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Sagitta siamensis, a new benthoplanktonic Chaetognatha living in marine meadows of the Andaman Sea, Thailand

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Abstract: A new benthoplanktonic chaetognath, *Sagitta siamensis*, is described from near-shore waters of Phuket Island (Thailand), in the Andaman Sea, where it lives among submerged vegetation. It is related to the species of the "*hispida*" group. In the laboratory, specimens have been observed swimming in the sea water but also sometimes adhering to the wall of the jars, and the eggs are benthic and attached on the substratum. Their fins are particularly thick and provided with clusters of probably adhesive cells on their ventral side and edges. This is the first mention of such fins in the genus *Sagitta* but the adhesive apparatus do not resemble that found in the benthic family Spadellidae and is less evolved. A review of the morphological characteristics of the species of the "*hispida*" group is done as well as their biogeography.

Résumé : Un nouveau chaetognathe benthoplanctonique, *Sagitta siamensis*, est décrit des eaux néritiques de l'île Phuket (Thaïlande) en mer des Andaman, où il vit dans la végétation immergée. Il est proche des espèces du groupe "*hispida*". Au Laboratoire, les spécimens ont été observés nageant dans l'eau mais parfois aussi adhérant aux parois des récipients et les œufs sont benthiques, fixés sur le substratum. Leurs nageoires sont très épaisses et munies, sur leur face ventrale et sur les bords, de cellules probablement adhésives. De telles nageoires sont observées pour la première fois dans le genre *Sagitta*, mais leur système adhésif ne ressemble pas à celui de la famille benthique des Spadellidae, étant moins évolué. Une revue des caractères morphologiques et de la biogéographie des espèces du groupe *"hispida"* est présentée.

Keywords : Chaetognatha, *Sagitta*, Andaman Sea, taxonomy, biogeography.

Introduction

During the last ten years or so, many new chaetognath species (~30) have been described, most of them belonging to the deep benthoplanktonic family Heterokrohniidae (living at depths > 700 m, in the water masses immediately above the bottom) or to the benthic family Spadellidae. Planktonic species are the best known chaetognaths, and today discovery of new species essentially occurs in restricted unstudied areas where particular hydrological conditions are found. That is the case of the very shallow neritic waters not investigated during oceanographical cruises, such as those off the west coast of Thailand.

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Materials

In December 1994, one of us (TG) collected more than 100 specimens of a benthoplanktonic *Sagitta* among the seagrass beds (*Enhalus acoroides*) at Thachatchai on the North coast of Phuket Island (Thailand) in the Andaman Sea (Fig. 1). Many features of these specimens indicate that they belong to a species of *Sagitta* new to science for which the name *S. siamensis* is proposed owing to its geographical origin. Specimens have been caught by towing an Ockelmann sledge among the *Enhalus* meadows, at shallow

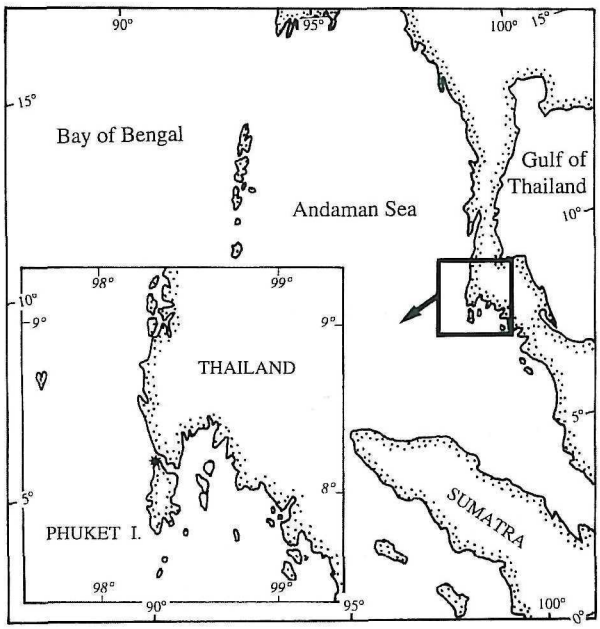

Figure 1. Aire de récolte (astérisque) de *Sagitta siamensis* n.sp. sur la côte nord de l'île Phuket (Thaïlande).

Figure 1. Sampling area (asterisk) of *Sagitta siamensis* n.sp. on the north coast of Phuket Island (Thailand).

depths of ~ 1.5m. During sampling, the sea water temperature was 30° C and salinity 31‰. Some specimens were kept alive for laboratory experimentation and some other (~ 20) preserved in 5% formalin for a systematic study.

Sagitta siamensis sp.nov.

Type locality: Thachatchai, Phuket Island, Thailand.

Material examined. Holotype: a quasi mature individual, 7.7 mm long, and one *paratype* are deposited in the National Science Museum Tokyo (NSMT-ch.26 and ch 27 respectively). Two other paratypes were presented to the Muséum national d'Histoire naturelle, Paris (UE 881).

Etymology: The specific name of this new *Sagitta* indicates its geographical origin, Siam being the old name of Thailand.

Description: Length of specimens varies from 6.2 to 7.7 mm. Body firm with large head. Tail represents 29.5 to 32.4% of body length without tail fin (Fig. 2). Anterior teeth, 6-8 at each side, slightly flattened. Posterior teeth 10-12, thin. Both anterior and posterior teeth ornamented with imbricate, longitudinal ridges; teeth tips multicuspate (Fig. 3 A-D). Hooks, 6-8, normally bent, smooth. Vestibular organs regularly mamillated, located just behind the posterior teeth (Fig. 3A, B). Eyes rounded, with a large square black pigmented area, corresponding to the pigment

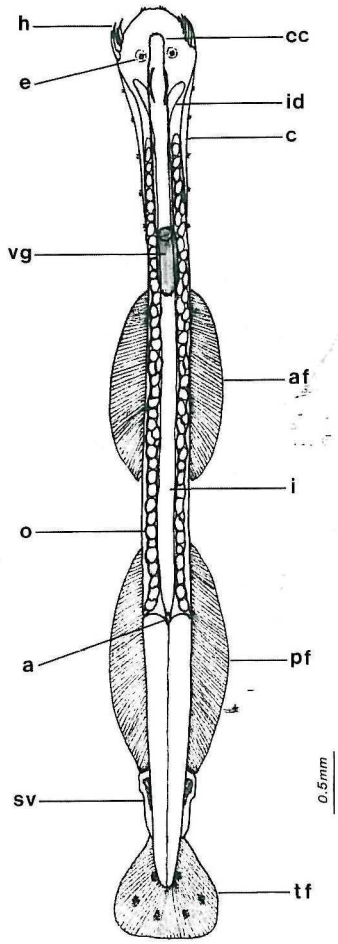

Figure 2. Habitus de *Sagitta siamensis* n.sp. (vue dorsale). a = anus, af = nageoires antérieures, c = collerette, cc = couronne ciliée, e = yeux, h = crochets, i = intestin, id = diverticules intestinaux, o = ovaires, pf = nageoires postérieures, sv = vésicules séminales, tf = nageoire caudale, vg = ganglion ventral.

Figure 2. Habitus of *Sagitta siamensis* n.sp. (dorsal view). a = anus, af = anterior fins, c = collarette, cc = corona ciliata, e = eyes, h = hooks, i = intestine, id = intestinal diverticula, o = ovaries, pf = posterior fins, sv = seminal vesicles, tf = tail fin, vg = ventral ganglion.

cell (Fig. 3E); parts of some sensory cells are seen grey-coloured against the latter. Collarette firm, from neck to beginning of ventral ganglion, thicker laterally than dorso-ventrally, with scattered sensory ciliated receptors. A few cells of collarette-like tissue are seen on the anterior part of the tail fin. Corona ciliata extending from the end of cerebral ganglion to the anterior third of the ventral ganglion (Fig. 2). In one specimen, it is constituted of two parts as it is interrupted at the level of neck. Presence of a pair of conspicuous intestinal diverticula. Both lateral and caudal fins particularly thick and rigid, totally covered with rays. Their ventral side and edges provided with patches of

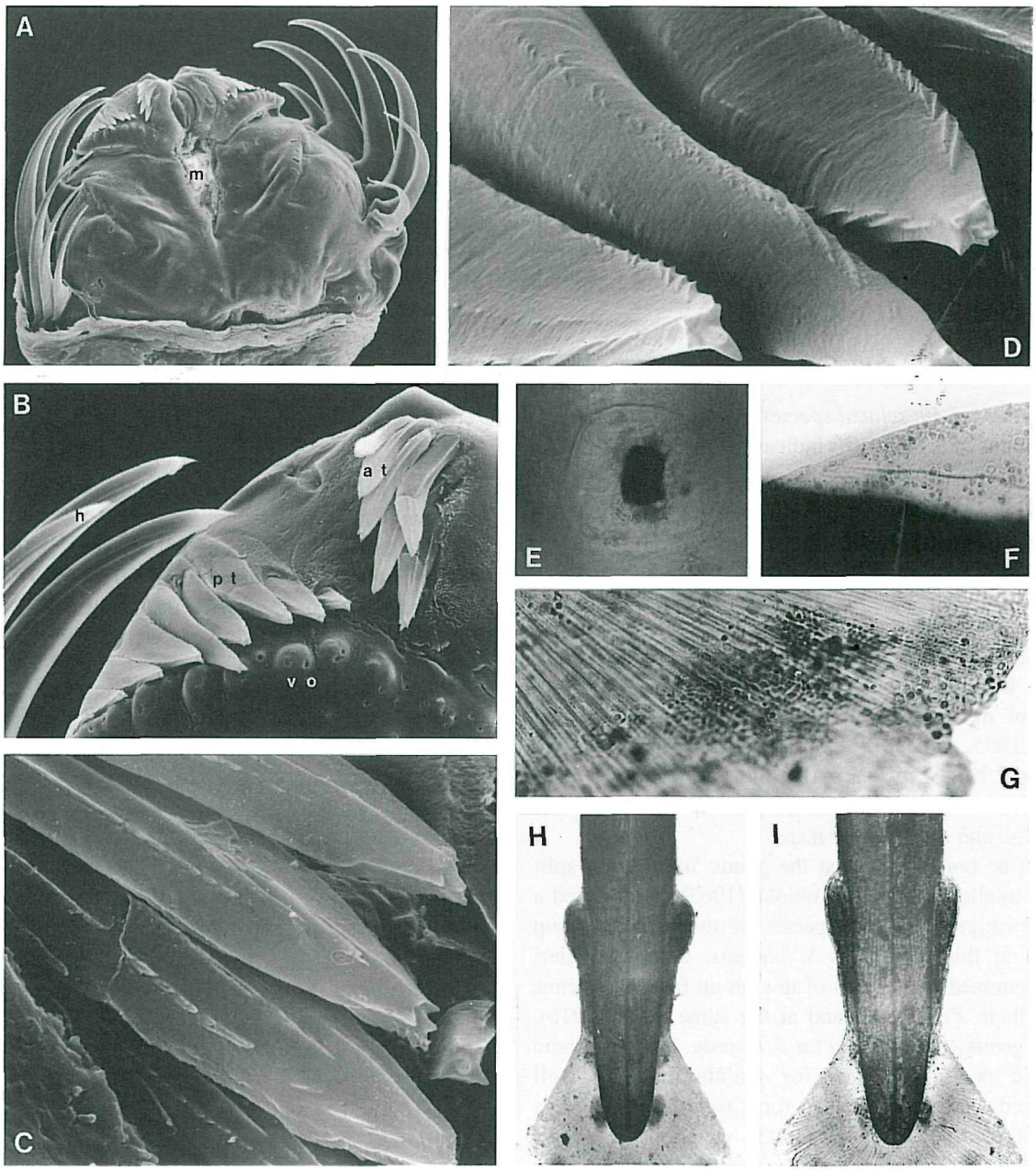

Figure 3. *Sagitta siamensis* n.sp. A-D : photographies au MEB de la face ventrale de la tête (A), détails de l'armature de la tête (B), dents antérieures (C) et postérieures (D). E-I = photographies photoniques de l'œil droit (E), de cellules (adhésives ?) sur les nageoires postérieures (F, G) et de vésicules séminales à différents stades de maturité (H, I). at = dents antérieures, h = crochets, m = bouche, pt = dents postérieures, vo = organes vestibulaires. Grossissement : A x 100, B x 520, C x 2400, D x 2850, E x 250, F x 100, G x 180, H et I x 50.

Figure 3. *Sagitta siamensis* n.sp. A-D: SEM photographs of ventral side of head (A), details of head armature (B), anterior teeth (C) and posterior teeth (D). E-I = light photographs of the right eye (E), (adhesive ?) cells on posterior fins (F, G) and seminal vesicles at different stages of maturity (H, I). at = anterior teeth, h = hooks, m = mouth, pt = posterior teeth, v o = vestibular organs. Magnification: A x 100, B x 520, C x 2400, D x 2850, E x 250, F x 100, G x 180, H and I x 50.

(adhesive?) cells (Fig. 3F, G). Anterior fins, beginning at the level of the posterior end of the ventral ganglion or slightly before, as wide as posterior fins. Posterior fins longer than the anterior ones, extending to the seminal vesicles (Fig. 2). They lay much more on the tail (>2/3) than on the trunk; ratio T/C (part on trunk/part on caudal segment or tail) =

0.42 to 0.49. Interval between anterior and posterior fins is 6 to 6.9% of body length and 1/4 of the length of posterior fins. The anterior and posterior halves of each lateral fin are roughly symmetrical.

Ovaries long, reaching almost the level of neck, but no specimen available for the systematics study was fully mature (Fig. 2). Ova arranged dorsoventrally in one or two rows. The seminal vesicles touch both the posterior fins and the tail fin. Each vesicle consists of a swollen anterior part often subrectangular and a narrower but longer posterior sperm reservoir (Fig. 3H, I).

Discussion

Comparisons with related species

The habitus of *S. siamensis* indicates that it belongs to the "*hispida*" group established by Alvariño (1965, 1967). Some authors (Silas and Srinivasan, 1967; Dallot, 1971) have added *S. bombayensis* Lele and Gae, 1936 to this group, but the location of its anterior fins, beginning far behind the ventral ganglion, and the absence of intestinal diverticula are not consistent with the features of the group. On the other hand, *S. erythraea* described from a single specimen (Casanova, 1985) can now be considered as a member of this group which thus comprises: *S. hispida* Conant, 1895, *S. ferox* Doncaster, 1903, *S. robusta* Doncaster, 1903, *S. tokiokai* Alvariño, 1967, *Sagitta ferox* f. *americana* Tokioka, 1959, *S. galerita* Dallot, 1971, *S. erythraea* and *S. siamensis* n.sp.

It must be pointed out that the genus *Sagitta* was split into nine smallest genera by Tokioka (1965) who created a genus *Parasagitta* for the species of the *hispida* group described at this date, plus *S. elegans*. Later on, Bieri (1991a) removed the species of this group from this genus to name them *Ferosagitta* and at the same date (1991b), created a genus *Adhesisagitta* for *S. hispida*. Such an erratic taxonomic position argues for maintaining the well charaterized genus *Sagitta* s.l. As for *S. robusta* and *S. ferox*, badly described by Doncaster (1903), we adopt Alvariño's definitions (1962) which seem to be the most used in papers dealing with systematics and ecology.

Three specific characters allow to differentiate immediately the new species from the other species of the *hispida* group: the thickness and rigidity of fins (see below, adaptation to habitat), the large part of posterior fins on tail, and the original square pigment cell. *Sagitta siamensis* is more particularly related to *Sagitta ferox* f. *americana* to *S. galerita* and *S. erythraea*, owing to the angular aspect of the anterior part of the seminal vesicles. Indeed, in *S. robusta* this part of the mature vesicles is rounded and very prominent (Fig. 4A) while in the three other species, such as *S. ferox* (Fig. 4B), there is no distinct anterior part. Although the shape of the seminal vesicles is roughly the same in the four related species, small differences are noticeable. In *S. galerita* (Fig. 4C, D) and *S. ferox* f. *americana*, they are surmounted by a swelling of epidermis, but in the former, it is clearly apart from the vesicles while in the latter the swelling totally fills the space between the vesicles and the body. This swelling is absent in *S. siamensis* (Fig. 3H, I) and *S. erythraea* (Fig. 4E), but in the latter the seminal vesicles are small and well separated from the tail fin by a length equal to their own length; moreover, remnants of a thick foamy epidermis tissue are seen between one vesicle and the tail fin.

As previously said, the position of the posterior fins on the body is characteristic in *S. siamensis*. Indeed, more than 2/3 of their length is on the tail, so that the ratio T/C is ≤ 0.49. For *S. galerita*, this ratio is 0.55 to 0.66, and for *S. ferox* f. *americana*, Tokioka (1959) only indicated that more than half of the fins length lie on the tail. This ratio is unknown in *S. erythraea*.

The aspect of the pigment cell of the eyes immediately differenciates *S. siamensis* (Fig. 3C) from its closest relatives. In *S. ferox* f. *americana*, Tokioka (1959) said that it is "rather large, slightly elongate and curved", but unfortunately he did not give a drawing. In *S. galerita* from Tuléar (Madagascar), it looks like a kind of stylized lily flower with stumpy branches (Fig. 4F); in specimens from the Gulf of Aqaba, the pigment cell is slightly more elongated antero-posteriorly (Fig. 4G). In both cases, two bundles of fiber-like structures (distal segments of sensory cells?) are seen against the outer anterior and posterior sides of the pigment cell, and two pale grey pigmented areas (conical bodies of other sensory cells?) against its inner side. In *S. erythraea* (Fig. 4H), the pigment cell looks like that of *S. galerita* from Tuléar.

The extent of the corona ciliata on the dorsal side of the trunk is also different. In *S. ferox* f. *americana*, it is about one and a half times as long as the head, while it is two and a half in *S. galerita*, reaching thus the level of the beginning of the ventral ganglion; it has not been observed in *S. erythraea*. It is longer in *S. siamensis* compared to the other two species.

Lastly, the anterior teeth are in number often equal to or more numerous than, the posterior teeth in *S. ferox* f. *americana,* while they are always less numerous than the posterior teeth in the other species of the group. The tip of posterior teeth is different, when observed with SEM, from *S. galerita,* where it consists of a small smooth area perforated with a hole and surrounded by a fringe of setae-like structures (Fig. 4I, J); it is unknown in *S. ferox* f. *americana* and *S. erythraea*. The posterior teeth of *S. galerita* are particularly interesting. Indeed, they seem to be hollow, a peculiarity which has never been observed previously (Furnestin, 1982; Bone *et al.*, 1983; Thuesen & Bieri, 1987). This may represent an evolutionary step towards more efficient

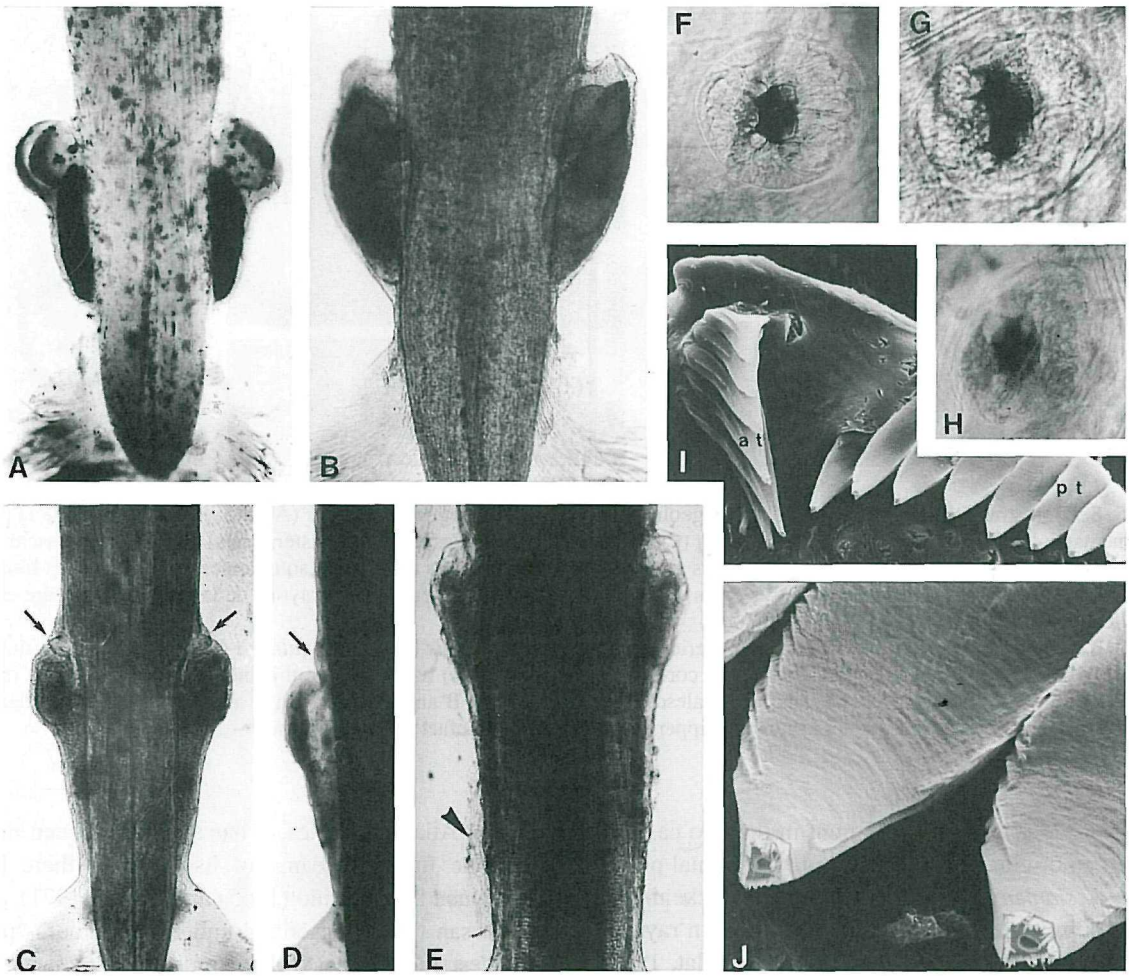

Figure 4. Caractéristiques morphologiques de *Sagitta robusta* (A), *S. ferox* (B), *S. galerita* des eaux malgaches (C, F, I, J) et du golfe d'Aqaba (D, G), et *S. erythraea* (E, H) : photographies photoniques des vésicules séminales (A-E) et des yeux du côté gauche (F-H) ; photographies au MEB des dents (I) et de l'extrémité distale des dents postérieures (J). Les flèches montrent l'épaississement épidermique surmontant les vésicules séminales en C et D et la tête de flèche la collerette entre la vésicule séminale et la nageoire caudale en E. at = dents antérieures, pt = dents postérieures. Grossissement : A-E x 50, F-H x 250, I x 480, J x 2850.

Figure 4. Morphological characteristics of *Sagitta robusta* (A), *S. ferox* (B), *S. galerita* from the waters of Madagascar (C, F, I, J) and the Gulf of Aqaba (D, G), and *S. erythraea* (E, H): light photographies of seminal vesicles (A-E) and left eyes (F-H); SEM photographs of teeth (I) and tip of posterior teeth (J). Arrows indicate the swelling of epidermis above the seminal vesicles in C and D and arrowhead the collarette tissue between the seminal vesicle and tail fin in E. at = anterior teeth, pt = posterior teeth. Magnification : A-E x 50, F-H x 250, I x 480, J x 2850.

delivery of venom by chaetognaths. A full account of this subject can be found in Thuesen (1991).

Adaptation to a benthoplanktonic habitat

Sagitta siamensis is a benthoplanktonic species since one of us (TG) observed that specimens kept in the laboratory swim but also are sometimes attached by their ventral side to the wall of glass jars, like *Spadella cephaloptera*. Moreover, like in this species too, eggs are laid on the wall of the jars. *Sagitta hispida* is the only other *Sagitta* known to attach its eggs on the substratum and to live near the bottom in west tropical Atlantic areas with dense marine vegetation. That is why Bieri (1991a) said it was "quasi-planktonic", a way of life that we call benthoplanktonic. Egg laying in chaetognaths has been reviewed by Pearre (1991) and it appears that most of the planktonic species have pelagic eggs, which are shed either separately (*Sagitta*) or embedded in a gelatinous mass (*Pterosagitta draco*). Some other species keep their eggs in a marsupium (*Eukrohnia*).

The particular way of life of *S. siamensis* is probably reflected in their curious thick and rigid fins, which contrast to the thin and soft fins of the related truly planktonic species (Fig. 5A, B). Indeed, the benthic species of the family Spadellidae are all characterized by thick and rigid

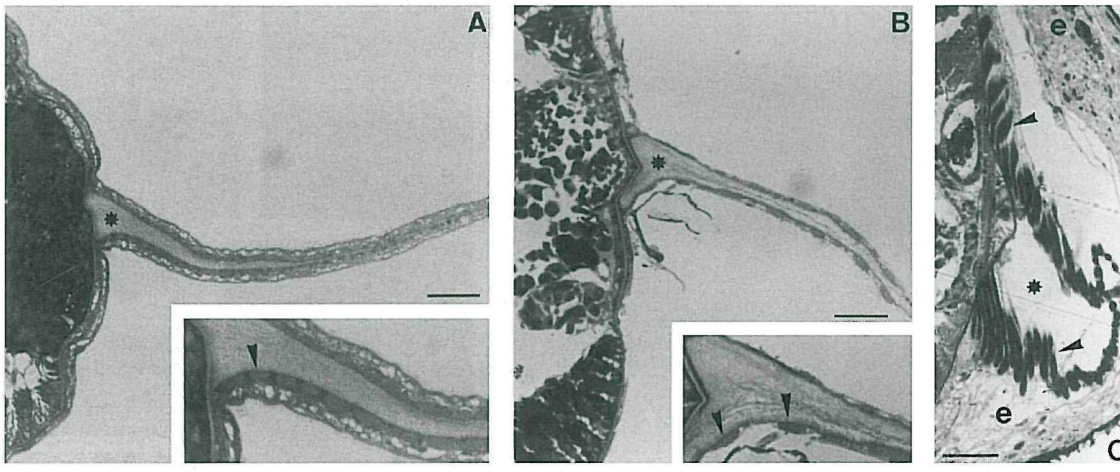

Figure 5. Sections transversales au niveau d'une nageoire postérieure chez *Sagitta siamensis* (A) et *S. galerita* (B) et de la partie postérieure d'une nageoire latérale chez *Paraspadella gotoi* (C). Noter que 1/ l'axe des nageoires (astérisques) a la même épaisseur en A et B alors que le corps est nettement plus massif en B, 2/ les rayons des nageoires (têtes de flèches) sont coalescents en A mais libres en B et C (encarts en A et B), et 3/ l'épiderme (e) est très épais en C (l'espace entre l'épiderme et les rayons de la rangée supérieure est un artéfact). Échelles = 50 µm.

Figure 5. Transverse sections at the level of a posterior fin in *Sagitta siamensis* (A) and *S. galerita* (B) and of the posterior part of a lateral fin in *Paraspadella gotoi* (C). Note that 1/ the core of the fins (asterisks) has the same thickness in A and B while the body is obviously stouter in B, 2/ fin rays (arrowheads) are coalescent in A but free in B and C (inserts in A and B), and 3/ the epidermis (e) is very thick in C (the space between the epidermis and upper set of rays is an artefact). Bars = 50 µm.

fins. But the rigidity of fins is different in the two cases. It results from an original coalescence of the proximal part of the rays in *S. siamensis* and to an important thickening of the epidermis in spadellids (Fig. 5B, C) where fin rays are free as in planktonic chaetognaths (Duvert & Salat, 1990). Moreover, on the ventral side and edges of fins of *S. siamensis*, clusters of large cells with large nuclei are seen (Fig. 3F, G), differing from both patches of sensory cells and from epidermal cells, commonly found on most chaetognath species. These large cells do not exist on the fins of the planktonic related species that we observed, *S. galerita*, *S. hispida* from the Gulf of Guinea, *Sagitta robusta* and *S. ferox*, and they probably have an adhesive function. *Sagitta siamensis* is not a truly benthic species as are species of spadellids. Its adhesive apparatus is not as well developed as in *Spadella* (Fig. 6A-C), where numerous adhesive papillae are scattered over the major part of the ventral body surface, but the thickening and strengthening of its fins appear as a first step in adaptation towards a benthic habitat. It must be pointed out that we have not observed such a trend in the specimens of *S. hispida* from the Gulf of Guinea, and that this feature has not been mentioned in specimens from the west tropical Atlantic often observed on seagrass.

Taxonomy and Biogeography

All the species of the *"hispida"* group but one are found in the tropical Indo-Pacific. Indeed, *S. hispida* is typically a tropical Atlantic species. It has sometimes been mentioned from the Indian Ocean, but its presence there has been questioned by Alvariño (1965) and Dallot (1971). Silas and Srinivasan (1968) described under this name a species off the West Indian coast which indeed might be *S. hispida*. Nevertheless the abundance of *S. hispida* is surprizing (558 specimens from 27 stations) as well as the absence of *S. neglecta*, a species common in this area, so that a misidentification cannot be ruled out. All the species of the *"hispida"* group are more or less related and their taxonomic status has been lengthily debated. *Sagitta robusta* and *S. ferox* have only been clearly separated in 1962 by Alvariño. Recently Bieri (1991) suggested that *S. galerita* might be a variant of *S. robusta* in spite of the fact that differences between them have been well established by Dallot (1971). Since then, *S. galerita* and *S. robusta* have been found together on one station in the middle of the Red Sea and in the Malagasy waters, off Tulear (Casanova, 1985 and unpublished data). Photographs of their mature seminal vesicles (Fig. 4A, C, D) undoubtedly prove the existence of two distinct species. Besides *S. ferox* f. *americana* has been synonymized with *S. robusta* by Alvariño (1962) - since Tokioka (1959) confused *S. robusta*, and *S. ferox* - but Dallot (1971) pointed out striking differences between the two species. Moreover, according to Dallot *S. ferox* f. *americana* is related to *S. galerita* and both species might be subspecies of a single

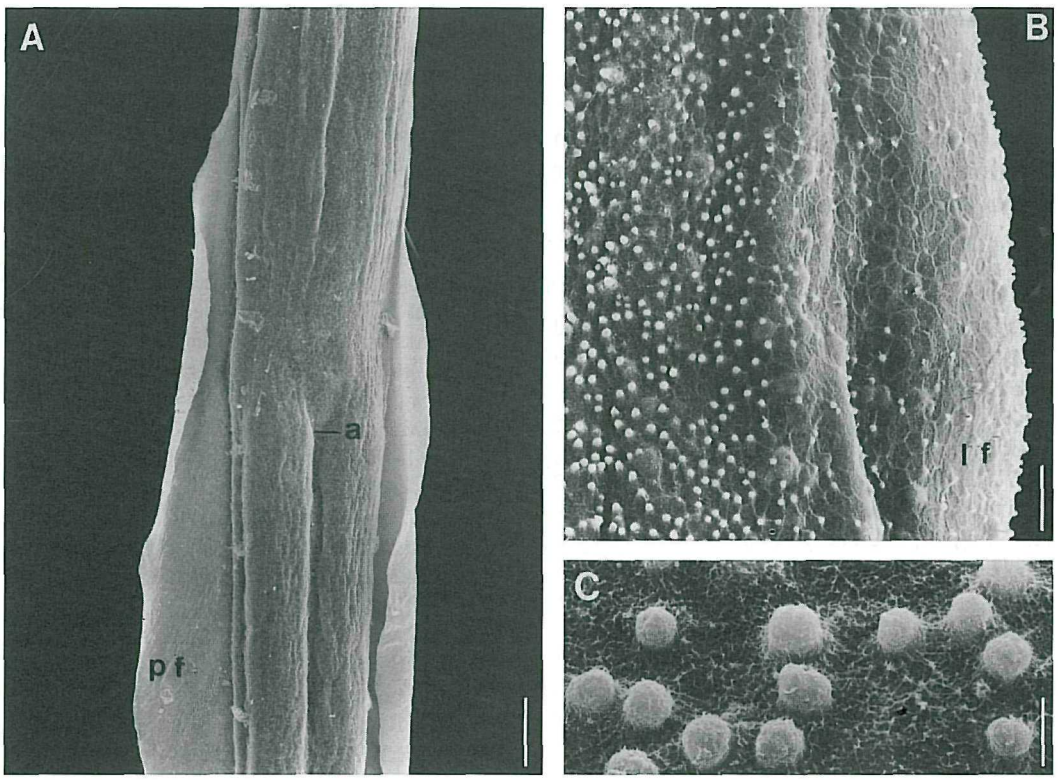

Figure 6. Observations au MEB de la face ventrale de *Sagitta siamensis* (A) et *Spadella cephaloptera* (B et C). A. Tronc et région caudale ; absence de papilles adhésives. B. Région caudale avec de nombreuses papilles adhésives. C. Agrandissement des papilles adhésives. a = anus, lf = nageoire latérale, pf = nageoires postérieures. Échelles : A = 100 µm, B = 25 µm, C= 5 µm.

Figure 6. SEM observations of ventral side of *Sagitta siamensis* (A) and *Spadella cephaloptera* (B and C). A. Trunk and tail region; no adhesive papillae are found. B. Tail region with numerous adhesive papillae. C. higher magnification of adhesive papillae. a = anus, lf = lateral fin, pf = posterior fins. Bars : A = 100 µm, B = 25 µm, C = 5 µm.

species which then would be named *S. americana* (Tokioka, 1959). Further studies are needed to resolve definitely the relationships of this group of species, but it is now established that *S. ferox* f. *americana* is distinct from *S. robusta* (see Dallot, 1971). It is also different from *S. galerita* as shown by Dallot (1971): aspect of the pigment cells of eyes, length of corona ciliata and number of anterior teeth. These differences are as marked as those separating *S. erythraea* and *S. siamensis* from *S. galerita*. So, *S. ferox* f. *americana* is probably a "good species" as suggested by Dallot.

Sagitta ferox and *S. robusta* are more or less widely distributed in the tropical waters of the Pacific and the Indian Oceans (Alvariño, 1962, 1969). All the others species from these oceans have restricted neritic ranges. *Sagitta galerita*, the best known, is said to be outer neritic in the Nosy-Bé area (north of Madagascar), since it is rare in samples far offshore and near the shore and abundant above 100 m depth (Dallot, 1971), where the salinity is the highest (~35‰). It has the same distribution in the Red Sea where it is abundant in the shallow (~50m) and hypersaline (~42‰) waters of the Gulf of Suez (Ducret, 1973), and accidentally found in the open sea (Casanova, 1985); specimens from the Gulf of Aqaba are the largest (12.5mm) so far recorded (Casanova, 1988) nevertheless they have undoubtedly all the features of *S. galerita*. *Sagitta americana* might be the East Pacific twin species of *S. galerita*, found between California and Peru, a more oceanic species caught between 300 and 0m (Shellback Expedition 1952). *Sagitta erythraea* is perhaps a near-shore species from the Red Sea, since the single known specimen has been caught in the open sea. *Sagitta siamensis* occupies very shallow waters and exhibits adaptative characters to a benthoplanktonic habitat: thick fins, provided with probably adhesive cells, and egg laying on the substratum. This last feature represents the sole adaptation observed in some west Atlantic populations of *S. hispida* living in a habitat similar to that of *S. siamensis*.

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