.

Telson and furca (Fig. 10B). The posteroventral, spine-like setae of the telson are 275 μm long, extend well beyond the spinose ventral margins of the furcal rami, and are armed with two dorsal rows of denticles (Fig. 10B, ts). The furcal rami are 410 μm long, 80 μm high at the base, and taper distally with three abrupt steps and a very slight distal upswing (Fig. 10B, fr). The dorsal margin is lined with short, needle-like setae. The proximal part of the ventral margin is armed laterally with 12 short spines on the left ramus, 13 on the right. Three setae arise from the ventral margin, the first at midlength, the second at 80% length, and the third subapically. The first one is simple, the second has short dorsal and ventral setules proximally, and the third has longer, more widely spaced setules, but only ventrally. The single apical seta has short setules along the dorsal side. There are three long, biserially setulate, medial setae, the first two of which arise quite far proximally.

Discussion

Comparison

The present specimen closely resembles the only known specimen of *Synagoga paucisetosa*, a male captured at a depth of 3459 m in the central equatorial Atlantic (Grygier, 1990). That specimen was bigger than the present one, with a carapace 2.04 mm long and 1.64 mm high. Features that they uniquely share within the genus include: the general form of the antennule with the sixth segment longer than the fifth, a single spine at the base of the two setae on antennular segment 4, and three setae on antennular segment 5 (other species have more); five setae on the second exopodal segment of leg 1 (other species have more); the extreme length of the telsonic spine-like setae; and three medial setae on each furcal ramus, although there may also be as few as three in the Indian Ocean juvenile (Grygier, 1988).

A possible palisade ("row of cuticular ctenae") was observed only posteriorly and posteroventrally in *S. paucisetosa*, but the ornamentation of the carapace was examined much more closely in the new species than in any other of the genus. The anterior pit in each valve is relatively half as deep as in *S. paucisetosa* and has a different, radial pattern of internal striations. That species also has obvious gut diverticula.

At the level of detail shown by Grygier (1990), the antennules of the two species are identical except: 1) *S. millipalus* has a longer spinule row and bigger spinules on the claw; 2) the ornamentation of the two setae of the fourth segment is different (denticles along the ventral edge in *S. paucisetosa*); and 3) the sixth segment has divergent rather than parallel margins in *S. paucisetosa*. The posterior ramus of the frontal filament complex in *S. paucisetosa* is about 30% longer than the ventral ramus rather than nearly the same length, and no basal aesthetasc was observed. The tip of the oral cone lies a little more proximally relative to the thoracopods in *S. millipalus*; in fact, the new species has the least ventrally protruding oral cone in the genus.

The thoracopods are comparably slender in both species, but in *S. paucisetosa*, the

proximal exopodal segment is considerably longer than the distal one in legs 2–5, rather than the same length or shorter. The leg setation differs in that *S. millipalus* has no medial seta on the basis in leg 4 but has a medial seta on the second endopodal segment in legs 2–5, while *S. paucisetosa* has the former and lacks the latter. Also, *S. millipalus* has one exopodal seta fewer on leg 6. The lateral margin of the proximal exopodal segment bears many thin, moderately robust setae in *S. paucisetosa*, rather than the single robust seta found in the new species. With regard to leg 1 in *S. paucisetosa*, there is a discrepancy in Grygier (1990) between the illustration and the setation table; the values for positions 3 and 6–7 were inadvertently reversed in the table, so this species actually has the same exopodal setation and unarmed basis in leg 1 as *S. millipalus*.

The penis of *S. paucisetosa* could not be examined in detail, but it is relatively at least one-third smaller than in *S. millipalus*, and the flexible part of the shaft and the distal setae of the rami are relatively shorter.

The posteroventral telsonic setae are relatively somewhat longer compared to the telson and furcal rami in *S. millipalus*, and have two rather than one reported row of denticles. The furcal rami have fewer ventral spines in the new species (12–13 vs 19–20).

Carapace ornamentation

Previous studies. Four previous studies have examined the bivalved carapaces of ascothoracidans with SEM. Grygier (1988) examined the outer surface and anterior inner surface of a Tessmann's larva (presumably an ascothoracid-larva belonging to the family Lauridae) caught in plankton. Itô & Grygier (1990) examined the outer and posterior inner surfaces of another laurid ascothoracid-larva, that of *Baccalaureus falsiramus* Itô & Grygier. Jensen et al. (1994) examined the outer surface of the second-instar ascothoracid-larva of *Ulophysema oeresundense* Brattström. Finally, Grygier & Itô (in press) reported the external ornamentation of adult female *Waginella metacrinicola*, a species in a genus that exhibits a degree of morphological plesiomorphy similar to that of *Synagoga*.

Palisade. Grygier's (1988) and Itô & Grygier's (1990) laurid ascothoracid-larvae have no palisade like that of the present species. Instead they have three or more concentric, submarginal, comb-like rows of thin spines that are separate to the base. The feather-like, anterior spine arrays of these larvae are absent in *Synagoga millipalus*, and these larvae also lack guard setae, having instead some enlarged spine rows (see also the light microscopical study of a laurid ascothoracid-larva by Grygier (1992)). Grygier & Itô (in press) showed an extremely hairy valve margin, at least ventromedially, in *Waginella metacrinicola*, but no palisade per se. While posterior guard setae have been described by light microscopy in many ascothoracidans, lanceolate setae like those observed here, which are apparently independent of the spine rows, have not been noted explicitly before. The enlarged spine rows and the arrays of barbed setae in various species probably all serve to groom the natatory setae of the thoracopods and furca.

Pores. Jansen et al. (1994) noted "pores with a raised lip" and sparse setae on the carapace of larval *Ulophysema oeresundense*, a situation comparable to *Synagoga millipalus*. On the other hand, Grygier & Itô (in press) described and named several kinds of pores on the outer surface of the carapace of *Waginella metacrinicola*: "gland cones" on the flat ventral side, which are hemispherical protrusions 9–10 μm wide surrounding a collapsed tube; "pitted gland-tubes" found over the whole outer surface, which are collapsed tubes arising within a 2–4 μm wide circular pit; and "collared gland-tubes" 4–6 μm wide that are found in a precise arrangement along the medial rim of the ventral face. Furthermore, the ventral surface is covered with villus-like processes. None of these features is found in *Synagoga millipalus*. Grygier & Itô (in press) inferred that some of them may be related to the sessile habit of *W. metacrinicola*, whereby the ventral side of the carapace is attached to a host crinoid.

Pits. The pair of pits anteriorly on the inner side of each carapace valve in *S. millipalus* is almost certainly homologous to the pair of large, anteroventral carapace pores of *Waginella* spp. (see discussion of this point by Grygier (1990)). Those of *W. metacrinicola* have a lattice-like inner surface, with a pore opening in each rectangular, ridge-bounded cell of the lattice (Grygier & Itô, in press). It was impossible to see far inside the present pits with SEM, but no pores were observed except possibly in the innermost, blebby region; the parallel diagonal ridges in two sets along the outer region evidently represent a different kind of structure than the rectangular lattice. The apertures of the internal pit pores in *W. metacrinicola* are elongate ovals, almost slits, similar to pores on the external surface of the carapace in *S. millipalus*.

Other organs. The field of tiny pores found medially at the posterior angle of each carapace valve has not been noticed in any other ascothoracidan. It joins an assortment of peculiar, poorly known organs reported on the carapaces of various larvae: the anterodorsal marginal row of pits in second ascothoracid-larvae of *Parascothorax synagogoides* Wagin (Grygier, 1991), the anterodorsal patch of minute hair sensilla at the anterior angle of the carapace valve in second ascothoracid-larva of *Ascothorax gigas* Wagin (Grygier & Fratt, 1984), and the anterior reticulate with several pores observed on a laurid ascothoracid-larva (Grygier, 1992).

Lattice organs

The structures now called lattice organs would once have been included among the mysterious organs just listed, having been observed by light microscopy in several ascothoracidans. Itô & Grygier (1990) first examined them with SEM and called them "cardic organs" (from Latin *cardo*: hinge) because of their proximity to the anterior and posterior ends of the dorsal hinge (two pairs anteriorly, three posteriorly). But in various forms, and with a normally 2+3 arrangement, they are now known to be a synapomorphic feature of the Thecostraca, present in cypridiform larvae of ascothoracidans, thoracican and acrothoracican cirripedes, and rhizocephalans (Jensen et al., 1994), as well as facetotectan cyprids (Grygier, unpubl. data; P.G. Jensen & J.T.Høeg, pers. comms.).

In those few ascothoracidans yet examined closely, the lattice organs have the form of a recumbent tube in a trough; the tube is a keel rather than a free, seta-like structure (Jensen et al., 1994). *Synagoga millipalus* is the first ascothoracidan known in which the lattice organs and their keels are all in line with each other and parallel to the valve edge. In contrast, all five pairs converge posteriorly in ascothoracid-larvae of Lauridae and *Ulophysema oeresundense* (cf. Itô & Grygier, 1991; Grygier, 1992; Jensen et al., 1994). Grygier & Itô (in press) found only the anterior two pairs with SEM in adult female *Waginella metacrinicola*; they are either oriented at a high angle to the valve margin and converge anteriorly or are more or less perpendicular to the margin.

A pore opens at the posterior end of the tube (keel) in all five pairs of lattice organs in the two laurid ascothoracid-larvae and in those of *Ulophysema oeresundense*. Jensen et al. (1994) considered this arrangement to represent the plesiomorphic state in their study of lattice organs in the cyprid larvae of the Cirripedia. However, two of the lattice organs in *Synagoga millipalus* have a reverse structure, with the pore opening at the anterior end. The reversed state in the most anterior of the three rear organs is for now unique to *S. millipalus* within the Thecostraca and may be assumed to be an autapomorphy for some clade of ascothoracidans. However, Jensen et al. (1994) considered the other reversal, that of the most anterior of the five lattice organs, to be characteristic of the Thoracica and Rhizocephala. The utility of this particular feature of lattice organs in any cladistic study of the Cirripedia is now weakened, because both states occur in the outgroup Ascothoracida. The present specimen is not an ascothoracid-larva, but an adult male, and may not be strictly comparable to cyprid larvae or the ascothoracid-larva of *Ulophysema*. Nonetheless, *Synagoga* probably undergoes very little morphological change with maturation, and there is no good reason to exclude it from consideration on the grounds of non-homologous instars.

Acknowledgments

M.J. Grygier was supported by an international fellowship from the Dan Charitable Trust Fund for Research in the Biological Sciences. S. Ohtsuka acknowledges grant support from the Fujiwara Natural History Foundation and thanks the captain and crew of TRV "Toyoshio-maru" for technical assistance. Learned criticism of the SEM interpretations by P.G. Jensen and W. Klepal is appreciated.

References

- Gruvel, A. 1905. Monographie des Cirrhipèdes ou Thécostraces. Masson, Paris (reprinted 1964, A. Asher, Amsterdam), 472 pp.
- Grygier, M.J. 1983a. Revision of *Synagoga* (Crustacea: Maxillopoda: Ascothoracida). J. Nat. Hist., 17: 213–239.
- . 1983b. Ascothoracida and the unity of Maxillopoda. In: Schram, F.R. (ed.), Crustacean Phylogeny (Crustacean Issues 1), pp. 73–104. A.A. Balkema, Rotterdam.
- . 1988. Larval and juvenile Ascothoracida (Crustacea) from the plankton. Publ. Seto Mar. Biol. Lab., 33(4/6): 163–172.
- . 1990. Five new species of bathyal Atlantic Ascothoracida (Crustacea: Maxillopoda) from the equator to 50°N latitude. Bull. Mar. Sci., 46(3): 655–676.
- . 1991. Redescription, ontogeny, and demography of *Parasothorax synagogoides* (Crustacea:

- Ascothoracida), parasitic on *Ophiophthalmus normani*, a dominant ophiuroid in the bathyal basins off southern California. Proc. San Diego Soc. Nat. Hist., 6: 1–20.
- . 1992. Laboratory rearing of ascothoracid nauplii (Crustacea: Maxillopoda) from plankton at Okinawa, Japan. Publ. Seto Mar. Biol. Lab. 35(4/5): 235–251.
- & Fratt, D.B. 1984. The ascothoracid crustacean *Ascothorax gigas*: redescription, larval development, and notes on its infestation of the Antarctic ophiuroid *Ophionotus victoriae*. Antarct. Res. Ser., 41(2): 43–58.
- & Itô, T. in press. SEM-based morphology and new host and distribution records of *Waginella* (Ascothoracida). In, Schram, F.R. & Høeg, J.T. (eds.), New Frontiers in Barnacle Biology (Crustacean Issues 8). A.A. Balkema, Rotterdam.
- Itô, T. & Grygier, M.J. 1990. Description and complete larval development of a new species of *Baccalaureus* (Crustacea: Ascothoracida) parasitic in a zoanthid from Tanabe Bay, Honshu, Japan. Zool. Sci., 7(3): 485–515.
- Jensen, P.G., Moysc, J., Høeg J. & Al-Yahya, H. 1994. Comparative SEM studies of lattice organs: putative sensory structures on the carapace of larvae from Ascothoracida and Cirripedia (Crustacea Maxillopoda Thecostraca). Acta Zool. (Stockh.), 75(2): 125–142.
- Newman, W.A. 1974. Two new deep-sea Cirripedia (Ascothoracica and Acrothoracica) from the Atlantic. J. Mar. Biol. Assoc. U. K., 54: 437–456.
- Norman, A.M. 1888. On the Zoological Station at Naples. II. Report on the occupation of the table. Brit. Assoc. Adv. Sci. Ann. Rep., 1887:85–86.
- Norman, A.M. 1913. *Synagoga mira*, a crustacean of the order Ascothoracida. Trans. Linn. Soc. Lond., Zool., 11: 161–169.
- Okada, Y.K. 1926. Contribution à l'étude des Cirripèdes Ascothoraciques. II. Note sur l'organisation de *Synagoga*. Bull. Mus. Natl. Hist. Nat., 50: 69–73.
-