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FROM PIPEFISH TO SEAHORSE — A STUDY OF PHYLOGENETIC RELATIONSHIPS

By

EARL S. HERALD

Steinhart Aquarium, California Academy of Sciences

Valuable information about the relationships within the pipefish and seahorse family, Syngnathidae, can be obtained by careful study of the brood pouch. As is well known, it is the syngnathid male, and not the female, that carries the eggs during incubation. Depending upon the subfamily and genus, the eggs may be attached to the underside of either the abdomen or the tail. They may be attached loosely, imbedded singly in spongy sockets, or crammed into a covered pouch. Bony pouch-protecting plates and pouch folds may either be present or absent. Most ichthyologists are in agreement on Duncker's (1915) subfamily classification based upon these criteria (table 1). From this table it will be noted that the abdominal-pouch syngnathids (Gastrophori) do not have a sealed pouch equivalent to the tail-pouch *Hippocampus* (Urophori). The term Protourophori is given to the hypothetical group of tail-pouch pipefishes corresponding to the Nerophinae. Although not one of this type is known from the fossil record, the other three subfamilies of the Urophori (Solegnathinae, Syngnathinae, and Hippocampinae) must surely have evolved through this stage at some time in their development.

Detailed studies of the manner in which the brood-pouch folds close over the eggs have not previously been made. The method of closure (herein designated by the letters BPC) shows to best advantage on males that have had a full clutch of eggs in the pouch for only a few days.

TABLE 1

Classification of the pipefishes and seahorses (Syngnathidae)

	Egg and Brood Pouch Position	
	GASTROPHORI (under abdomen)	UROPHORI (under tail)
(a) Eggs loosely attached to ventral surface of male, but not isolated from one another.	1. NEROPHINAE	1. (proto-urophorinae)
(b) Eggs imbedded singly, isolated from each other in spongy mass on ventral surface of male; no protecting plates or covering membranes.	2. SYNGNATHOIDINAE	2. SOLEGNATHINAE
(c) Eggs isolated through imbedding in spongy matrix; lateral protecting plates or membranous brood pouch coverings or both present.	3. DORYRHAMPHINAE	3. SYNGNATHINAE
(d) Eggs contained in sealed brood pouch having single post-anal opening; pouch protecting plates present *(Acentronura)* or absent *(Hippocampus)*.		4. HIPPOCAMPINAE

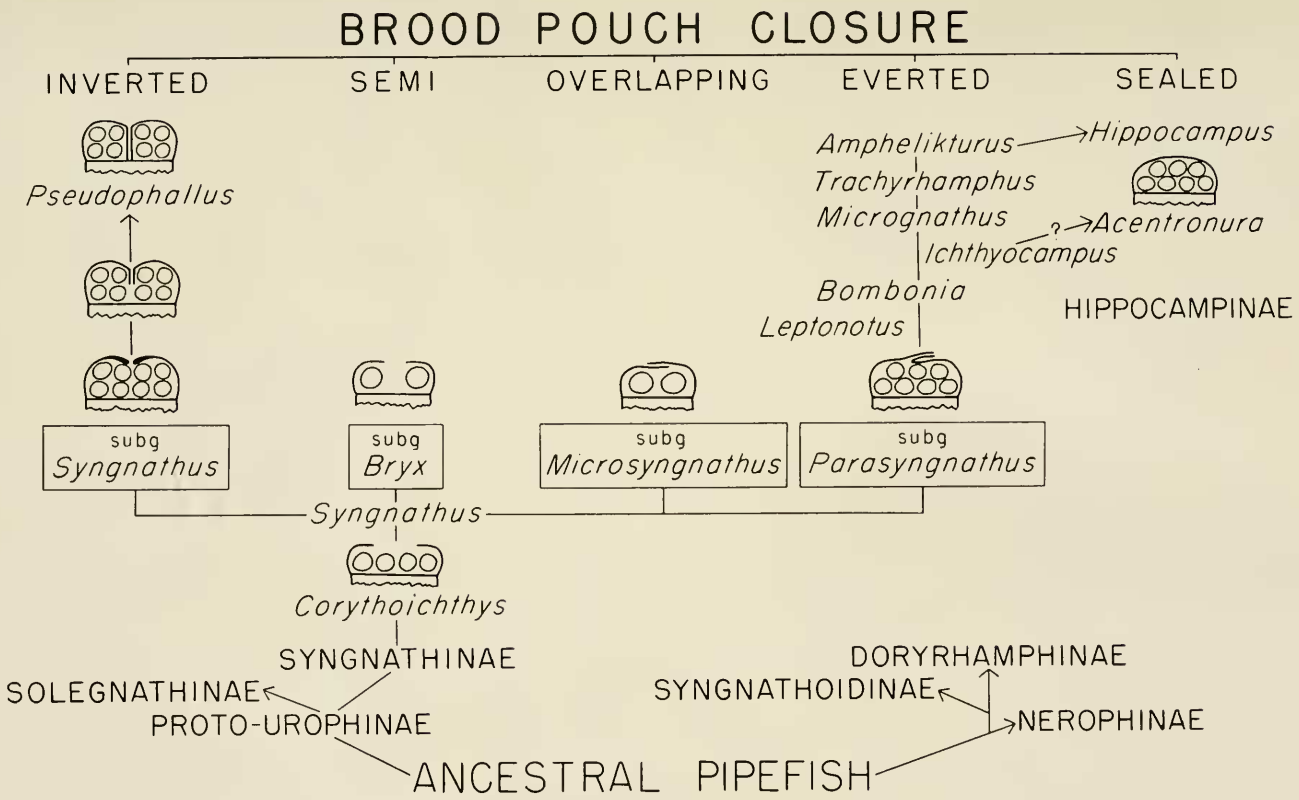

Fig. 1. Hypothetical development of the brood pouch.

At times it may be necessary to examine a series of males of a single species before suitable individuals illustrating the BPC can be found. If the pouch is empty, or if the eggs have reached the advanced embryo stage so that the covering pouch folds have become expanded by the growing progeny, the character of the BPC may not be fully evident.

Given sufficient material, all syngnathine pipefishes with brood-pouch folds can be assigned to one of the four groups diagrammed in fig. 1.

The most generalized type of pouch within the subfamily Syngnathinae is that of the semi-brood-pouch closure, which is well represented by *Corythoichthys*. In this genus the eggs are one layer in depth and four to six in width; they are not completely covered by the brood-pouch folds so that the eggs in the center are exposed. Males of the following species have been examined and all fit into semi-BPC: the Atlantic *Corythoichthys albirostris* and *C. brachycephalus*, and the Pacific *C. intestinalis*, *C. ocellatus*, *C. schultzi*, *C. flavofasciatus*, and *C. nigripectus*. The Atlantic species have pouch-protecting plates and usually have the eggs covered to a greater extent than do the Pacific species which lack the protecting plates.

Bryx, a subgenus of *Syngnathus*, is similar to *Corythoichthys* in that it also is a member of the semi-BPC group, but the eggs are arranged in only two rows.

From this semi-BPC any of the other types may have developed. If a species of *Corythoichthys* were to elongate the brood-pouch folds without developing thickenings at the free ends, the folds would then be capable of overlapping as found in overlapping-BPC. This closure method is characteristic of a group of small pipefishes including the Atlantic American *Syngnathus dunckeri* and the Pacific American *Syngnathus arctus* and *Syngnathus coccineus*. These may now be grouped under a new subgeneric name, *Microsyngnathus*, herein designated.[1]

If the underlapping edge of the brood-pouch folds were to be turned outwardly back upon itself, this would be the type designated as everted brood-pouch closure. Such closure is characteristic of those pipefishes which are in the direct evolutionary line leading from the primitive open-pouch pipefish to the complex closed-pouch seahorse. This trend, indicated in fig. 1, is shown in detail in fig. 2.

The everted-BPC series begins with pipefishes such as the Atlantic *Syngnathus elucens* and the China Sea *Syngnathus argyrostictus*. These can be assigned to the subgenus *Parasyngnathus*.[2] *Leptonotus* as shown

[1] *Microsyngnathus*, new subgenus of *Syngnathus*; genotype *Syngnathus dunckeri* Metzelaar; diagnosis: small pipefishes usually less than 100 mm. of the overlapping-brood-pouch closure type; eggs usually arranged in two rows.

[2] *Parasyngnathus* Duncker, 1915, a subgenus of *Syngnathus;* genotype *Syngnathus argyrostictus* Kaup; diagnosis: pipefishes of the genus *Syngnathus* with everted-brood-pouch closure.

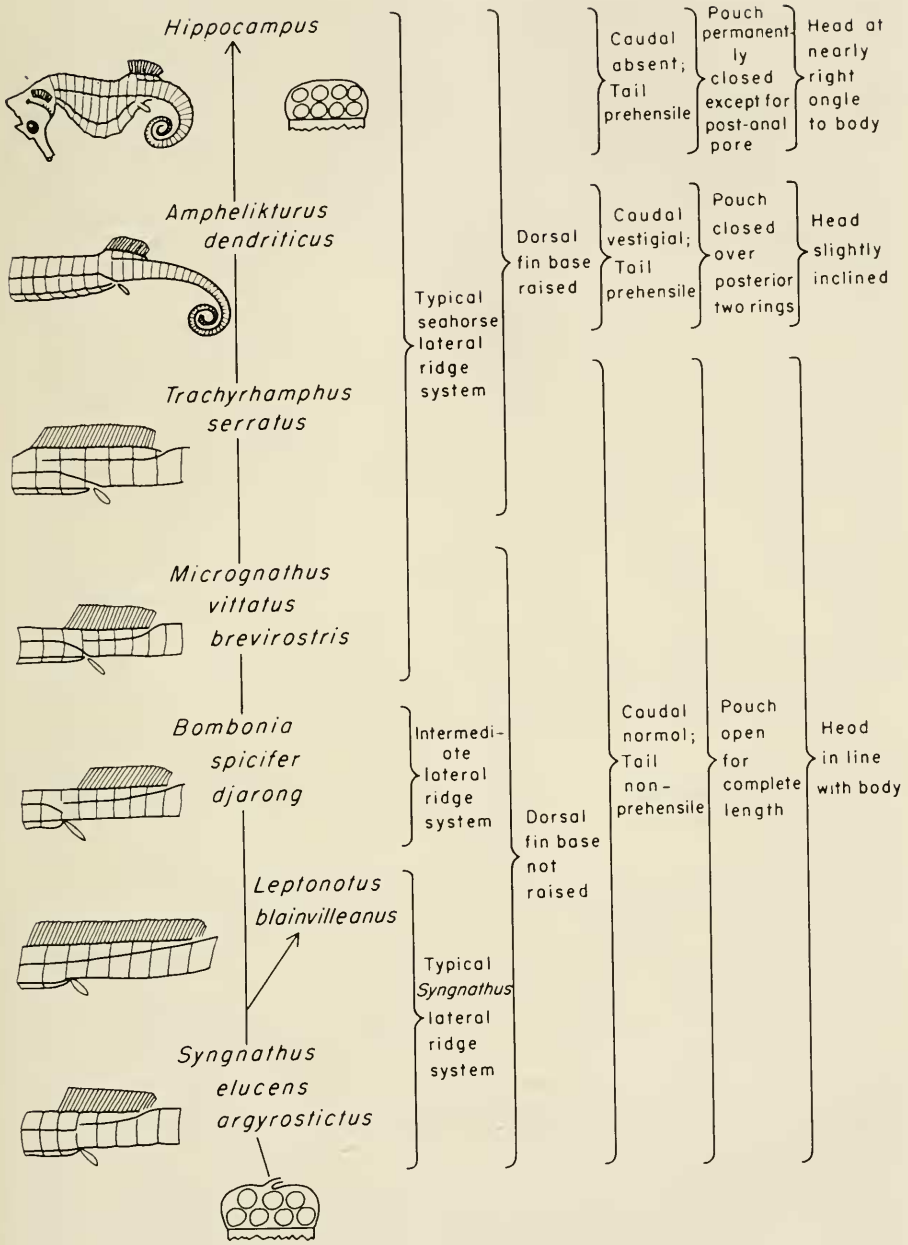

Fig. 2. Hypothetical evolutionary sequence from a typical Syngnathine pipefish with everted-brood-pouch closure to a typical seahorse.

by *L. blainvilleanus,* is perhaps not on the direct line of evolution, for in this genus the lateral trunk and tail ridges are continuous rather than subcontinuous (fig. 3). However, two species previously placed under *Syngnathus,* viz., *S. spicifer* and *S. djarong,* are certainly transitional and should be considered intermediate between *Syngnathus* and *Micrognathus.* This is indicated by the lateral trunk ridge being deflected ventrad at the anus but not continuous with the inferior tail ridge as is the case in the next genus, *Micrognathus.* Because of this transitional ridge system, *Syngnathus spicifer* and *S. djarong* can be given generic recognition under *Bombonia* Herre, 1927.[3]

Micrognathus is the next genus in the everted-BPC series. Of the nine species in the subgenus *Micrognathus,* only two, the Atlantic *M. vitatus* and the Pacific *M. brevirostris,* have had suitable males that indicate that they may be assigned to the everted-BPC series. The other subgenus of *Micrognathus* is *Anarchopterus* Hubbs, 1935. It is principally confined to the Caribbean with only two species, both of which have smooth bodies and lack the anal fin. One species, *M. (Anarchopterus) crinigerus,* is definitely of the everted-BPC type, and for the other more material is needed. It should be noted that there is a tendency within the species of *Micrognathus* as well as in *Ichthyocampus* for the posterior end of the egg-filled pouch to assume an overlapping-BPC although the anterior end will usually be of the everted-BPC type.

Trachyrhamphus, as illustrated by the species *T. serratus,* is not greatly different from *Micrognathus* except for two features, the presence of a raised dorsal-fin base, and the loss of the pouch-protecting plates.

Amphelikturus, with a single species, *A. dendriticus,* is the genus of the Syngnathinae most closely related to the typical seahorse. The dorsal base is raised, the caudal is vestigial, the tail is prehensile, the pouch is closed for the two most posterior rings, and the head is moderately bent. From here it is only a slight jump to the true seahorse, *Hippocampus,* which also has the raised dorsal base and the prehensile tail but has lost the caudal fin. The pouch is permanently sealed for most of its length with the exception of a small post-anal pore. The head is conspicuously bent at right angles to the body.

There are three genera which have the *Micrognathus-Hippocampus* type ridge pattern and probably belong to the everted-BPC series. Unfortunately, suitable males of these three, *Yozia, Halicampus,* and *Halichthys,* have not as yet been available. All three have the raised dorsal

[3]*Bombonia* Herre, 1927, genus of the Syngnathinae; genotype *Bombonia luzonica* Herre = *Syngnathus djarong* Bleeker; diagnosis: pipefishes of the everted-BPC type which have a lateral ridge system intermediate between *Syngnathus* and *Micrognathus,* i.e., lateral trunk ridge deflected ventrad at the anus but not continuous with the inferior tail ridge.

Duncker (1915) lists *Syngnathus cyanospilus* Bleeker as belonging to this deflected ridge group. The single male I have examined appears to have everted-BPC, but definite verification will have to await examination of more specimens.

base. *Haliichthys* has also lost the caudal fin and has gained a prehensile tail.

The seahorse subfamily, Hippocampinae, is made up of two genera: (1) *Hippocampus*, the typical seahorse, which was developed through the everted-BPC series, and (2) the pseudo-seahorse, *Acentronura*, which obviously did not evolve in the same manner. Both of these fused-pouch genera are alike in having a prehensile tail without a caudal fin, in having a raised base for the dorsal fin, and in having the head at an angle to the body. *Acentronura* and *Hippocampus* both have a ridge system in which the lateral trunk ridge is continuous with the inferior tail ridge. A significant difference, however, is that the lateral tail ridge is entirely missing on *Acentronura*. Likewise, *Acentronura* has lateral protecting plates in the brood pouch, these being absent in *Hippocampus*.[4] In the subfamily Syngnathinae there are only three genera, *Urocampus, Penetopteryx,* and *Ichthyocampus* which have the same kind of ridge pattern as *Acentronura*. Of these three, *Urocampus* lacks the pouch-protecting plates, *Penetopteryx* lacks the dorsal and pectoral fins, but *Ichthyocampus* has all three structures missing from the others. Possibly then, *Ichthyocampus* may be the modern representative of a form through which the pseudo-seahorse, *Acentronura,* has evolved.

Of the 18 species in the genus *Ichthyocampus* only four have a ridge pattern like that of *Acentronura: Ichthyocampus bikiniensis* from the Marshall Islands, *I. bannwarthi* from Suez, *I. pawnei* from the Bahamas, and *I. filum* from southern Australia and New Zealand. The last species is definitely in the everted-BPC series, but for the others sufficient material has not been available. In addition to the *Acentronura* type ridge system, *Ichthyocampus* has two additional ridge patterns; subgeneric designations are available for all three.[5] *Ichthyocampus pictus* is the only other species in the genus that without question can be assigned a BPC group—in this case also the everted type. There are two possibilities for the development of the *Ichthyocampus-Acentronura* group—either they were derived from the main *Hippocampus* line somewhere between *Bombonia* and *Micrognathus* or they arose even earlier than that, before the development of the *Parasyngnathus* group.

Most of the species in the genus *Syngnathus* belong to the type subgenus, *Syngnathus*, characterized by inverted-BPC (genotype *Syng-*

[4]Most of the genera and species in the everted-BPC series have the protecting plates. The exceptions are *Yozia, Trachyramphus,* and *Corythoichthys.*

[5]The three *Ichthyocampus* subgenera are (1) *Larvicampus* Whitley 1948, genotype *Festucalex runa* Whitley = *Ichthyocampus filum* Günther, lateral trunk ridge continuous with inferior tail ridge, everted-BPC; (2) *Ichthyocampus* Kaup 1856, genotype *Syngnathus carce* Hamilton, lateral trunk ridge deflected ventrad at anus but not continuous with inferior tail ridge, BPC probably everted type; (3) *Festucalex* Whitley 1931, genotype *Syngnathus cinctus* Ramsey, lateral trunk ridge ending free near or beyond anal ring, and without ventral deflection, BPC unknown. Another subgenus of *Ichthyocampus* has been described, viz., *Bulbonaricus* Herald, 1953. Although it has the *Festucalex* ridge pattern, its future relationship based on BPC remains to be determined.

nathus acus L.). The most primitive development of the inverted-BPC series is to be found in such species as *Syngnathus californiensis, S. auliscus, S. schlegeli,* and *S. rostellatus,* and in the genus *Stigmatopora.* In all of these the contacting edges of the brood-pouch folds are only moderately thickened and usually extend slightly, if at all, into the brood pouch. One of the variations of this closure is that found in *S. typhle* in which the contacting pouch folds are covered with vertical or oblique grooves. All males of this species do not show the character to equal extent, but in some it is so remarkably developed that there may appear to be innumerable small fimbriae attached to the edges of the brood-pouch folds and directed into the pouch.

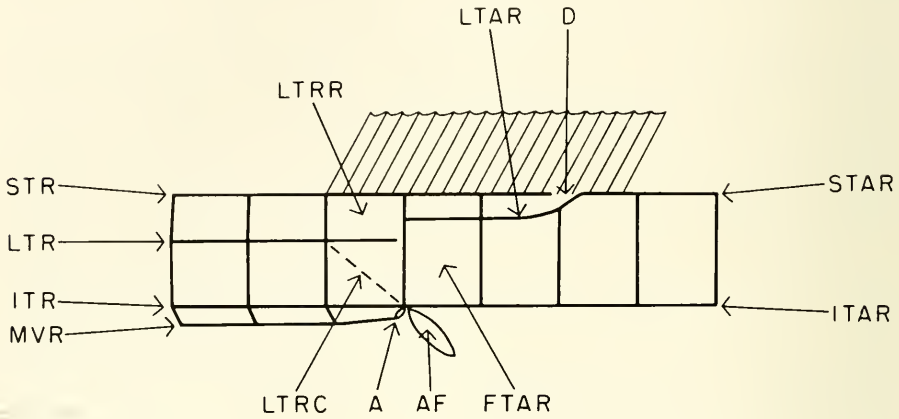

Fig. 3. Diagram of the middle part of the body of a hypothetical syngnathid illustrating the terms used in describing this family: (A) anus; (AF) anal fin; (D) discontinuous part of superior tail ridge; (FTAR) first tail ring; (ITAR) inferior tail ridge; (ITR) inferior trunk ridge; (MVR) midventral abdominal ridge; (LTAR) lateral tail ridge; (LTR) lateral trunk ridge; (LTRC) lateral trunk ridge continuous with inferior tail ridge; (LTRR) last trunk ring; (STAR) superior tail ridge; (STR) superior trunk ridge.

The majority of the species of the inverted-BPC group belong to the *Syngnathus fuscus—S. floridae* group, which may be defined as differing from the previous group only in that the folds extend about half way into the center of the pouch, but do not completely divide it. At times it may be difficult to assign a species to one or the other of these groups since the difference between them is only one of degree. Generally speaking, however, the former group often has the eggs crammed into the center area of the pouch as well as on the sides, whereas in the latter group the eggs are usually on both sides with a partial septum in between,

formed by the contacting brood-pouch folds. The septum does not go entirely through the pouch so that there may be eggs in the center portion in the most dorsal section. Other members of this second group are *Syngnathus scovelli, S. pelagicus, S. louisianae, S. springeri,* and *S. carinatus.* One interesting development is found in the Chesapeake Bay population of *S. floridae* which has the contacting edges of the brood pouch folds covered with small papillae. These are usually visible only under a microscope.

The greatest development of pouch division in the inverted-BPC series is to be found in the genus *Pseudophallus* with three known species limited to Central America. These are *P. mindi* of the Atlantic and *P. starksi* and *P. elcapitanensis* of the Pacific. In this genus the contacting surfaces of the brood-pouch folds completely divide the pouch so that the eggs on the two sides of the pouch are entirely separated.

From figure 1 it will be noted that the genus *Syngnathus* breaks down into four subgenera, *Syngnathus, Parasyngnathus, Bryx,* and *Microsyngnathus,* these designations being dependent upon the method of closure of the brood pouch. *Bryx* and *Microsyngnathus* represent the end development within the genus of semi- and overlapping-BPC, respectively. With its inverted-BPC the subgenus *Syngnathus* has the greatest number of species, but the ultimate development of this type of closure is in another genus, *Pseudophallus. Parasyngnathus,* representing the everted-BPC group, has given rise to a number of genera ending with the true seahorse, *Hippocampus.* In some manner not yet fully understood, *Parasyngnathus* and the members of the everted-BPC group are related to the development of the *Ichthyocampus - Acentronura* evolutionary sequence.

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