

Egg Pouches and Other Reproductive Structures in Pelagic Chaetognatha¹

ANGELES ALVARÍO²

ABSTRACT: Some specimens of *Eukrobnia bathyantartica* David from the collections obtained by the United States Antarctic Research Program were observed which had marsupial sacs full of eggs, and hanging from the opening of the oviducts. The eggs in the sacs, in various specimens, appeared at different stages of development, from the gastrular stage up to the eclosion of the larvae.

THE BREEDING PATTERN in Chaetognatha either is seldom mentioned or is hidden in the pertinent literature among other subjects related to the group. For this reason a review of the breeding characteristics merits specific attention.

Norgaard (1905) was the first to indicate the brood sacs in *Eukrobnia*, when he stated: "In samples from the Vest Fiord there were specimens with eggbags. The wider part of the fin was bent downwards, this forming a hollow in which the eggs lay tightly pressed together."

Similarly, Ritter-Zahony (1910) observed: "Die Eier waren vollständig aus den Ovarien ausgetreten und bildeten zwei pflaumenförmige, von einer gallertigen Hülle umgebene Ballen am Rücken des Tieres." He included illustrations of this sac for *E. hamata* (Möbius). However, considering the extension of the laminar part of the fin, the species probably corresponded to *E. bathypelagica* Alvaríño. Ritter-Zahony (1910) also explained: "Diese Eiersäckchen lagen nebeneinander zu einem am Rumpf-, drei Vierteln am Schwanzabschnitt."

Ritter-Zahony (1911), describing *E. fowleri*, stated: "Eiersäckchen, die wie bei *E. hamata* von den eigentümlich deformierten Seitenflossen umhüllt waren." He also noticed small brooding sacs in *E. hamata* from the Antarctic. These specimens probably belonged to *E. bathyantartica* David.

Kuhl (1928) made similar observations for *Eukrobnia*.

At Point Barrow, Alaska, MacGinitie (1955) observed two mature specimens of *E. hamata* 40 mm long "carrying young in a marsupium formed by folding of the posterior lateral fins." He also explained that when the material was brought to the laboratory "some of the young, which were 3 mm long, began escaping from the marsupium."

Tchindonova (1955) stated that the majority of the specimens of *E. fowleri* were sexually mature, with ovarian sacs that had already ruptured. This probably refers to the brooding sacs.

David (1958) indicated that one specimen of *E. bathyantartica* had "an egg-shaped opaque structure appended to the oviduct." He also suggested that in *E. bathyantartica* and *E. fowleri* "the seminal vesicles function as spermatophores and are attached intact to the external opening of the oviducts by a fine tube which is probably the vas deferens." David (1958) was unable to find a single specimen of *E. fowleri* or *E. bathyantartica* with mature seminal vesicles, and thus he considered the sacs observed attached to the oviducts to be remains of the seminal vesicles. These small sacs, which are also illustrated in David's figures 2a and 3c might be the brooding sacs beginning to develop.

Ghirardelli (1959a) was also able to observe specimens of *E. bathyantartica* and explained: "le spermatofores hanno la forme di un fiasco, limitato esternamente da una membranella anista resistente. Questa membrana forma un prolungamento (simile appunto al collo di un fiasco) che si trova infilato nell' orificio genitali femminile, i cui bordi si presentano assai rilevati.

¹ Contribution from the Scripps Institution of Oceanography, La Jolla, California. These studies have been supported by the Marine Life Research Program, the Scripps Institution's component of the California Cooperative Oceanic Fisheries Investigations; and by the National Science Foundation (NSF GB-2861). Manuscript received September 15, 1967.

² Scripps Institution of Oceanography, La Jolla, California 92037.

In un solo esemplare la spermatofore era intera; in altri, invece, soltanto la membranella lacerata sporgeva dagli orifici genitali. Nessuno degli esemplari esaminati ha purtroppo le vescicole seminali mature a ciò impossibile ogni supposizione sul come si formino le spermatofore."

It is unfortunate that neither David (1958) nor Ghirardelli (1959a) studied the structure of these sacs or their contents to ensure identification. Ghirardelli (1959b), commenting on the sac with mature eggs in *Eukrohnia*, stated, "le poche uova devono essere fornite di notevole quantità di materiali di riserva ed in oltre protette nella particolare tasca incubatrice."

Alvariño (1962), when first describing *E. bathypelagica*, stated, "the fins are broadest at the tail region, where they bend to the dorsal side. . . . This phenomenon is incipient in *E. hamata* and *E. fowleri*, but in *E. bathypelagica* is more conspicuous, as this part of the fin is broader." The species of *Eukrohnia* studied by Alvariño in 1962 did not include *E. bathyantartica*. She also stated for *E. bathypelagica*, "The laminar part of the lateral fins bends to the dorsal side, which helps drive the spermatozoa into the oviducts, and probably also bears the newly hatched eggs."

Schilp (1941) referring to *E. hamata* observed, "The ovaries project outside the body. The cause of this abnormality is unknown to me." The iridescent membranous funnels at the openings of the oviducts which he mentioned for *E. richardi* Germain and Joubin (probably *E. fowleri*) might be remnants of the incubatory sacs.

Alvariño (1967, 1968) illustrated some pieces of a saclike remnant hanging from the oviduct of *E. fowleri*. Dawson (personal communication) observed a marsupial sac filled with eggs hanging from the oviducts of specimens of *E. bathypelagica* collected at the ice-cap region of the Arctic.

Personal observations on specimens of *E. bathyantartica* from the antarctic and subantarctic regions, collected recently by the R. V. "Eltanin" during the United States Antarctic Research Program (U.S.A.R.P.), detected the sac containing eggs protruding from the opening of the oviducts. The brood sac (marsupial sac or brooding pouch) appeared of different sizes in various specimens, indicating various

stages of development. The mature eggs in this marsupial sac were observed at different stages of development, from the formation of the blastomeres to the various phases of development of the embryos, up to the larval stage ready for eclosion. Some specimens showed remnants of the sac hanging from the oviducts. Those specimens presented one sac at each side, and the widest part of the lateral fins was bent dorsally covering more or less completely the marsupial sacs.

The brooding phases could be outlined as follows: Stage I, brood sac developing (Fig. 1A); Stage II, brood sac filled with mature eggs, up to gastrula; Stage III, brood sac with eggs containing embryos in a single coil (Fig. 1B); Stage IV, brood sac with eggs containing double coiled embryos; Stage V, brood sac broken after the eclosion of the larvae (Fig. 1C).

The illustrations were obtained using the stereomicroscope with the drawing tube attachment.

In the illustrations (Fig. 1) the seminal vesicles are clearly visible, evidence that David's observation (1958) that "the 'ruptured sacs' attached to the oviduct were seminal vesicles," was an erroneous assumption.

Tokioka (1939), when describing *Bathyspaddella edentata*, indicated the presence of a "capsula-like opening at the seminal receptacle"—a small bag at the opening of the oviducts. This might have been related to the brood sacs beginning to develop.

Ritter-Zahony (1910) explained that in the genus *Krohnia* brooding sacs are not present. However, Schilp (1941) noticed small membranous sacs at level with the trunk-tail septum in *K. subtilis* (Grassi).

Sanzo (1937) observed the pelagic ootheca of *Pterosagitta draco* (Krohn) containing mature eggs. The gelatinous substance of the ootheca protects both the eggs and larvae from the various physico-chemical changes until eclosion. In the Straits of Messina, this author found gelatinous colonies 6.0 to 6.4 mm in diameter, with spherical transparent eggs 0.3 to 0.4 mm in diameter.

Hertwig (1880) observed free deposition of eggs in *Sagitta bipunctata* Quoy and Gaimard and in *S. serratodentata* Krohn.

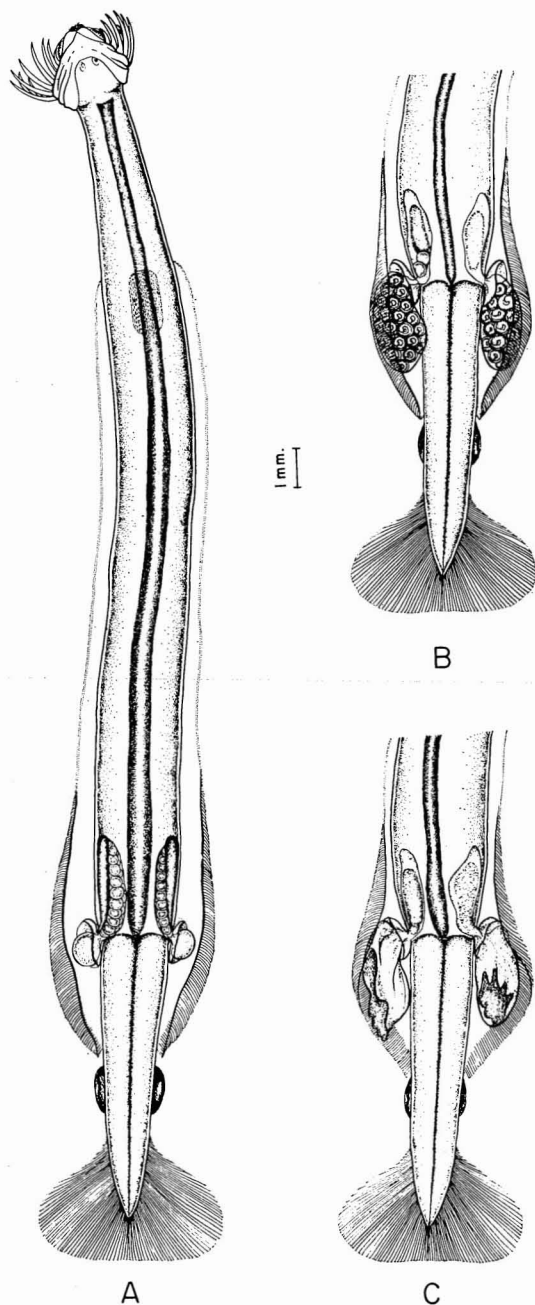


FIG. 1. *Eukrobnia bathyantartica*. A, Dorsal view of a full mature specimen; the ova arranged in two dorso-ventral rows; brood sac incipient. B, Posterior part, dorsal view; marsupial sacs (brood sacs) filled with eggs containing embryos in a single coil (Stage III). C, Posterior part, dorsal view; brood sac broken.

Conant (1896) witnessed the egg laying of *S. hispida* Conant at Beaufort, North Carolina. The eggs remained 20 to 30 minutes in each oviduct while a jelly coat thickened around each of them. They were pushed out by ovarian contraction and issued in two linear rows (one for each oviduct), totalling from 60 to 70 eggs.

Stevens (1910) observed the free discharging eggs in *S. elegans* Verrill. Huntsman and Reid (1921) found eggs of *S. elegans*, in various stages of development, free in the plankton of the Bay of Fundy and the Gulf of St. Lawrence.

Ghirardelli (1954) stated, "Anche le Sagitte depongono uova pelagiche spesso riunite in piccoli ammassi gelatinosi, talvolta però anche isolate."

Murakami (1959) observed in the laboratory specimens of *S. crassa* Tokioka in the process of free spawning of eggs. Elian (1960) observed eggs of *S. setosa* J. Müller and *S. euxina* Moltchanoff free in the plankton from the Black Sea.

Thorson (1936), Werenberg-Lund (1947), and MacGinitie (1955) suggested that the arctic animals show a tendency to brood their eggs or to provide some other method of protecting them until the embryos, the young larvae, or young animals develop. Ghirardelli (1959b) made similar observations for both the arctic and antarctic Chaetognatha. However, the species of *Eukrobnia* possess the brood pouch, and have world wide distribution (except *E. bathyantartica* which is mainly restricted to the antarctic-subantarctic regions), inhabiting different depths. The temperatures in the regions inhabited by the species are in many cases similar to those encountered in the Bay of Fundy or the Gulf of St. Lawrence, where free eggs of *S. elegans* at various stages of development were observed (Huntsman and Reid, 1921).

Thus it appears that the eggs of the species of chaetognaths belonging to the genus of highest evolutionary rank are probably better equipped for survival, either by means of the chemical composition of the vitellus or by the nature of the involucrum of the egg.

Table 1 is a summary of the breeding characteristics of the Chaetognatha which may have some evolutionary significance.

I wish to express my appreciation to Professor

TABLE 1
COMPARISON OF BREEDING CHARACTERISTICS OF SIX GENERA OF CHAETOGNATHA

GENERA	GENERIC NOTATIONS	BREEDING CHARACTERISTICS
<i>Eukrobnia</i>	One pair of fins (from tail to ventral ganglion); one pair of sets of teeth	Brood sac or marsupium
<i>Bathyspadella</i> ?	One pair of rayed fins (from tail to near the ventral ganglion); no teeth	Probably as in <i>Eukrobnia</i>
<i>Krobnitta</i>	One set of paired fins (from tail to posterior part of trunk); anterior pair of sets of teeth	Somewhat similar to <i>Eukrobnia</i>
<i>Heterokrobnia</i>	One set of paired rayed fins (from tail to level of posterior end of ventral ganglion) with a constriction about mid-length; two pairs of sets of teeth	Unknown
<i>Pterosagitta</i>	One set of paired fins (from tail to level of posterior septum); trunk covered by thick cuticulae (collarette); two pairs of sets of teeth	Pelagic jelly ootheca
<i>Sagitta</i>	Two sets of paired fins; two pairs of sets of teeth	Free eggs covered by thick involucre

M. W. Johnson for reading the manuscript, and for his valuable advice and encouragement.

REFERENCES

- ALVARIÑO, A. 1962. Two new Pacific Chaetognatha; their distribution and relationships to allied species. *Bull. Scripps Inst. Oceanogr.* 8(1):1-50.
- 1967. The Chaetognatha of the NAGA Expedition (1959-1961) in the South China Sea and the Gulf of Thailand. Reports of the NAGA Expedition, vol. 4, pp. 1-197.
- 1968. Quetognatos del Atlántico. Distribución y notas asenciales de Sistemática. *Trabajos Inst. Español Oceanografía*. In press.
- CONANT, F. S. 1896. Notes on the chaetognaths. *Johns Hopkins Univ. Circ.* 15(126):82-85.
- DAVID, P. M. 1958. A new species of *Eukrobnia* from the southern ocean with a note on fertilization. *Proc. Zool. Soc. London* 131(4):597-606.
- ELIAN, L. 1960. Observations systematiques et biologiques sur les Chaetognathes qui se trouvent dans les eaux Roumaines de la Mer Noire. *Rapp. Comm. int. Mer Mediterranée* 15(2):359-366.
- GHIRARDELLI, E. 1954. Sulla biologia della riproduzione in *Spadella cephaloptera* Bush (Chaetognatha). *Mem. R. Accad. Sci. Ist. Bologna, Cl. Sci. Fis., Ann.* 242, ser. 11(1):3-19.
- 1959a. Habitat e biologia della riproduzione nei Chaetognati. *Arch. Oceanogr. Limnol.* 11(3):1-18.
- 1959b. L'apparato riproduttore femminile nei Chaetognati. *Accad. Naz. dei XL, ser. 4*, 8:1-46.
- HERTWIG, O. 1880. Die Chaetognathen, ihre Anatomie, Systematische und Entwicklungsgeschichte. Eine Monographie. *Jena. Zeitschr. Naturw.* 14 (N.F. bd. 7):196-302.
- HUNTSMAN, A. G., and M. E. REID. 1921. The success of reproduction in *Sagitta elegans* in the Bay of Fundy and the Gulf of St. Lawrence. *Trans. Roy. Canadian Inst.* 13(2):99-112.
- KUHL, W. 1928. Chaetognatha. *Tierwelt der Nord- und Ostsee* 7(1):1-24.
- MACGINITIE, G. B. 1955. Distribution and ecology of the marine invertebrates of Point Barrow, Alaska. *Smiths. Misc. Coll.* 128(9):1-201.
- MURAKAMI, A. 1959. Marine biological study on the planktonic chaetognaths in the Seto Inland Sea. *Bull. Naikai Reg. Fish. Research Lab.* 12, Contrib. 81,86, pp. 1-186.
- NORDGAARD, O. 1905. Hydrological and Biological investigations in Norwegian Fiords. *Bergens Museum Marine Investigations. Chaetognatha*, p. 46.
- RITTER-ZAHONY, R. 1910. Die Chätognathen. *Fauna Arctica* 5(1):249-288.

- 1911. Revision der Chätognathen. Deutsche Südpolar-Expedition, 1901–1903, 13, Zool. 5:1–71.
- SANZO, L. 1937. Colonia pelagica di uova di Chetognati (*Spadella draco* Krohn). Mem. R. Com. Talassogr. Ital. 239:1–6.
- SCHILP, H. 1941. The Chaetognatha of the SNELLIUS Expedition. Temminckia 6:1–99.
- STEVENS, N. M. 1910. Further studies on reproduction in *Sagitta*. J. Morphol. 21(2):279–319.
- TCHINDONOVA, J. G. 1955. Chaetognatha of the Kurile-Kamchatka Trench. Trudy Inst. Oceanol. 12:298–310. (In Russian.)
- THORSON, G. 1936. The larval development, growth, and metabolism of arctic marine bottom invertebrates. Medd. Grønland 100(6): 1–155.
- TOKIOKA, T. 1939. Three new Chaetognatha from Japanese waters. Mem. Imperial Marine Observatory, Kobe, Japan 7(1):129–139.
- WESENBERG-LUND, E. 1947. Syllidae (Polychaeta) from Greenland waters. Medd. Grønland 134(9):1–58.