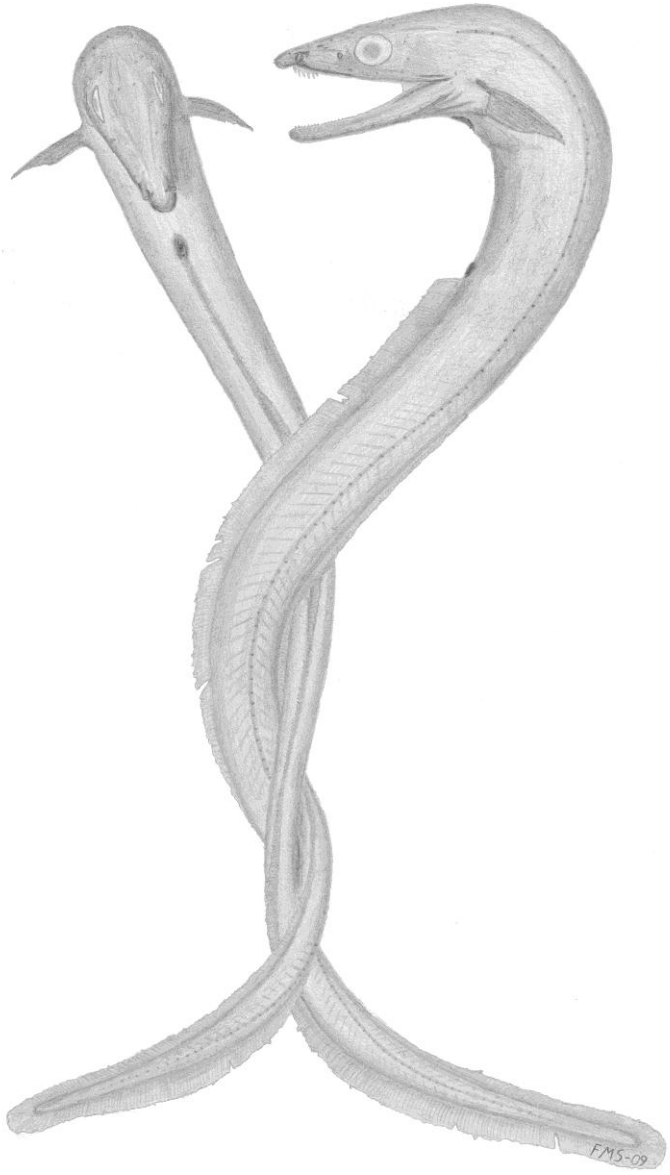
Morphological and genetic variation in North Atlantic synaphobranchid eels in relation to species diagnostics



Master of Science thesis, Marine Biodiversity

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Abstract

Synaphobranchus eels are difficult to identify at species level. A literature study of previous taxonomic work on these species revealed several inconsistencies concerning the diagnostic characters of *Synaphobranchus kaupii* and *Synaphobranchus affinis*. One hundred and eleven specimens from the mid-Atlantic ridge and a type specimen of *S. affinis* were examined morphologically, and the DNA barcode region of the mitochondrial COI gene was sequenced from 60 of these specimens. The results of this examination showed an ontogenetic change in most morphometric characters and that most of the previously used diagnostic characters, namely dorsal fin origin in relation to the vent, predorsal length, scale shape and pattern, and dentition, cannot distinguish between the species *S. kaupii* and *S. affinis*. All the examined MAR-ECO specimens are in accordance with the original description of *S. kaupii* by Johnson (1862) and have a high number of vertebrae, hence all are identified as *S. kaupii*. The type specimen of *S. affinis* may represent a member of a cryptic species that closely resembles *S. kaupii*, separable by having a lower number of vertebrae, but a geographical expansion of this study is needed to resolve this taxonomic issue.

1 Introduction

1.1 *Synaphobranchus*

Synaphobranchus is a genus in the eel family Synaphobranchidae (Anguilliformes). For the full taxonomic position, see Appendix I. Synaphobranchids constitute an important part of the deep-sea fauna at the continental slope and rise in temperate as well as tropical waters (Sulak and Shcherbachev 1997). The genus *Synaphobranchus* consists of six valid species, *S. kaupii* Johnson, 1862, *S. affinis* Günther, 1877, *S. brevidorsalis* Günther, 1887, *S. dolichorhynchus* (Lea, 1913), *S. oregoni* Castle, 1960, and *S. calvus* Melo, 2007. *S. dolichorhynchus* is only found as leptocephali larvae. All these species, except *S. calvus*, are recorded in the North Atlantic (Robins and Robins 1989, Lea 1913, Sulak and Shcherbachev 1997). Detailed information about the biology and distribution of the studied species are available in Appendix II. The identification of the *Synaphobranchus* species is difficult due to their similar external morphology, broad overlap in body proportions (Robins 1971), and unclear characters (Smith 2002). Sulak and Shcherbachev (1997) state that several characters must be considered together during the species identification of these fishes.

The *Synaphobranchus* specimens collected during the 2004 MAR-ECO cruise (www.mar-eco.no) proved difficult to identify in the field, and all specimens were initially named *S. kaupii.* The specimens were later revised, primarily following the key provided by Sulak and Shcherbachev (1997), and most of them were considered to be *S. kaupii,* but also many were identified as *S. affinis*. A picture of two of the MAR-ECO specimens is shown in figure 1. Subsequent debate ensued due to discrepancies with the character combinations, especially concerning the dentition of the palate and scales, and the fact that it was difficult to see any clear difference between the species. This resulted in the questioning of which character(s) that should be most emphasized in the identification of these species and whether the variation of the diagnostic characters in these eels had been sufficiently understood. (Ingvar Byrkjedal and Gunnar Langhelle, Bergen Museum, personal communication). A combined molecular and morphological analysis seemed appropriate to solve this taxonomic issue

Figure 1: Two of the MAR-ECO specimens. ME 17379-1, 617 mm total length, and ME 17379-2, 490 mm total length.

1.2 The taxonomic history of *Synaphobranchus kaupii* and *S. affinis*

In this synopsis of the taxonomic history of *Synaphobranchus kaupii* and *Synaphobranchus affinis*, I focus on the diagnostic characters used by most authors, namely the origin of the dorsal fin, the shape and pattern of the scales, and the total number of vertebrae.

The taxonomic history of *Synaphobranchus* begins in 1862 with James Yates Johnson`s description of the genus and the new species *Synaphobranchus kaupii* (Johnson 1862). He states that this genus forms the type of a new family of Apodes, the Synaphobranchidæ. This family is different from other families, except the Symbranchidæ (now known as Synbranchidae), by having gill openings close together ventrally, and from the Symbranchidæ by having pectoral fins. The genus is described as having a single gill opening, internally divided by a membrane; scales present; teeth on jaws, vomer and the mesial line of the palate (here "vomer" probably means the premaxillary-ethmoid complex, and "the mesial line of the palate" means the vomer). The description of the new species *S. kaupii* is detailed and it includes a drawing of the upper jaw and palate, seen ventrally, and measurements of one of the larger specimens. Johnson does not give the number of specimens on which the description was based, but it must have been more than one. The specimens were deposited in the British Museum. He describes the dorsal fin origin as "the dorsal fin commences behind the vent, a little posterior to the commencement of the second third of the total length". The scales are described as "small oval scales, set obliquely

and at right angles to each other". Number of vertebrae is not described. The specimens were obtained at Madeira.

In "Catalogue of the fishes in the British Museum" (Günther 1870), Albert Günther synonymises *Synaphobranchus kaupii* Johnson, 1862 with *Muræna pinnata* Gronovius (in Gray 1854) under the name *Synaphobranchus pinnatus*. He obviously believes that *S. kaupii* is the same species as described by Gronow, but that the genus *Synaphobranchus* is the proper genus for this species. It seems that Günther examined four specimens, all from Madeira, including the types of *S. kaupii*. The description is rather short, mostly concerning the dentition. The origin of the dorsal fin is described as "vent somewhat in advance of the origin of the dorsal fin". There is no description of scales or vertebrae at species level, but "body scaly" is mentioned in the description of the genus.

Laurence Theodore Gronow (Laurentius Theodorius Gronovius) describes the species *Muræna unicolor, maxillare superior longiore* (nr. 161) in his "Musei Ichthyologici, tomus secundus" (1756), from the collection of Arnoldius Vosmaerius. The description of the pectoral fins and the possible ventral gill opening makes it likely that he is describing a synaphobranchid species. There is no description of scales or vertebrae, and the position of the median fins is just referred to as equal to species number 45 in his book "Museum Ichthyologicum" (1754). The species number 45 is called *Muræna unicolor, maxilla inferior longiore*, but it is not described in any detail. There are just a lot of references to other books, which I have been unable to obtain. There are no figures of species number 45 or 161.

John Edward Gray purchased a collection and manuscript at an auction in London a long time after Gronow`s death in 1777, and published the manuscript with the title "Catalogue of Fish collected and described by Laurence Theodore Gronow, now in the British Museum" (Gronow 1854). Gronow`s description of the group Muræna is detailed, and he describes the gill openings as narrow and positioned on the sides in most, but in others as a single opening beneath the pectoral fins, and lacking in some cases. Pectoral fins absent in some. He also describes the group as not covered with scales that can be seen by the naked eye, but in a note he states that other authors claim to have seen scales on fish in this group. The group

Muræna is further divided into paragraphs, and the species *Muræna pinnata* is placed in § 4: Operculis branchialibus pinnisque pectoralibus utrinque, meaning gill covers and pectoral fins on both sides. The description of *Muræna pinnata* is very short: “Muræna unicolor; maxilla superior longiore; pinnis pectoralibus aperturisque branchialibus utrinque” meaning unicolored muraena, upper jaw longest, with pectoral fins and gill openings on both sides. And it is referred to as being the same as the species *Muræna unicolor, maxilla superior longiore*, species number 161 in “Musei Ichthyologi, tomus secundus” (1756).

After the HMS *Challenger* expedition in 1873 - 1876, Albert Günther published some preliminary notes on new fishes in 1877 (Günther 1877). Here he describes the species *Synaphobranchus affinis* from off Inoshima, Japan. The description is short and without measurements or figures. The origin of the dorsal fin is described as “dorsal fin commencing at some distance behind the vent”, and the description of the scales as ”epidermoid productions rudimentary, lanceolate, obliquely arranged, imbedded in the skin”. The only parts of the description that are essentially different from Johnson`s description of *S. kaupii* (Johnson 1862), are “allied to *S. brevidorsalis*” (note: the first description of *S. brevidorsalis* is published in 1887), the description of the scales as “lanceolate” (Johnson: oval), and the color as “blackish brown” (Johnson: dull brown). There is no statement on how many specimens that were examined. A picture of one of the type specimens is shown in figure 2.

Figure 2: One of the syntypes of *S. affinis*, 371 mm total length.

In the report on the deep-sea fishes collected during the HMS *Challenger* expedition in 1873-1876 (Günther 1887), *S. affinis* Günther, 1877 was placed together with *S. kaupii* Johnson, 1862 and *Muræna pinnata* Gronovius, as synonyms of *Synaphobranchus pinnatus*. Nineteen specimens were examined including 11 types of *S. affinis*. Eighteen of them were from around Japan and the Philippines, and one specimen from the coast of Brazil. According to this description "the dorsal fin commences above or at a very short distance behind the vent", and the scales are "rudimentary, lanceolate, oblique". Günther also describes the new species *Synaphobranchus brevidorsalis* in this report.

In 1888, L. Vaillant published a report from the scientific expeditions of the *Travailleur* and the *Talisman* from the coasts of Morocco and Sudan, the Canary Islands, the Azores, and the Cape Verde islands (Vaillant 1888). The author uses the scientific name *Synaphobranchus pinnatus* Gray, and 56 specimens of this species were collected during these expeditions. Vaillant questions whether the merging of *kaupii*/*affinis* and *M. pinnata* is valid. However, the author concludes that there is no reason to complicate the taxonomy any further and retains the species name *pinnatus* and the genus name *Synaphobranchus*. Further, the author states that there is one possible important difference (if not a spelling mistake by Johnson) in the body depth between Johnson`s example and the examined specimens. Johnson`s example has a body depth that goes 10 times in the total length. The examined specimens have a body depth that goes 20 times in the total length. The author claims that the scales are easily lost, and are not present in many individuals. One scale measures 3.55 mm in length and 1.5 mm in width. The otoliths and digestive tract are described in detail. Johnson (1862) states that the swim bladder is long and stretches more than one third of the body length, but these specimens have swim bladders that goes further into the caudal region, as a thin tube posteriorly. An example of measurements, from probably only one individual, is shown.

E. W. L. Holt described the new genus *Nettophichthys* and the new species *Nettophichthys retropinnatus* in 1891 (Holt 1891). He puts the genus in the family Murænidæ. The description is detailed, but lacks measurements and figures. The genus and species is

described as scaleless and with no pectoral fins. The dorsal fin originates “at a point somewhat posterior to median”. The description of the genus and species is based on one much injured specimen with a total length of 5 inches. This species name was synonymized with *S. pinnatus* in 1906 by E. W. L. Holt and L. W. Byrne.

David Starr Jordan and Bradley Moore Davis published a preliminary review of the eels of American and European waters in 1892 (Jordan and Davis 1892). Here, *Synaphobranchus pinnatus* is listed with the synonyms *Muræna pinnata* Gronow, *S. kaupii* and *S. affinis*. The dorsal fin is described as “dorsal fin beginning ¼ to ½ head`s length behind vent”. Scales are not mentioned at species level, but number of vertebrae is recorded as 146. No mention of the number of specimens examined. The description is short, but with some measurements.

A review of eels of Japan was published by David Starr Jordan and John Otterbein Snyder in 1901 (Jordan and Snyder 1901). Here the name *Synaphobranchus affinis* reappears. They state that this species is very close to the *S. pinnatus* of the Atlantic, but that *S. pinnatus* is “evidently different, having the dorsal much further back”. The dorsal fin of *S .affinis* is described as “dorsal fin beginning very close behind vent”. It is otherwise a short description with some proportions listed. The number of specimens examined is referred to as numerous. They describe the new species *Synaphobranchus iraconis* that is distinguished by “the greater length of the tail, the larger mouth, larger pectoral, and especially the anterior insertion of the dorsal”. It is also stated that this species is related to *S. brevidorsalis*. The description is short with some proportions listed and based on one specimen. An identification key for the *Synaphobranchus* species is provided and it is based solely on the insertion of the dorsal fin: *S. affinis* with dorsal fin inserted directly over or very slightly behind vent, and *S. iraconis* with dorsal fin insertion 3/5 of head length behind vent. There is also a description of the new species *S. jenkinsi*. Schematic drawings of the species are presented.

C. H. Gilbert published a description of the new species *Synaphobranchus brachysomus* from Hawaii in 1905 (Gilbert 1905). The description is detailed and with measurements. The scales are described as narrow and elliptical and arranged in groups with their axis at right angles to each other, absent on fins and the underside of the head. The origin of the dorsal fin varies somewhat in position, but reaches in front of the vent in only one specimen. The author states that this species is most closely related to the species *S. pinnatus* and *S. affinis*, but differs from them by a much shorter trunk and white fin margins. The number of specimens examined is not stated, but it includes at least three specimens. A drawing of the fish is presented.

In a report of fishes from the Irish Atlantic Slope, published in 1906, E. W. L. Holt and L. W. Byrne describe characters of some young *Synaphobranchus pinnatus* (Holt and Byrne 1906). The description is based on at least three specimens, one of them with a total length of 118 mm. From an examination through a microscope, they believe they can see the incipience of scales. Origin of the dorsal fin is not mentioned, but measurements from one specimen are presented. The authors withdraw Holt`s own description of *Nettophichtys retropinnatus* because it was based on a badly damaged specimen of *S. pinnatus*.

In 1909, R. E. Lloyd described the new variety *Synaphobranchus pinnatus* var. *brevidorsalis* (Lloyd 1909). He states that “this variety closely resembles *S. pinnatus* in all but one character, namely, the length of the dorsal fin. In this it resembles *S. brevidorsdalis*”. He describes the origin of the dorsal fin as beginning one head length behind the level of the vent. The scales are described as “in the mosaic-like arrangement of the elongated scales the specimen resembles *S. pinnatus* and differs from *brevidorsalis*”. The description is of one specimen from the Arabian Sea, of 70 cm length.

Louis Roule described the new variant *Synaphobranchus pinnatus* var. *parvipinnis* in 1916 (Roule 1916). The description is based on a specimen from the waters off Portugal with a total length of 282 mm. The description is short and states that it differs from *S. pinnatus* in

several aspects, e.g. the origin of the dorsal fin is more anterior without reaching the level of the vent.

Tanaka described the new species *Synaphobranchus taketæ* in 1916 (Tanaka 1916). The description is in Japanese and I have not been able to locate a translation.

In 1927, Einar Koefoed published a report on the fishes from the sea-bottom from the *Michael Sars* deep-sea expedition in 1910 in the North Atlantic (Koefoed 1927). Forty-two specimens were examined with total lengths of 10 to 55 cm. He states that the distance from the vent to the origin of the dorsal fin varies from ½ head lengths to more than 1 head length, and that this character cannot be used to distinguish the species *S. pinnatus* and *S. brevidorsalis*. However, he points to the difference in the description of scale shapes between these species. He questions whether the species *Synaphobranchus brachysomus* Gilbert, 1905 is distinct from *S. pinnatus*. There is a table with measurements and measurements expressed as percent of total length or head length. There is also a table showing the variation in the distance from the vent to the origin of the dorsal fin.

In 1937, Anton Fr. Bruun published some contributions to the life-histories of the Synaphobranchidae, based on material collected during several "Dana"-expeditions (Bruun 1937). The study is detailed, based mainly on the leptocephali, but adult considerations are also dealt with. He points out that the connection between adults and leptocephali has only been made for a few species, one of them being *S. kaupii* (the author uses the spelling *S. kaupi*; this common misspelling is commented in Appendix IX) and this connection is based on the number of myomers in the larvae connected to the number of vertebrae in adults. He discusses the previous taxonomy of *S. kaupii* and considers it almost impossible that Gronow`s (1854) description includes *S. kaupii*, based on his description of the position of the gill slits. He concludes that "Günther has not proved any identity between *M. pinnata* Gronow-Gray and *S. kaupi* Johnson" and that "*M. pinnata* was so badly defined, that it should be cut out altogether, as an unrecognizable species, whilst *S. kaupi* should remain as

type for both the genus and family, in accordance with Johnson`s view". He states that *S. pinnatus* var. *parvipinnis* "may be a chance variant of the same species", and finds it unlikely that the many species described from Japan (*affinis*, *brevidorsalis*, *bathybius*, *iraconis*, *jenkinsi* and *taketae*) and *brachysomus* from Hawaii, are well defined. He describes the leptocephali of *S. kaupii* in detail. He states that it seems unlikely that *S. kaupii* is found outside of the North-Atlantic, based on the investigations of the leptocephali. He also describes the distribution and biology of *S. kaupii* leptocephali, and that this species seems to share the same reproductive pattern as *Anguilla anguilla* and *Conger conger*. Measurements of adults and larvae are listed in tables. Three specimens from the Western Atlantic had vertebrae numbers of 147, 151 and 152. Bruun describes the new species *Synaphobranchus indicus* based on eight leptocephali. Their number of myomeres varies from 129 to 138. He also separates them as two subspecies, *S. indicus indicus* and *S. indicus occidentalis*, based on position and extension of the lateral spot, and geography.

K. Matsubara published an article on the morphological variation found in *Synaphobranchus pinnatus* in 1938 (Matsubara 1938). The study is based on 39 specimens collected from waters near Hokkaido and Tyosi, Japan, with total lengths of 472 – 806 mm. The author focuses most on the variation found in the origin of the dorsal fin. In this character, the examined specimens include all known species of *Synaphobranchus*, and intermediate forms between them, and the author concludes that they all are referable to *Synaphobranchus pinnatus* (Gronow). Further he states that "it is absolutely impossible to divide the genus into several species as noted above" (i.e. by the dorsal fin), and that the seven species and two varieties known, *S. pinnatus* (Gronow), *S. brevidorsalis* Günther, 1887, *S. brachysomus* Gilbert, 1905, *S. pinnatus* var. *brevidorsalis* Lloyd, 1909, *S. pinnatus* var. *parvipinnis* Roule, 1916, *S. affinis* Günther, 1877, *S. iraconis* Jordan & Snyder, 1901, *S. jenkinsi* Jordan & Snyder, 1901, and *S. taketae* Tanaka, 1916 (note: the author uses the spelling *S. takedae*), should all be considered as one species with variable dorsal fin origin, namely *Synaphobranchus pinnatus* (Gronow).

J. R. Norman and Ethelwynn Trewavas published measurements and merisistic characters of synaphobranchid specimens in the British Museum and some other specimens in 1939 (Norman and Trewavas 1939). They discuss the work of Matsubara (1938) and point out that no vertebrae counts were made. Here, 13 specimens of *S .kaupii* from the Atlantic and off Cape Point had vertebrae counts from 146 – 151. The holotype of *S. iraconis* Jordan and Snyder, 1901 has 146 vertebrae, and the authors state that "this species, known only from Japan, is very doubtfully distinct from *S. kaupii*". *S. affinis* is listed with the synonyms *S. brachysomus* and *S. taketae*. Nine specimens, included type of *S. affinis* and holotype of *S. brachysomus*, have vertebrae counts from 135 – 137. They state that *S. affinis* might be confined to the North Pacific and that it is distinguished from *S. kaupii* by the lower number of vertebrae and "rather longer head and pectoral fin, and somewhat more anterior insertion of dorsal fin". The species *Synaphobranchus indicus* Bruun?, 1937, ("Bruun?" is how it is spelled in this article) has 131 and 132 vertebrae in two specimens, and the authors states that "this form is very close to *S. affinis*". Tables with measurements and vertebrae counts are provided for all species. A figure of the scales of *S. kaupii* is presented.

Kiyomatsu Matsubara and Akira Ochiai published a study of the taxonomy of the genus *Synaphobranchus* in 1951 (Matsubara and Ochiai 1951). The article is in Japanese, but with a summary in English. All tables and figures are also written in English. 40 specimens of *S. kaupii* with total lengths of 492 – 811 mm, and five specimens of *S. affinis* with total lengths of 303 – 586 mm were examined, all from Japanese waters. They distinguish *S. kaupii* and *S. affinis* based mainly on differences in number of vertebrae, scale shape, and shape of upper pharyngeal teeth. The biometrics of *S. affinis* falls mostly within the range of *S. kaupii*, but *S. kaupii* has on average a dorsal fin origin a little posterior to that of *S. affinis*. Vertebrae are more numerous in *S. kaupii* (142 – 150) than in *S. affinis* (133 – 138). The scales are reported as being wider in *S. affinis* than in *S. kaupii* and a figure of this is shown. Tables of meristic characters and measurements are provided, and also a diagram of the frequency of vertebrae numbers in *S. kaupii*. A figure shows the variation of the origin of the dorsal fin in *S. kaupii*.

P. H. J. Castle published an article on deep-water eels from New Zealand in 1961 (Castle 1961) where he examined four specimens of *S. affinis* with total lengths of 437 - 469 mm. *S. affinis* is listed with the synonyms *S. pinnatus* Günther, 1887 (part), *S. brachysomus* Gilbert, 1905 and *S. taketae* Tanaka, 1916. The description is detailed and includes drawings of the fish, scales, and dentition. The scales are described as "present over most of body surface but absent from fins. They are closely packed and regularly arranged in groups of three to four at an acute angle to the lateral line, but less regularly arranged on the dorsal and ventral midlines; scales of adjacent groups are disposed at right angles to one another; each scale is oval and imbedded in a shallow depression covered by a very thin, pigmented epidermis". The dorsal fin origin is described as "originating at the level of, or just posterior to, level of vent". The vertebrae counts are 131 – 135.

In 1964, P. H. J. Castle published an article about the family Synaphobranchidae in the report from the Galathea expedition (Castle 1964). One specimen of *S .kaupii* (the author uses the spelling *S. kaupi*) of 266 mm total length from off Kenya was examined. The description is detailed with measurements, meristic counts, and drawings of the fish, its head, dentition and scales. The scales are described as "scales present over whole of body except head and fins, with scaled area beginning above origin of lateral line. Scales much as in *Histiobranchus* but a little less elongate". In the description of the genus, he states that *S. kaupii* and *S. affinis* together have clearly distinct scales from other members of the genus. The dorsal fin origin is described as "originating a little less than length of head behind level of vent". Vertebrae 144. He states that *S. kaupii* and *S. affinis* can be separated on the basis of vertebrae count, *S. kaupii* with 142 – 151 and *S. affinis* with 131 – 138 vertebrae.

Catherine H. Robins published a thorough and detailed article of the synaphobranchids from the Straits of Florida in 1971 (Robins 1971). Forty-six specimens of *S. affinis* with total lengths of 193 – 515 mm, and 13 specimens of *S. kaupii* (the author uses the spelling *S. kaupi*) with total lengths of 296 – 740 mm were examined. Many of the specimens are sexed and both genders are represented in both species. She states in the introduction that "although the synaphobranchids of the Straits of Florida are distinct entities and are

currently identified with the species described by Johnson, Günther, Gilbert and Castle, additional study of Pacific collections may necessitate some taxonomic changes in the Synaphobranchidae". The cephalic lateral line pores and osteology of the species are studied in detail, but without any major differences found between *S. kaupii* and *S. affinis.* She claims that the species within *Synaphobranchus* are best separated by differences in scale pattern and number of vertebrae, and that the body proportions are very variable within species and with broad overlap between species and can therefore not be used as diagnostic characters. The scales of *S. affinis* are described as "most scales of *S.affinis* are ovoid and are arranged in a loose basket-weave pattern similar to the more compact and regular arrangement of scales of *Anguilla*. Some scales, particularly those close to the midline or lateral line are subcircular or trapezoidal". The scales of *S. kaupii* are described as "elongate ovals, tightly arranged in a basket-weave pattern which is more compact than in *S. affinis*". The vertebrae number for *S. affinis* is 128 – 139, with an average of 133.1, and for *S. kaupii* 146 – 150 with an average of 148.0. Measurements and counts are listed for each specimen in tables. There are also tables of frequency distributions for several of the characters. Many drawings of the osteology, and one figure showing the difference in scale pattern between the species, are presented. The osteological descriptions are based on one specimen of *S. kaupii* and three specimens of *S. affinis*.

Osamu Okamura and Yoshihiko Machida published some records of fishes from Japan in 1987 (Okamura and Machida 1987). Three specimens of *S. kaupii* with total lengths of 602-874 mm, and one specimen of *S. affinis* with total length of 546 mm were examined. The description is rather short, but with measurements and meristics. The scales of *S. kaupii* are described as "elongate-oval, placed in groups, and scales of each group being at right angles to those of adjacent groups". The dorsal fin of *S. kaupii* is described as "originating above or posterior to the vent". 149 vertebrae are reported for *S. kaupii* and 137 for *S. affinis*. The authors state that *S. affinis* "closely resembles *S. kaupii*, but differs in having broader scales, minute teeth on outer patch of pharyngeal bone, and more numerous lateral line pores and vertebrae" (the last part of this statement must be a mistake considering the numbers given earlier in the text).

In the book “Fishes of the Western North Atlantic” from 1989, Catherine H. Robins and C. Richard Robins wrote the chapter on the family Synaphobranchidae (Robins and Robins 1989). A key to the species is provided, and *S. kaupii* (the authors use the spelling *S. kaupi*) and *S. affinis* are separated as follows:

-Scales very elongate (3-4 times as long as wide), small, regularly arranged in aligned clusters of 4-5 set at right angles to other such groups; vertebrae usually 144-152; dorsal-fin origin behind level of anus; vomerine teeth uniserial, but zig-zag anteriorly……..…….*S. kaupi*

-Scales oval, not so regularly arranged; vertebrae 128-140 (rarely slightly fewer); dorsal-fin origin at or just posterior to level of anus; vomerine teeth uniserial……*S. affinis*

A figure showing scale pattern, dorsal fin origin, and number of vertebrae is presented on the same page as the identification key. Later in the article is another figure of the scale patterns of the different species (note: the scale pattern and shape for the species *S. affinis* are drawn very differently in the two figures). The description of the species is thorough and detailed. *S. kaupii* is listed with the synonyms *S. pinnatus* Günther, 1870, *Nettophichthys retropinnatus* Holt, 1891, *S. iraconis* Jordan and Snyder, 1901, and *S. pinnatus* var. *parvipinnis* Roule, 1916. *S. affinis* is listed with the synonyms *S. pinnatus* Günther, 1887, *S. brachysomus* Gilbert, 1905, *S. taketae* Tanaka, 1916, *S. indicus* Bruun, 1937, and *S. indicus occidentalis* Bruun, 1937. In the text, the number of vertebrae in *S. affinis* is reported as 125 – 140 (but 128 – 140 in the key). There are figures of the fish and their dentition for both species. The number of examined specimens are, in addition to Catherine Robins` study in 1971, 26 from the West Atlantic, 11 from the West Pacific, and about 1000 uncatalogued specimens from the Bahamas for *S. kaupii*, and 10 from the Eastern Atlantic, 39 from the Western Atlantic, 4 from the Indian Ocean, 11 from Indonesia-Philippines, at least 47 from Japan, and 4 from Hawaii for *S. affinis*.

In 1995, Okamura published records of 23 specimens of *S. kaupii* (the author uses the spelling *S. kaupi*) from around Greenland with total lengths of 255 – 570 mm (Okamura 1995). He states that this species is separated from other congeneric species by the number of vertebrae, scale pattern, position of dorsal fin origin and a single prevomerine tooth patch. The description is rather short, but with measurements and meristics. The scales are

described as “very elongated, regularly aligned in clusters of four or five, set at right angles to adjacent clusters”. Number of vertebrae is 143 – 152. A picture of one specimen is presented.

In 1997, Kenneth J. Sulak and Yuri N. Shcherbachev published an article on zoogeography and systematics of some synaphobranchid genera (Sulak and Shcherbachev 1997). They claim that the identification of synaphobranchids is often difficult and that “a simple dichotomous key is inappropriate for identification of synaphobranchid eels”. 466 specimens of *S. kaupii* and 379 specimens of *S. affinis* were examined. An identification key is provided and it separates the two species as follows:

11A. -PME (note: premaxillare-ethmoid complex)elongate, oval shaped, with a dominant, linear, median series of 6-8 nearly equal teeth (lateral teeth present as well, but set low along the margins of the toothpatch and less evident); scales in very regular, grouped, right-angle basketweave pattern; 3-6 scales per group, typical length:width ratio 3:1 - 4:1; dorsal fin origin relatively far behind vent – by a distance of more than one pectoral fin length; musculature dense, very firm upon preservation; color gray, brown, or black with a silvery iridescent tone; vomerine teeth uniformly very small – the largest only as long as the smallest lateral PME tooth; Lateral line pores in front of vent 27-33; total length to 905 mm; Vertebrae 141- 150…….…..*S. kaupii*

11B. -PME short, oval or club-shaped, with irregularly placed teeth of variable size…….…12

12A. -Dorsal fin origin approximately opposite vent (sometimes slightly ahead or behind, but if behind vent – then never by a distance exceeding one pectoral fin length); scaled in fairly regular, right-angle basketweave pattern; 2-3 scales per group, length:width ratio 2:1 - 3:1; color blackish; musculature very firm; skin resilient, seldom frayed or parted around scales in preserved specimens; body slender, even in large adults: vomer without enlarged teeth anteriorly – largest tooth only subequal to smallest PME tooth; lateral line pores in front of vent 25-29; total length to 1600 mm; vertebrae 129 – 150…. ……..…….. *S. affinis*

A table of number of vertebrae in specimens from several parts of the world is presented, based on some of the material examined in the study and on literature sources. This table shows that only specimens of *S. affinis* from the western North Pacific and eastern North Pacific (three specimens altogether) fall within the vertebrae range for *S. kaupii*. Figures of

the cephalic lateral line system, the dentition of the vomer and the premaxillare-ethmoid complex, and scale patterns are presented, showing the differences between the species.

Marcelo R. S. Melo published a description of the new species *Synaphobranhcus calvus* and notes on the other species in the same genus, in 2007 (Melo 2007). Five specimens of *S. affinis* with total lengths of 382 – 561 mm, and four specimens of *S. kaupii* with total lengths of 291 – 548 mm were examined. Tables of measurements and meristic data are presented. An identification key to the species is provided and it separates *S. kaupii* and *S. affinis* by the origin of the dorsal fin (far behind anal-fin origin in *S. kaupii*, and at level of, or a little behind anal-fin origin in *S. affinis*) and lateral line pores to the level of dorsal fin origin. The scales of *S. kaupii* are described as "very elongate, small, regularly arranged in a right angle basket-weave pattern of four to six scales". He discusses the previous records of *S. kaupii* in the western South Atlantic and concludes that "there is no evidence of the presence of *Synaphobranchus kaupii* in the western South Atlantic so far". He reports the first record of *S. affinis* in the area. There is no mention of the vertebrae number, but the number of lateral line pores is shown.

Armando J. Almeida and Manuel Biscoito published new records of *Synaphobranchus* species from off the Azores in 2007 (Almeida and Biscoito 2007). Six specimens of *S. kaupii* and six specimens of *S. affinis* were examined. There are no descriptions of the species, but a table of measurements and number of vertebrae is presented. The authors state that "amongst our material, the origin of dorsal fin in *S. affinis* is always closer to the origin of anal fin than it is in *S. kaupii*, which can be a useful character to separate the two species, as it has been already pointed out by Sulak and Shcherbachev (1997)". *S. kaupii* is reported with 145 - 152 vertbrae, and *S. affinis* with 135 - 150.

A summary of this taxonomic history: Günther (1887) united the species *S. kaupii* and *S. affinis* under the name *S. pinnatus*. *S. affinis* was separated from *S. pinnatus* by Jordan and Snyder (1901) and *S. kaupii* became the valid name again after Bruun`s (1937) dismissal of

the name *pinnatus*. The origin of the dorsal fin was considered as a very important diagnostic character by Jordan and Snyder (1901) and the number of vertebrae were eventually considered important, starting with Bruun (1937). The origin of the dorsal fin was found useless as a discriminating character by several later studies (Matsubara 1938, Matsubara and Ochiai 1951, Robins 1971) and scales and vertebrae were considered as the discriminating characters (Matsubara and Ochiai 1951, Robins 1971). The value of the dorsal fin origin as a diagnostic character gained emphasis again in later taxonomic studies (Almeida and Biscoito 2007, Melo 2007, Robins and Robins 1989, Sulak and Shcherbachev 1997). The taxonomic history shows a general disagreement and inconsistency concerning the values of and ranges of the applied diagnostic characters.

1.3 Molecular techniques in taxonomy

Traditional morphological identification of species has some limitations. Phenotypic plasticity and variation in characters can lead to misidentifications and problems with morphologically cryptic species. Also, morphological keys are often usable for only one life stage or gender, and the use of keys often demands a high level of expertise. Use of modern genetic techniques can yield a better taxonomical resolution than through morphological studies (Hebert et al. 2003). Ideally, molecular techniques and traditional morphological analysis should be used together, and correct identification of species and use of voucher specimens are necessary (Ward et al. 2005).

After the discovery of the structure of DNA in 1953, DNA sequences have been incorporated into all aspects of biology. Several technical advances in recent decades have had a major influence on the application of DNA sequences to studies of taxonomy and systematic. DNA sequencing was a slow and difficult task before the development of the Polymerase Chain Reaction (PCR). The development of efficient thermal cyclers and primers in the early 1990s greatly increased the ease of generating DNA data (Simon et al. 2006). Some authors now want a taxonomic system based largely on DNA sequence data, see e.g. Tautz *et al*. (2002, 2003), but this is of course hotly debated, see e.g. Lipscomb *et al*. (2003).

Variation in DNA sequences is used in taxonomy to discriminate taxa (Hebert et al. 2003). Studies show that sequences within species are generally more similar than sequences between species, but there are exceptions that create taxonomic uncertainties, e.g. hybridization (Ward et al. 2005). Sequence data from mitochondrial genes is most widely used in animal systematics. Advantages of mitochondrial DNA (mtDNA) include the fact that sequences are generally easy to obtain and show variation at a range of taxonomical levels (Simon et al. 2006, Simon et al. 1994). Analysis of gene regions that evolve relatively rapidly will be more suited to studies involving short divergence times than less variable genes, but several markers may be suitable for any given application. One mtDNA gene that has received much attention in recent years is the cytochrome c oxidase subunit I gene (COI). Cytochrome c oxidase is the mitochondria`s terminal enzyme in the respiratory chain. It catalyzes the electron transfer from cytochrome c to oxygen and reduces the oxygen to water. This enzyme is complex, with 13 subunits in mammals (Ward and Holmes 2007). COI comes with two broad advantages for molecular systematic research: there are robust "universal" primers for this gene, allowing use in many higher animal groups, and this gene evolves rapidly and permits discrimination of closely related species (Hebert et al. 2003).

In a study of COI sequences in insects, Hebert et al. (2003) showed a 100 % identification success (n=150) at species level, and they suggest that a region of the COI gene could be used as a global identification system for animals. This "DNA barcode" delineates species by one sequence or a group of very similar sequences. The Kimura 2-parameter (K2P) differences of the sequences within species in this study were always small (average 0.25 %), and the differences between congeneric species were much larger (average 6.8 %).

Cytochrome oxidase I in vertebrates has a total length of about 1545 basepairs. A region of about 650 basepairs has been adopted as the barcode region (Ward and Holmes 2007). Species identification by use of the barcode region has been investigated in various taxa over the last few years (www.barcodinglife.org). Clare *et al.* (2007) examined 87 species of Neotropical bats and all could be identified by the barcode region. The average K2P distance within these species was 0.60 %, between congenerics 7.80 %. In a study by Ward *et al.* (2005), all 207 fish species analyzed could be separated by COI barcoding. Here, the average K2P distance within species was 0.39 %, within genera 9.93 %, and within families 15.5 %. This study indicated that COI barcodes are very efficient and reliable for identifying fish

species. A later study involving 388 species of jawed fish showed an average within-genera K2P distance of 9.54 %, with a range of 0.35 – 21.96 %. All species except for two (with possible hybridization issues) were separated well by sequencing the barcode region (Ward and Holmes 2007).

1.4 Aims of this study

The problems concerning the identification of the MAR-ECO specimens and the inconsistency of the taxonomic history of *S. kaupii* and *S. affinis* make a reappraisal of the status of these species appropriate. New contributions to their taxonomy are hereby made due to the availability of many specimens and the application of modern molecular genetic techniques. This study incorporates more morphometric and meristic characters than previous studies, and DNA sequences have previously not been applied to the taxonomy of these eels. All studied characters are analyzed, but the traditionally used diagnostic characters have received special attention. Sulak and Shcherbachev (1997) described the dentition on the vomer and the premaxillare-ethmoid complex, and these characters are also studied in detail.

The aims of this study are: to describe the observed morphological variation and identify and define possible groupings, to assess the molecular variation in COI over the range of the morphological variation in the material and identify possible cryptic species, and to analyze the validity of previously used diagnostic characters, with focus on the origin of the dorsal fin, number of vertebrae, shape and pattern of the scales, and the dentition of vomer and the premaxillare-ethmoid complex.

2 Materials and methods

2.1 Material examined

Most of the specimens from the MAR-ECO cruise in 2004 were collected by bottom trawls. A few were collected with pelagic trawls and longlines. The type specimens of *Synaphobranchus affinis* and *S. brevidorsalis* were provided by the British Museum of Natural History. These were collected during the HMS *Challenger* expedition 1873-76. The gear used for these collections is not specified, but was likely to have been either dredges or bottom trawls.

Tissue samples were taken from all the MAR-ECO specimens. An L-shaped cut was made in the dorsal region of the fish and muscle tissue was placed in 96 % ethanol. Skin tissue was not sampled due to possible contamination. Scalpel and forceps were cleaned and burned between each sample. Every tissue sample was labeled with the specimen`s identification number.

The specimens used in the molecular analysis were selected to cover the range of the morphological characters and geographical distribution as far as possible. Both extreme and middle values were covered. Table 1 lists the genetically examined MAR-ECO specimens. COI-sequences were also retrieved from GenBank (www.ncbi.nlm.nih.gov/Genbank/) for use in the molecular analyses: four sequences of North Atlantic *S. kaupii*, accession numbers EU148341, EU148342, EU148343, and EU148344, one sequence of a Pacific *S. kaupii*, accession number NC005805, one sequence of *Diastobranchus capensis*, accession number EF609343, and two sequences of *Ilyophis brunneus*, accession numbers EU148213 and EU 148214.

The syntypes of *S. affinis* and *S. brevidorsalis* were fixated in formalin and thus no DNA sequences could be obtained from them.

Table 1: Genetically examined MAR-ECO material. The tissue samples are located at Bergen Museum, ZMUB

Identification number	Individual number	No.
ME 1196	-	1
ME 4756	4, 5, 6, 7, 8	5
ME 4758	3, 4, 5, 6, 8, 10	6
ME 4772	2, 5, 7, 8, 9	5
ME 4774	1, 2, 3, 7	4
ME 4816	3, 4, 5, 6, 7, 8	6
ME 4830	3, 7	2
ME 7469	-	1
ME 10799	1, 2, 3, 4, 11, 12, 13	7
ME 11502	1, 3, 8, 10, 17	5
ME 12195	1, 2, 3, 5, 6, 8, 10, 23	8
ME 12263	1, 2, 4, 5, 7, 8	6
ME 17379	1	1
ME 20793	1, 2, 3	3
Total		60

All specimens were given individual tags with identification number and were fixated in formalin or ethanol prior to the morphological examination. The formalin fixation was done by injecting 6 % formalin into the viscera of the fish before soaking the fish in 4 % formalin for 5 days. Then they were placed in a tub with running water for 24 hours. The specimens were wrapped in cloth and stored in 75 % ethanol.

The morphologically examined material is listed in table 2. Figure 3 and 4 show maps of the stations and series where the examined material was collected.

The type specimen of *S. brevidorsalis* was examined in this study to see how a more clearly distinct species of *Synaphobranchus* would compare to the other examined specimens.

Table 2: Morphologically examined material. The MAR-ECO (ME) specimens are located at Bergen Museum, ZMUB.

Identification number	No.	Total length	Position	Depth	Vessel	Station	Equipment	Collection date
ME 1196	1	206 mm	60°21'N, 28°25'W	850-1260 m	RV *G.O. Sars*	Series 1009	Pelagic fish trawl	10. June 2004
ME 4756	12	357-611 mm	42°56'N, 29°32'W	1702-1767 m	RV *G.O. Sars*	Series 1151	Bottom trawl	9. July 2004
ME 4758	10	501-590 mm	42°56'N, 29°32'W	1702-1767 m	RV *G.O. Sars*	Series 1151	Bottom trawl	9. July 2004
ME 4772	10	521-641 mm	42°56'N, 29°32'W	1702-1767 m	RV *G.O. Sars*	Series 1151	Bottom trawl	9. July 2004
ME 4774	10	380-654 mm	42°56'N, 29°32'W	1702-1767 m	RV *G.O. Sars*	Series 1151	Bottom trawl	9. July 2004
ME 4816	8	498-582 mm	42°56'N, 29°32'W	1702-1767 m	RV *G.O. Sars*	Series 1151	Bottom trawl	9. July 2004
ME 4830	9	484-598 mm	42°56'N, 29°32'W	1702-1767 m	RV *G.O. Sars*	Series 1151	Bottom trawl	9. July 2004
ME 7469	1	484 mm	41°43'N, 30°00'W	674-1494 m	RV *G.O. Sars*	Series 1135	Krill trawl	30. June 2004
ME 10729	1	364 mm	51°20'N, 28°52'W	3505-3527 m	RV *G.O. Sars*	Series 1159	Bottom trawl	16. July 2004
ME 10799	9	477-660 mm	51°34'N, 30°19'W	1237-1296 m	RV *G.O. Sars*	Series 1161	Bottom trawl	19. July 2004
ME 11502	10	417–693 mm	49°52'N, 29°38'W	981-1003 m	RV *G.O. Sars*	Series 1157	Bottom trawl	15. July 2004
ME 12195	17	440-668 mm	49°52'N, 29°38'W	966-1019 m	RV *G.O. Sars*	Series 1158	Bottom trawl	15. July 2004
ME 12263	8	461-547 mm	42°49'N, 29°38'W	2063-2107 m	RV *G.O. Sars*	Series 1150	Bottom trawl	8. July 2004
ME 17379	2	490-617 mm	42°25'N, 29°38'W	1580-1964 m	MS *Loran*	Series 10022	Longline	8. July 2004
ME 20793	3	398-436 mm	42°49'N, 29°38'W	2063-2107 m	RV *G.O. Sars*	Series 1150	Bottom trawl	8. July 2004
BMNH 1887.12.7.250 Syntype *S. affinis*	1	371 mm	35°11'N, 139°28'E	631 m	HMS *Challenger*	Station 232		12. May 1875
BMNH 1887.12.7.256 Syntype *S.brevidorsalis*	1	593 mm	02°33'S, 144°04'E	1958 m	HMS *Challenger*	Station 218		1. March 1875
Total	113	206-693 mm		631-3527 m				

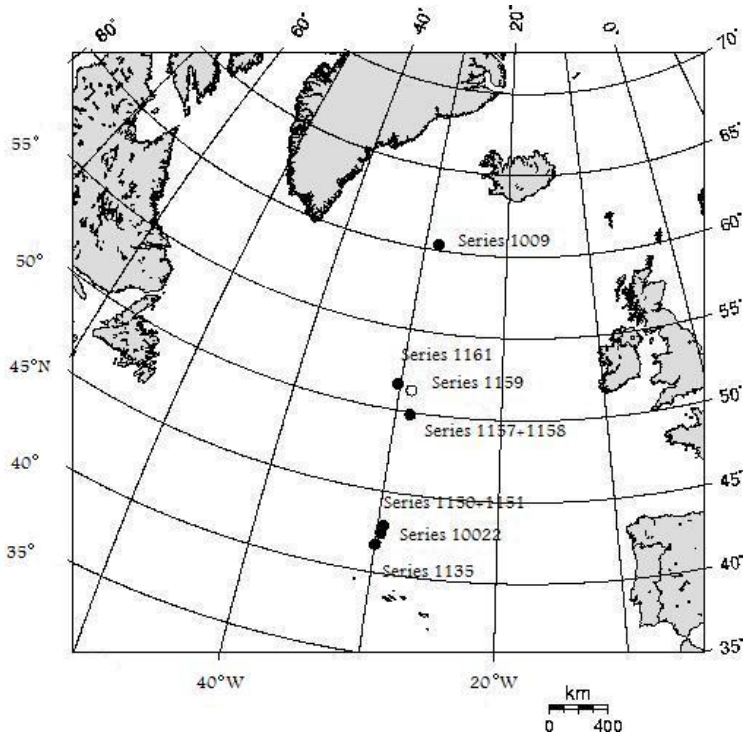

Figure 3: The MAR-ECO series, North Atlantic. Black dots denote both morphology and molecular study sites. White dots denote only morphological study.

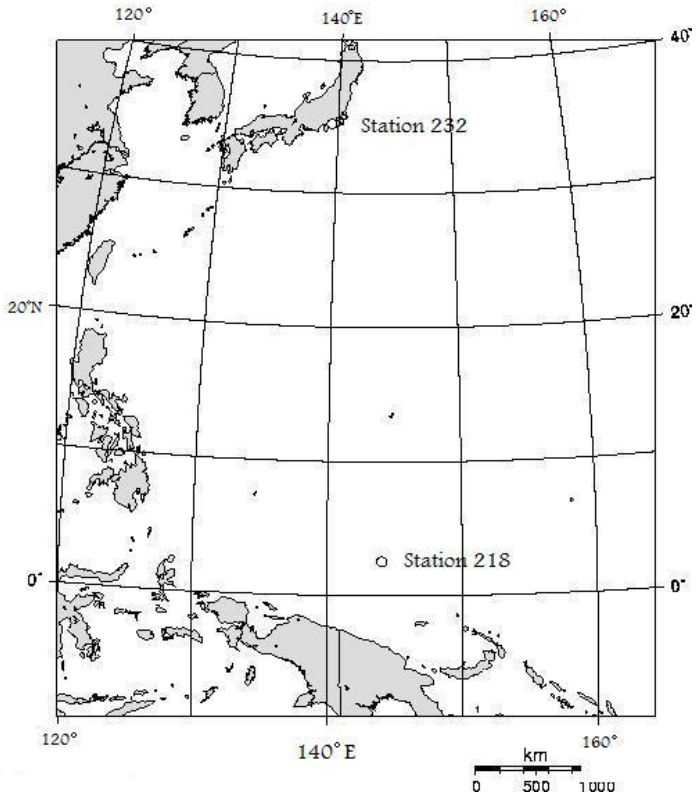

Figure 4: The HMS *Challenger* stations, Western Pacific.

2.2 Morphology

2.2.1 Morphometric characters

Total length, standard length, predorsal length, and preanal length were measured using a ruler of 1 mm accuracy. All other measurements were done with a vernier caliper of 0.1 mm accuracy. Every measurement, except pectoral fin length (the longest fin was measured), were taken from the left hand side of the specimens.

List of measured characters following Böhlke (1989):

- Total length, TL: From tip of snout to the end of the caudal fin.
- Predorsal length, PD: From tip of snout to the anterior origin of the dorsal fin.
- Preanal length, PA: From tip of snout to the anterior margin of anus.
- Head length, HL: From tip of snout to the dorsal edge of the pectoral fin base.
- Pectoral fin length, P: From the dorsal edge of pectoral fin base to the tip of the pectoral fin. Note: The fin tapers out to a thin tip, and this is sometimes lost. The fins on both sides of the body were measured and the longest was recorded.
- Upper jaw length, J: From tip of snout to end of the gape with mouth closed.
- Lower jaw length, LJ: From tip of lower jaw to the end of the gape with mouth closed.
- Snout length, S: From tip of snout to anterior margin of eye.
- Eye diameter, E: From anterior margin to posterior margin of eye.
- Length of gill slits, GS: From anterior to posterior margin of the gill slit.
- Interorbital width, IW: Distance between dorsal margins of eyes.
- Body depth, DA: From the vent to the top of the dorsum at a right angle.

List of additional measurements:

- Standard length, SL: From tip of snout to posterior end of tail, at the base of the caudal fin.
- Nose length, N: Distance between anterior and posterior nostril.
- Nostril to eye, NE: Distance between posterior nostril and anterior margin of eye.
- Anus to anal fin, AA: Distance between vent and anterior origin of the anal fin.

The measuring points are shown in figure 5. The projections are illustrated, but shortest distances were measured.

The distance from the level of the vent to the level of the dorsal fin origin expressed as number of pectoral fin lengths (DAP), was calculated. This is a diagnostic character for the studied species according to Sulak and Shcherbachev (1997) and Almeida and Biscoito (2007).

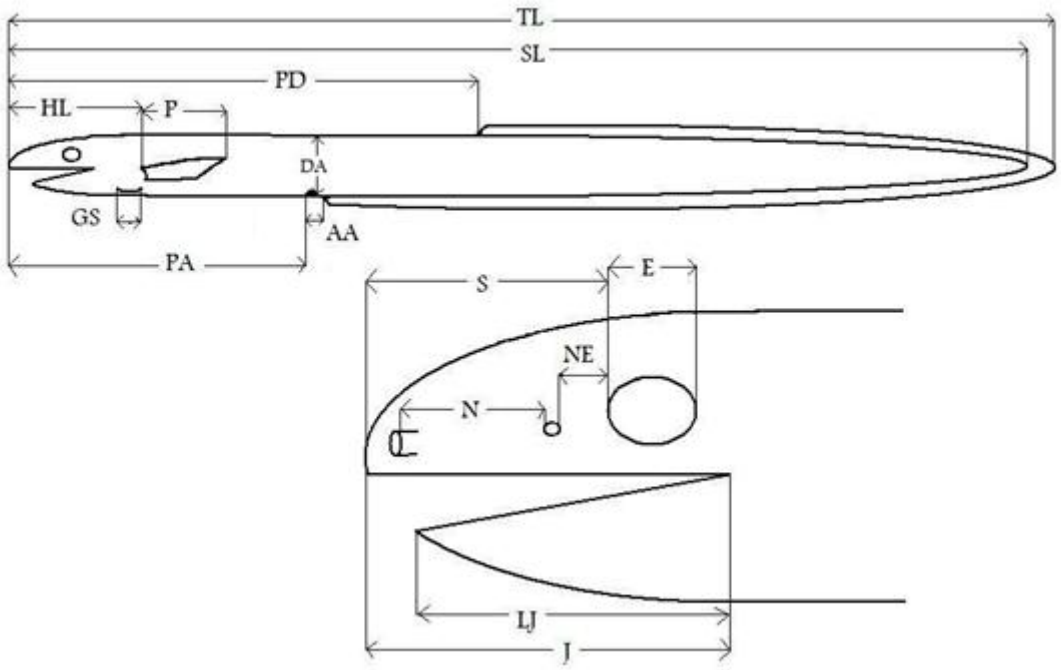

Figure 5: Schematic diagram over measurements. The projections are shown here, but the shortest distance between the measuring points were actually measured.

2.2.2 Meristic characters

A dissecting microscope was used when pores of the lateral line system were counted.

All individuals were x-rayed, so vertebrae and fin-rays could be counted. The specimens were pinned down on styrofoam with plastic strips and pins. Especially the tip of the tail needed to be pinned down because of its twists and curls. The specimens were tagged with lead-filled letters for identification. Because of the length of most specimens we had to take two x-ray pictures of each to get the entire length. A pin was inserted into the dorsum of the specimens as a reference point and this pin was included in both x-ray pictures. The x-rays

were taken by a Philips K 140 Be x-ray machine. The settings used were 25kV, 2mA, for 80 seconds.

The x-ray films were developed in a dark room, using the following protocol: 4 minutes in developer (AGFA G128, diluted: 1 part developer, 3 parts distilled water), rinse in water for about 30 seconds, 2 minutes in fix (AGFA G328), rinse in water. The films were hung to dry over night.

List of meristic characters following Böhlke (1989):

- Lateral line pores, LL: Number of pores in the lateral line canal along the body.
- Supraorbital pores, SO: Number of pores along the supraorbital canal.
- Infraorbital pores, IO: Number of pores along the infraorbital canal. I also include the adnasal pore (AD) in this count.
- Preopercularmandibular pores, POM: Number of pores along the preopercularmandibular canal.
- Frontal pores, F: Number of pores along the frontal canal.
- Supratemporal pores, ST: Number of pores along the supratemporal canal.
- Total vertebrae, V: Total number of vertebrae.
- Predorsal vertebrae, VPD: Number of vertebrae from anterior to and including the vertebra right under the dorsal fin origin.
- Preanal vertebrae, VPA: Number of vertebrae from anterior to and including the vertebra right above the anal fin origin.
- Dorsal fin rays, DR: Number of rays from the anteriormost ray of the dorsal fin to the midline of the caudal fin.
- Anal fin rays, AR: Number of rays from the anteriormost ray of the anal fin to the midline of the caudal fin.

One additional meristic character was registered:

- Preanal lateral line pores, LLA: Number of pores in the lateral line canal in front of the level of the vent.

The character number of lateral line pores has a lower n than most other characters due to damaged lateral lines on the posterior end of the tails of many specimens. Also, the anterior dorsal fin rays were very difficult to see on the x-ray pictures. This is the reason for the low n in the characters dorsal fin ray count and predorsal vertebrae. The anterior dorsal fin rays of the two type specimens from the Pacific were easier to locate.

2.2.3 Structural characters

A dissection microscope was used during the examination of scales and dentition.

List of structural characters:

- Pore positions of the cephalic lateral line system. Plotted in a schematic diagram.
- Scale shape and pattern: The scale shape was registered as one of three categories; a): elongate, b): oval, or c): more rounded. These categories are equal to the figure showing the scales of *S. kaupii* (category a)), *S. affinis* (category b)), and *S. brevidorsalis* (category c)), in Sulak and Shcherbachev (1997). The investigated area was close to the lateral line just above the vent. The categories are shown in figure 6.
- Dentition of the premaxillary-ethmoid complex, PME: The large teeth were schematically plotted. The plots could be placed into eight categories shown in figure 7. Category a): a straight median line. Category b): a straight median line with one tooth between this line and the margin. Category c): an uneven median line. Category d): a straight median line with one pair of parallel teeth. Category e): a straight median line with one pair of parallel teeth and one tooth between the median line and the margin. Category f): an uneven median line with one tooth between this line and the margin. Category g): a straight median line with two parallel pairs of teeth. Category h): a straight median line with two teeth on both sides of this line, symmetrically placed.
- Dentition of the vomer, VO: Registered as one of three categories, shown in figure 8. Category a): a straight uniserial line. Category b): an uneven uniserial line. Category c): at least one pair of parallel teeth.

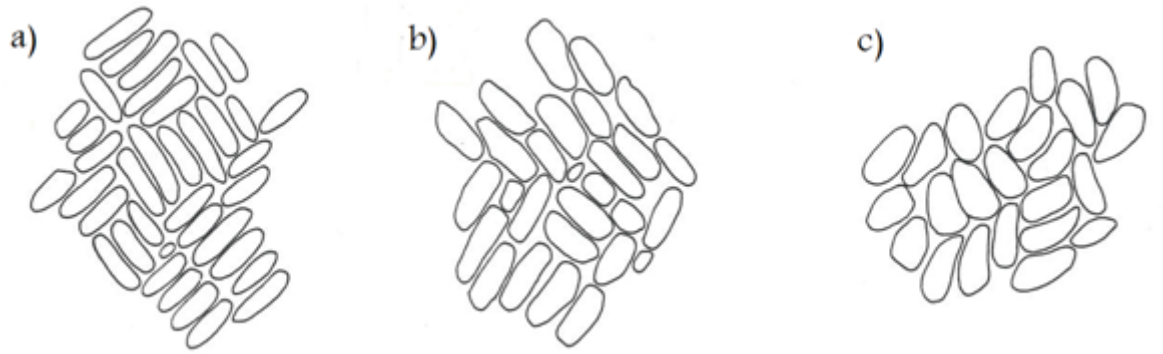

Figure 6: Categories of scale shape and pattern (near the lateral line above the vent). The drawings are taken from Sulak and Shcherbachev (1997), and according to their study: category a) is *S. kaupii*, b) is *S. affinis*, and c) is *S. brevidorsalis.*

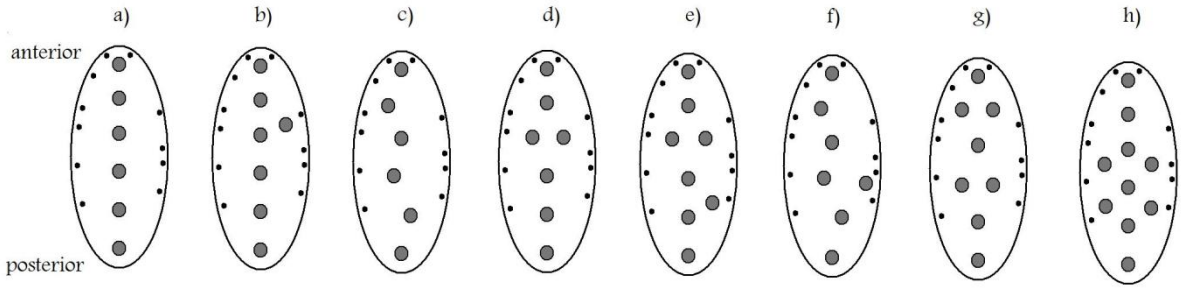

Figure 7: Schematic diagram of the categories of the dentition of the premaxillare-ethmoid complex, seen ventrally. The grey circles denote large teeth, and the small, black dots denote small teeth. There is no attempt to categorize the small teeth.

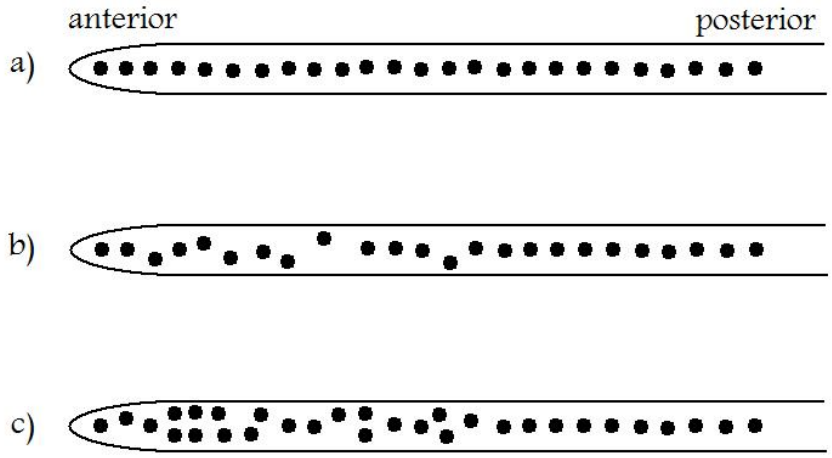

Figure 8: Schematic diagram of the dentition of the vomer, seen ventrally. Black dots indicate teeth. Category a) is a straight, uniserial line. Category b) is an uneven line, and category c) is more scattered, with at least some teeth in parallel lines.

One specimen (ME 12195-1) was dissected, and the results are shown in Appendix VI.

2.2.4 Statistical analyses

Univariate analyses:

Calculations, the Shapiro-Wilk test, histograms, regressions, F-tests, and plots are executed and made in the statistical program R, version 2.8.0 (R Development Core Team 2008). Commands and calculations executed in R are shown in Appendix IV. Bar plots of the meristic characters are made using Excel 2007. Range, mean, and standard deviation are calculated for all the morphometric and meristic characters. The distributions for the all variables are tested for normality using the Shapiro-Wilk test (Shapiro and Wilk 1965). The types of *S. affinis* and *S. brevidorsalis*, and Johnson`s measured example of *S. kaupii* (Johnson 1862), are tested against the MAR-ECO specimens by a test for outliers (Sokal and Rohlf 1995). This is done to examine if it is possible that these specimens can be included in the MAR-ECO population. All characters are plotted against the total length, and a linear model is fitted to the plot. F-tests are used to check whether a linear regression or the null model (the mean value) explains the plot better. This is done to check for character variation due to size. Only one specimen was smaller than 350 mm total length, namely ME 1196 (206 mm). Preliminary investigations showed that this specimen affected the regressions significantly, so this specimen is removed from this part of the analysis.

Multivariate analyses:

The multivariate analyses were performed in the statistical program CANOCO 4.5 (ter Braak and Smilauer 2002). Morphometric and meristic characters that have been previously used to separate *S. kaupii* and *S. affinis* were analyzed by ordination methods. Predorsal length, dorsal fin origin in relation to the vent, lateral line pores in front of the vent, number of vertebrae, and pectoral fin length were the chosen variables. CANOCO 4.5 does not allow empty spaces in the data set so this reduced the number of usable characters.

A preliminary Detrended Correspondence Analysis (DCA) was executed to see whether a linear or unimodal model was appropriate.

To check whether the specimens will differentiate into groups and to check for correlation between variables, a Principal Components Analysis (PCA) was executed. The different units for the different variables were compensated for by choosing the “center and standardize” option.

A Canonical Variate Analysis (CVA) was done to establish which characters that have power to discriminate between the species. This analysis demands that the specimens are put into predefined species prior to the analysis. The univariate analysis and PCA suggested that it was appropriate to use three groups: the MAR-ECO specimens, the *S. affins* type specimen, and the *S. brevidorsalis* type specimen. Settings for the CVA includes inter-species distances, Hill`s scaling, and Monte Carlo permutation test (999 permutations).

2.3 Molecular techniques

The gene selected for use in this study was the mitochondrial cytochrome c oxidase subunit I (COI). This gene was chosen based on its discriminating power at species level (Clare et al. 2007, Hebert et al. 2003, Ward and Holmes 2007, Ward et al. 2005). The primers used for amplification were primarily FishF2 and FishR2 (Ward et al. 2005) with additional use of LCO 1490 and HCO 2198 (Folmer et al. 1994) for some samples. The primer sequences are shown in table 3.

Table 3: Primer sequences

Primer	Sequence
Ward FishF2	5´ TCGACTAATCATAAAGATATCGGCAC 3´
Ward FishR2	5´ ACTTCAGGGTGACCGAAGAATCAGAA 3´
Folmer LCO 1490	5´ GGTCAACAAATCATAAAGATATTGG 3´
Folmer HCO 2198	5´ TGATTTTTTGGTCACCCTGAAGTTTA 3´

2.3.1 DNA extraction

DNA was extracted from ethanol preserved muscle tissue using the DNeasy blood & Tissue Kit from QIAGEN. The manufacturer`s protocol was followed with some minor modifications. Great care was taken to avoid contamination between the individual samples. An extraction negative control was also included in all rounds of DNA extractions using the same kit components and procedures, but without the addition of any tissue. This was done to check for possible DNA contamination of any of the extraction substances, and to check for cross-contamination from other DNA extracts.

DNA extraction protocol:

- About 2 mm^3 of muscle tissue was added to 180 µl of ATL buffer in a labeled 1.5 ml eppendorf-tube. 20 µl of Proteinase K (600 mAU/ml) was added. Tubes were vortexed, briefly centrifuged, and incubated at 56 °C for about 2 hours. During the two hours, the tubes were vortexed and centrifuged twice to ensure thorough mixing and complete tissue lysis.
- After incubation, 200 µl of AL buffer was added followed by vortexing for 15 seconds and brief centrifugation. The samples were then incubated at 70 °C for 10 min, followed by brief centrifugation.
- 200 µl of 96 % ethanol was then added, followed by vortexing for 15 seconds and brief centrifugation.
- The supernatant was then transferred from each eppendorf-tube to an individual spin column in a 2 ml collection tube. The caps were closed and the columns centrifuged at 8,000 rpm for 1 minute.
- The filtrate was discarded and the columns placed in a new QIA 2 ml tube. 500 µl of AW1 buffer was added and the caps closed. The columns were then centrifuged at 8,000 rpm for 1 minute.
- Again, the filtrate was discarded and the columns placed in a new QIA 2 ml tube. 500 µl of AW2 buffer was added, the caps closed, and columns were centrifuged at 14,000 rpm for 3 minutes.
- The columns were then placed in new 1.5 ml eppendorf-tubes. 200 µl of AE (elution) buffer was added to the column and the caps were closed. After incubation at room

temperature for 5 minutes to release the DNA from the column membrane, columns were then centrifuged at 8,000 rpm for 1 minute.

The eppendorf-tube containing the finished DNA extract was stored at 4 °C (long-term storage at -20 °C).

2.3.2 Polymerase Chain Reaction, PCR

All pre-PCR work was done on ice. All PCR reactions were done in 25 µl volumes. The "cocktail" of PCR-reagents contained (per sample): 14.5 µl dH_2O, 2.5 µl 10X PCR Buffer II, 2 µl $MgCl_2$ solution (25mM), 2 µl of 10 mM dNTPs, 1µl of each 10 µM primer (forward and reverse), and 0.2 µl AmpliTaq DNA Polymerase (5 U/µl), a total of 23.2 µl. 23 µl of this "cocktail" was put in a 0.2 ml tube. 2 µl of DNA extract was added, giving a total reaction volume of 25 µl. To check for possible contamination a negative control (PCR cocktail with no DNA added) was included in each round of the PCR reactions. A positive control (DNA known to amplify with these primers and PCR conditions) was also included to make sure every PCR reagent was added and that the thermal cycling had worked properly.

The thermal cycling program for the PCR reaction:

1. Denaturation at 94 °C for 1 minute and 30 seconds.
2. Denaturation at 94 °C for 30 seconds.
3. Primer annealing at 45 °C for 1 minute
4. Extension at 72 °C for 1 minute
5. Cycle to step 2 for 4 more times.
6. Denaturation at 94 °C for 30 seconds.
7. Primer annealing at 51 °C for 1 minute.
8. Extension at 72 °C for 1 minute.
9. Cycle to step 6 for 35 more times
10. Final extension at 72 °C for 5 minutes.

The PCR-products were stored at 4 °C prior to purification and sequencing.

All PCR reactions were performed on a "Peltier DNA Engine DYAD™ Thermal Cycler".

2.3.3 PCR product visualization and quantification

Gel electrophoresis (1 % agarose) was used to check and quantify the PCR products. Large gels were run at 90 mV for about an hour, to ensure good separation of the bands in the ladder to allow accurate DNA quantification. The gels were loaded with 4 µl of PCR-product and 1 µl of 5X loading buffer for each reaction. For each row of wells we loaded one well with 5 µl of ladder (ϕX 174). Gels were visualized under UV light in a SYNGENE UV-cabinet. GeneSnap software (Syngene) was used to capture gel images. The PCR-products (visible as single bands in the gel) were quantified using the computer program GeneTools (Syngene), using the known DNA quantities in the ϕX 174 ladder as a reference.

2.3.4 Purification of PCR products

Purification of PCR-products was done by addition of Exonuclease I (EXO) and Shrimp alkaline phosphatease (SAP) directly to the PCR product to remove unwanted dNTPs and primers. On ice, a cocktail consisting of 0.1 µl EXO (10 U/µl), 1.0 µl SAP (1 U/µl), and 0.9 µl of dH_2O per sample was prepared and 2 µl of this was added to 8 µl of PCR-product. After brief centrifugation, samples were placed in a thermal cycler and incubated at 37 °C for 30 minutes and then at 85 °C for 15 minutes (to deactivate the enzymes). The purified samples were stored at 4 °C.

2.3.5 Sequencing reaction

The primers used for amplification were also used for sequencing of the PCR products together with the BigDye Terminator v3.1 cycle sequencing kit (Applied Biosystems). For each sample, the sequencing reaction consisted of: 1 µl of sequencing buffer, 1 µl of Big Dye, 1 µl of primer (3.2 µM), and up to 7 µl of DNA (purified PCR-product) + dH_2O, to a total reaction volume of 10 µl. Separate sequencing reactions were performed for forward and reverse primers.

The thermal cycling program for the sequencing reaction:

1. Denaturation at 96 °C for 30 seconds.
2. Denaturation at 96 °C for 10 seconds.
3. Primer annealing at 50 °C for 10 seconds.
4. Extension at 60 °C for 4 minutes.
5. Cycle to step 2 for 29 more times.

Sequencing reactions were stored at -20 °C prior to delivery to the sequencing facility at the SARS Centre at Høyteknologisenteret i Bergen.

2.3.6 Sequence editing and analysis

DNA sequences were edited in MEGA 4 (Tamura et al. 2007). Sequence trace files were used to check any ambiguous base calls. All sites exhibiting variation were also checked carefully. This was done for both the forward and reverse reactions. Sequences with the reverse primers were reversed and the complimentary sequences were then able to be aligned with the forward sequences. After checking for conflicts between the forward and reverse sequence runs, the sequences were combined to form one single sequence for each sample. The alignment of the edited sequences was done using ClustalW, implemented in MEGA 4. Following editing and alignment, sequences were trimmed to equal lengths.

Five additional COI-sequences of *Synaphobranchus kaupii,* one sequence of *Diastobranchus capensis* and, two sequences of *Ilyophis brunneus* were added from GenBank. The *Diastobranchus* (same subfamily as *Synaphobranchus*) and *Ilyophis* (subfamily Ilyophinae) sequences were used as outgroups in subsequent analyses.

A matrix of Kimura two-parameter, K2P (Kimura 1980), distances was created for this data set using MEGA 4. The K2P model allows for differing rates of transitions (purine to purine or pyrimidine to pyrimidine changes) and transversions (changes from a purine to a pyrimidine, or vice versa) (Page and Holmes 1998, Kimura 1980). This model also corrects for multiple hits (multiple mutations at the same site) and assumes the four nucleotide frequencies to be equal. A phylogenetic tree was then constructed using the Neighbor-Joining (NJ) algorithm (Saitou and Nei 1987). NJ is fast and performs well on data where the divergence is small (Holder and Lewis 2003, Kumar and Gadagkar 2000). Support for nodes within the tree was estimated by 2000 bootstrap replicates.

3 Results

3.1 Morphology

The total length range in this study was 206 – 693 mm, with a mean value of 536.5 mm, but only one of the 113 examined specimens was shorter than 350 mm. The morphometric and meristic data set is listed in Appendix III.

3.1.1 Univariate analyses

The range, mean, standard deviation (SD), and number of examined specimens (n), of morphometric and meristic characters, are listed in table 4. Morphometric characters, located on or near the head, expressed as % of head length, are listed in Appendix V.

Table 4 also shows the test results of the Shapiro-Wilk normality test. This test tests the null hypothesis that the sample comes from a normally distributed population. A normal distribution of the observed morphological variation is expected when dealing with one species. If several species were examined, some kind of multimodal distribution would be expected. Three of the 16 measured characters reject the null hypothesis with the chosen critical probability value of 0.05. The morphometric characters standard length, eye diameter, and distance from posterior nostril to the eye are not normally distributed. Figure 9 shows histograms of the distributions of the measured characters. The distributions of lateral line pores, lateral line pores in front of vent, preopercularmandibular pores, and number of vertebrae are shown in figure 10. Lateral line pores and anal fin rays are the only meristic characters with a normal distribution according to the Shapiro-Wilk test. Of the cephalic lateral line pores, the preopercularmandibular pores showed some variation, but a normal distribution was rejected ($p < 0.0001$). Predorsal vertebrae and dorsal fin rays cannot be tested for normality due to the low number of data for these characters.

Table 4: Character statistics. The range, mean, SD, and "value" are expressed as a % of total length, except for one character (dorsal fin origin in relation to the vent) which has number of pectoral fin lengths as the dividing unit. The n denotes number of examined specimens, W is the test statistics calculated in the Shapiro-Wilk test, "included" shows whether the test for outliers includes the single sample in the MAR-ECO population or not. Bold numbers denote where the syntypes are outside of the MAR-ECO range.

								Test for outliers					
					Shapiro-Wilk test			Syntype *S. affinis*			Syntype *S. brevidorsalis*		
Morphometric characters	Range	Mean	SD	n	W	Norm. distr.	p-value	Value	Included	p-value	Value	Included	p-value
Standard length	97.6-99.0	98.59	0.24	111	0.9444	No	0.0002	97.8	no	<0.005	**97.1**	no	<0.001
Predorsal length	27.6-43.2	36.62	3.05	111	0.9840	yes	0.2070	32.1	yes	>0.10	**46.7**	no	<0.002
Preanal length	25.3-30.6	28.11	0.95	111	0.9945	yes	0.9437	27.0	yes	>0.20	**32.2**	no	<0.001
Head length	11.5-14.6	13.03	0.56	111	0.9861	yes	0.3101	14.3	no	<0.05	13.5	yes	>0.20
Upper jaw length	6.9-9.0	8.09	0.41	111	0.9889	yes	0.5035	7.7	yes	>0.20	7.1	no	<0.02
Lower jaw length	6.8-8.8	7.92	0.41	111	0.9921	yes	0.7752	7.4	yes	>0.20	7.0	no	<0.05
Snout length	3.5-4.8	4.09	0.25	111	0.9943	yes	0.9319	4.0	yes	>0.50	3.5	no	<0.05
Eye diameter	1.3-2.3	1.59	0.13	111	0.9137	No	<0.0001	1.8	yes	>0.20	1.8	yes	>0.10
Nostril to eye	0.3-0.8	0.57	0.08	111	0.9754	No	0.0376	0.5	yes	>0.50	0.4	yes	>0.05
Nose length	1.4-2.2	1.89	0.16	110	0.9897	yes	0.5750	1.5	no	<0.01	1.5	no	<0.05
Vent to anal fin	0.7-1.9	1.32	0.23	111	0.9832	yes	0.1792	0.9	yes	>0.10	1.5	yes	>0.50
Pectoral fin length	4.2-5.8	5.14	0.36	111	0.9888	yes	0.4948	**6.4**	no	<0.001	4.7	yes	>0.20
Body depth	3.1-8.9	5.75	1.06	103	0.9849	yes	0.2928	6.4	yes	>0.50	6.3	yes	>0.50
Gill slit length	1.1-2.2	1.60	0.22	111	0.9930	yes	0.8468	-	-	-	1.8	yes	>0.20
Interorbital width	1.0-2.2	1.62	0.20	108	0.9850	yes	0.2684	-	-	-	**2.5**	no	<0.001
Dorsal fin origin in relation to the vent	0.0-3.1	1.67	0.61	111	0.9885	yes	0.4719	0.8	yes	>0.10	3.1	no	<0.05
Meristic characters													
Lateral line pores	131-153	141.1	4.0	79	0.9828	yes	0.3669	139	yes	>0.50	**125**	no	<0.001
Lateral line pores to vent	29-34	31.4	1.2	111	0.9318	No	<0.0001	30	yes	>0.20	33	yes	>0.10
Supraorbital pores	6-7	6.0	0.1	109	0.0704	No	<0.0001	6	yes	>0.50	6	yes	>0.50
Infraorbital pores	7-9	8.0	0.2	108	0.2627	No	<0.0001	8	yes	>0.50	9	no	<0.001
Preopercularmandibular pores	10-13	12.1	0.6	106	0.7803	No	<0.0001	12	yes	>0.50	12	yes	>0.50
Vertebrae	145-152	148.0	1.7	111	0.9528	No	0.0006	**136**	no	<0.001	**127**	no	<0.001
Preanal vertebrae	29-34	31.9	1.1	101	0.9260	No	<0.0001	30	yes	<0.10	**35**	no	<0.01
Predorsal vertebrae	32-33	32.5	0.7	2	-	-	-	**35**	yes	>0.20	**50**	no	<0.05
Dorsal fin rays	325-360	342.5	24.8	2	-	-	-	**272**	yes	>0.20	**228**	yes	>0.10
Anal fin rays	265-325	294.9	16.7	16	0.9715	yes	0.8615	**241**	no	<0.01	**212**	no	<0.001

The results of the test for outliers are shown in table 4. With the chosen critical probability of 0.05, the type specimen of *S. affinis* is significantly different from the MAR-ECO population in four of the 14 morphometric characters. The test puts the *S. affinis* type specimen outside of the population for the characters standard length, head length, nose length, and pectoral fin length, but only pectoral fin length is outside of the range of the North Atlantic specimens. For the meristic characters, the *S. affinis* type specimen is significantly different from the MAR-ECO population in two of the 10 characters, namely vertebrae and anal fin rays. The low n for predorsal vertebrae and dorsal fin rays should be considered as the test includes the type specimen, but it falls outside of the ranges.

The syntype of *S. brevidorsalis* is significantly different from the MAR-ECO population in nine of the 16 measured characters, according to the test for outliers. It falls outside of the range in four characters: standard length, predorsal length, preanal length, and interorbital width. For the meristic characters it is significantly different in four of 10 characters by the test, but it falls outside of the range in six of 10 characters.

No type specimen of *S. kaupii* has been examined, but Johnson (1862) included some measurements of one individual in his description of this species. These measurements, expressed as inches and % of total length, are listed in table 5, together with the results of the test for outliers. This specimen falls outside of the MAR-ECO population in two characters: body depth and gill slit length.

Table 5: Morphometric characters from Johnson`s (1862) example.

			Test for outliers	
Character	Inches	% of total length	Included	p-value
Total length	32	-	-	-
Predorsal length	11.25	35.2	yes	>0.50
Preanal length	9.5	29.7	yes	>0.10
Head length	4.5	14.1	yes	>0.05
Eye diameter	0.5	1.6	yes	>0.50
Pectoral fin length	1.5	4.7	yes	>0.20
Body depth	3	9.4	no	<0.001
Gill slit length	0.9	2.8	no	<0.001

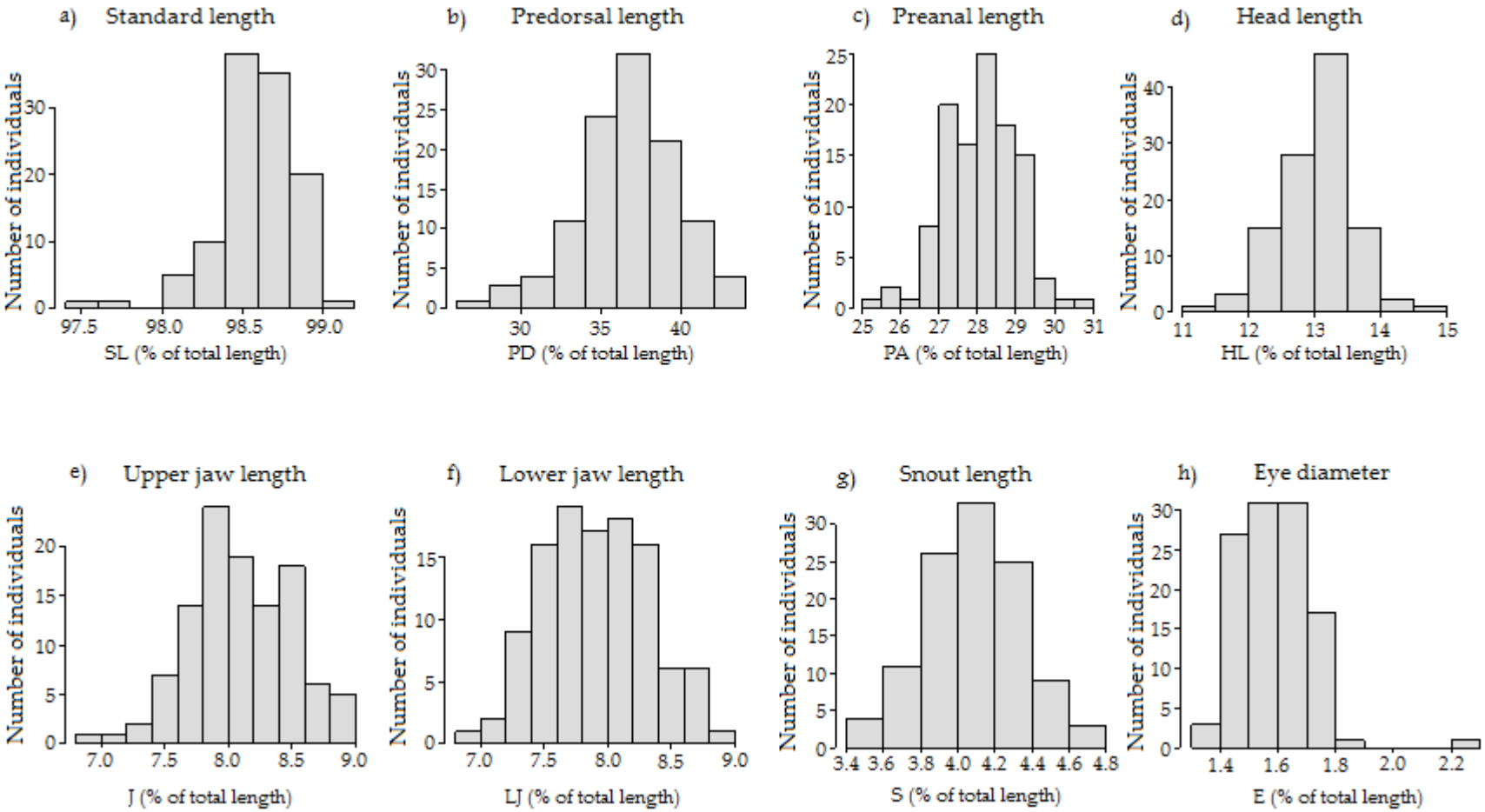

Figure 9: The distributions of the morphometric characters of the MAR-ECO specimens, expressed as % of total length. The character dorsal fin origin to vent (DAP) has number of pectoral fin lengths as unit.

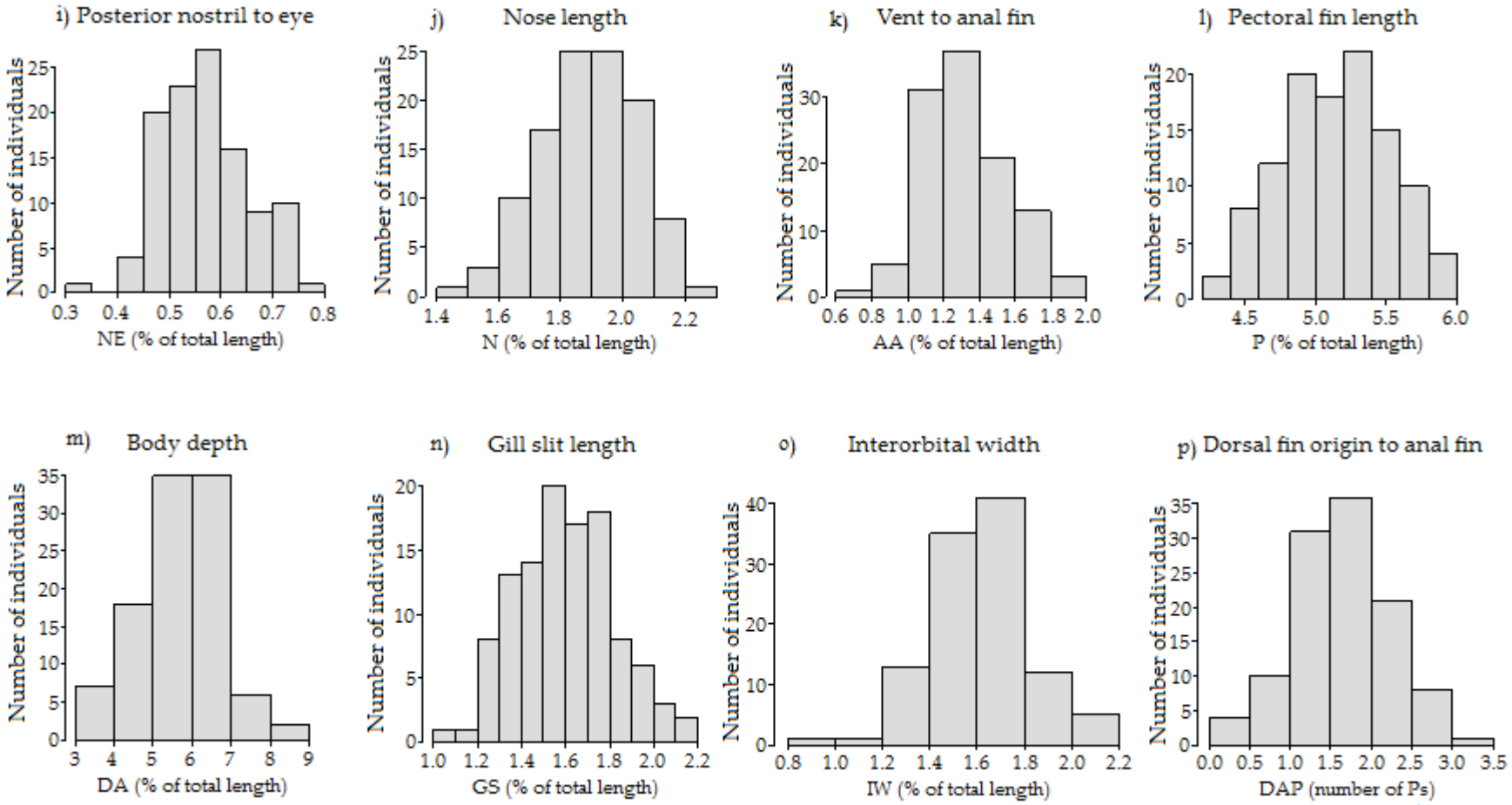

Figure 9 continued.

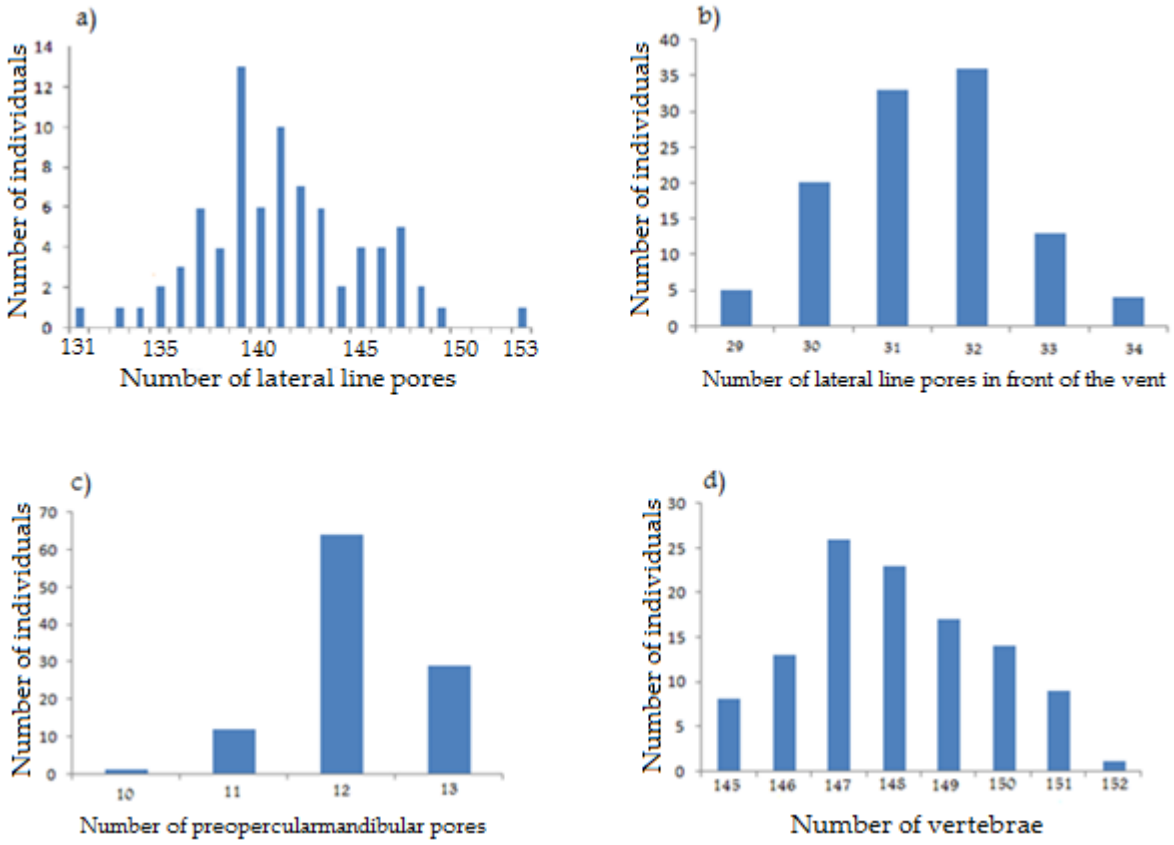

Figure 10: Distribution of meristic characters.

To check for variation due to ontogenetic changes, linear regressions were made for each of the characters plotted against the total length. Figure 11 shows the data distribution in relation to total length for the MAR-ECO specimens, and table 6 shows the p-values for the regression models and the regression formulae for the various characters. Predorsal length, distance from nostril to eye, distance from the vent to anal fin, gill slit length, and interorbital width, do not show any sign of relation to the total length, and the null model (the mean) is the best explanation of the data. Standard length, body depth, and dorsal fin origin in relation to the vent are increasing as the total length increases. Preanal length, head length, upper jaw length, lower jaw length, snout length, eye diameter, nose length, and pectoral fin length, show a decrease as the total length increases. None of the meristic characters showed any relationship to the total length. One specimen (ME 1196) was removed from the regression analyses. Its total length of 206 mm is much lower than the rest, and preliminary regression analyses showed that it affected the regression lines considerably. The measurements of this specimen are listed in table 7.

Table 6: Regression models and p-values. Due to the low value of the slope when considering millimeters, the scale in the regression formulae is set to decimeters, dm. “n” denotes the number of examined specimens.

Character	n	Regression	p-value	Regression formula
Standard length	110	yes	<0.0001	f(x) = 0.173x + 97.6
Predorsal length	110	no	0.1406	f(x) = 36.6
Preanal length	110	yes	0.0177	f(x) = -0.301x + 29.7
Head length	110	yes	0.0001	f(x) = -0.281x + 14.5
Upper jaw length	110	yes	0.0013	f(x) = -0.174x + 9.0
Lower jaw lenght	110	yes	0.0024	f(x) = -0.167x + 8.8
Snout length	110	yes	<0.0001	f(x) = -0.171x + 5.0
Eye diameter	110	yes	<0.0001	f(x) = -0.079x + 2.0
Nostril to eye	110	no	0.4353	f(x) = 0.6
Nose length	109	yes	<0.0001	f(x) = -0.095x + 2.4
Vent to anal fin	110	no	0.0510	f(x) = 1.3
Pectoral fin length	110	yes	<0.0001	f(x) = -0.306x + 6.8
Body depth	102	yes	<0.0001	f(x) = 0.773x + 1.6
Gill slit length	110	no	0.1907	f(x) = 1.6
Interorbital width	107	no	0.8824	f(x) = 1.6
Dorsal fin origin to anal fin	110	yes	0.0005	f(x) = 0.281x + 0.1

Table 7: Measurements of ME 1196

Character	Value
Total length	206 mm
Standard length	97.6 % of total length
Predorsal length	35.3 % of total length
Preanal length	27.1 % of total length
Head length	13.4 % of total length
Upper jaw length	7,9 % of total length
Lower jaw length	7.7 % of total length
Snout length	4.5 % of total length
Eye diameter	2.3 % of total length
Distance from nostril to eye	0.3 % of total length
Nose length	2.0 % of total length
Distance from vent to anal fin	0.7 % of total length
Pectoral fin length	5.6 % of total length
Body depth	3.5 % of total length
Gill slit length	1.4 % of total length
Interorbital width	1.3 % of total length
Dorsal fin origin in relation to the vent	1.5 pectoral fin lengths

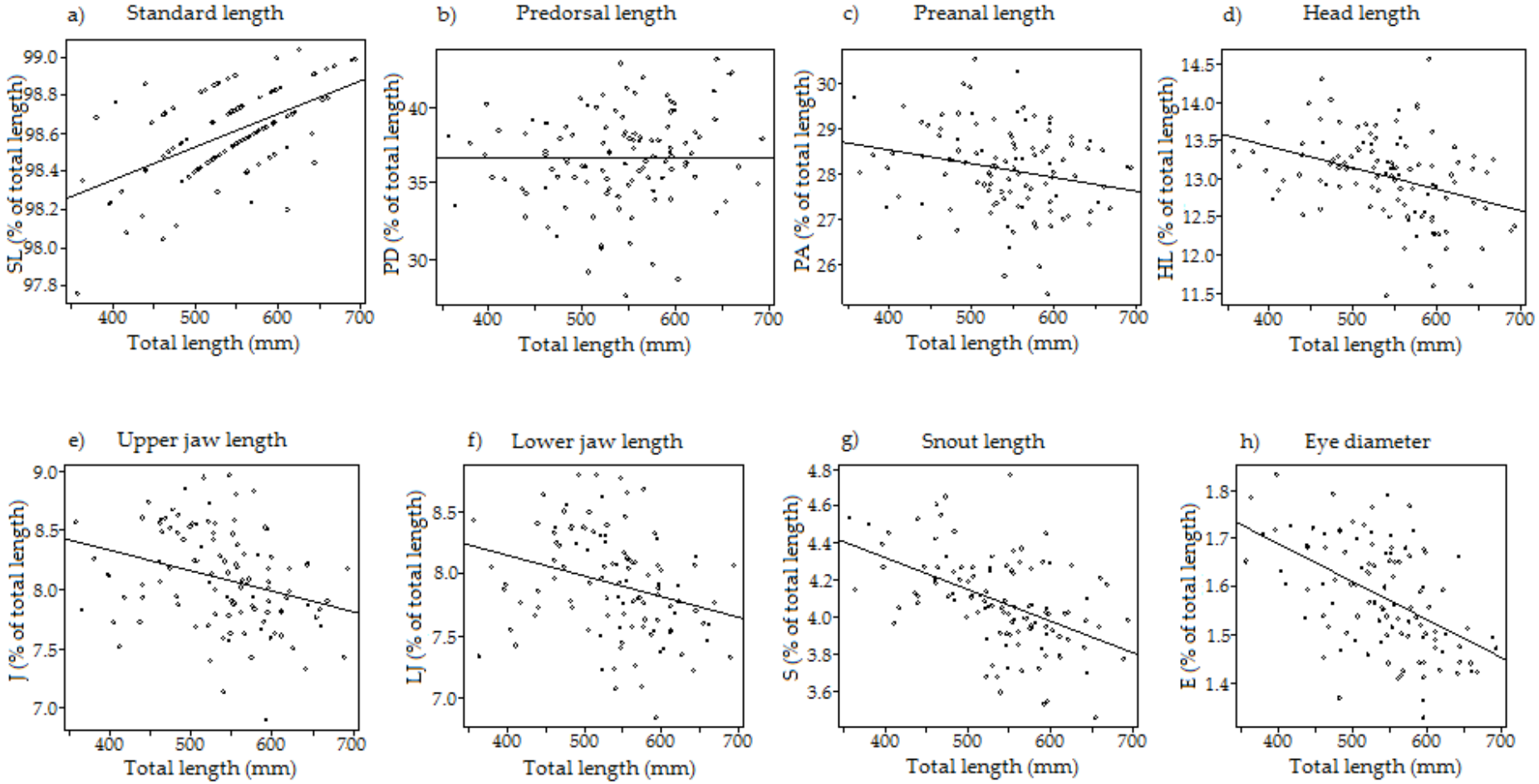

Figure 11: Linear regressions of the measured characters, with respect to the total length.

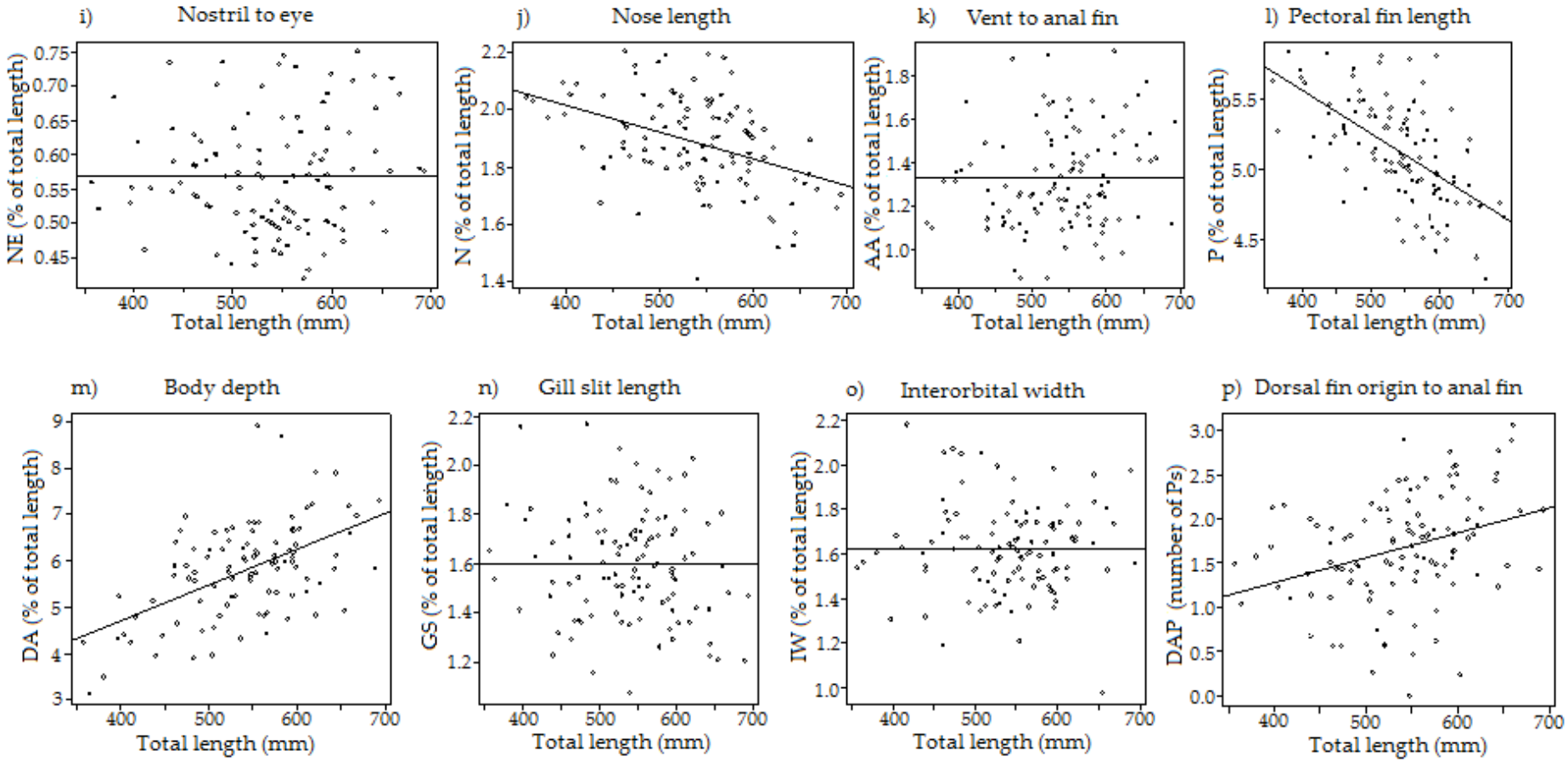

Figure 11 continued

Figure 12 shows the positions of the pores of the cephalic lateral line system. All but one of the 113 examined specimens had 6 supraorbital pores. The single specimen with 7 supraorbital pores had one extra pore between number 3 and 4, but had only 6 supraorbital pores on the other side of the head. 8 infraorbital pores were most common; only two specimens had 7 and three had 9 pores (the extra pores were located on different places). The type of *S. brevidorsalis* had 9 infraorbital pores, but only 8 on the other side of the head. Asymmetry in the cephalic lateral line system and the lateral line was observed in 9 specimens, but not all specimens were checked. More variation was seen in the preopercularmandibular pores, mainly between pore number 4 and 10. Twelve pores were most common (62 of 109). The one specimen with 10 preopercularmandibular pores was lacking pore number 10 and 11, but these were present on the other side of the head. The number of pores in the frontal canal (F) is 2. The number of supratemporal pores (ST) is 3, but one specimen had only 2 pores, and three specimens had 4 supratemporal pores. Two specimens had 2 adnasal pores (AD). Except for the 9 infraorbital pores on one side of the *S. brevidorsalis* type, both type specimens showed the pattern seen in figure 12, and this exact pattern was shared by 65 of the MAR-ECO specimens.

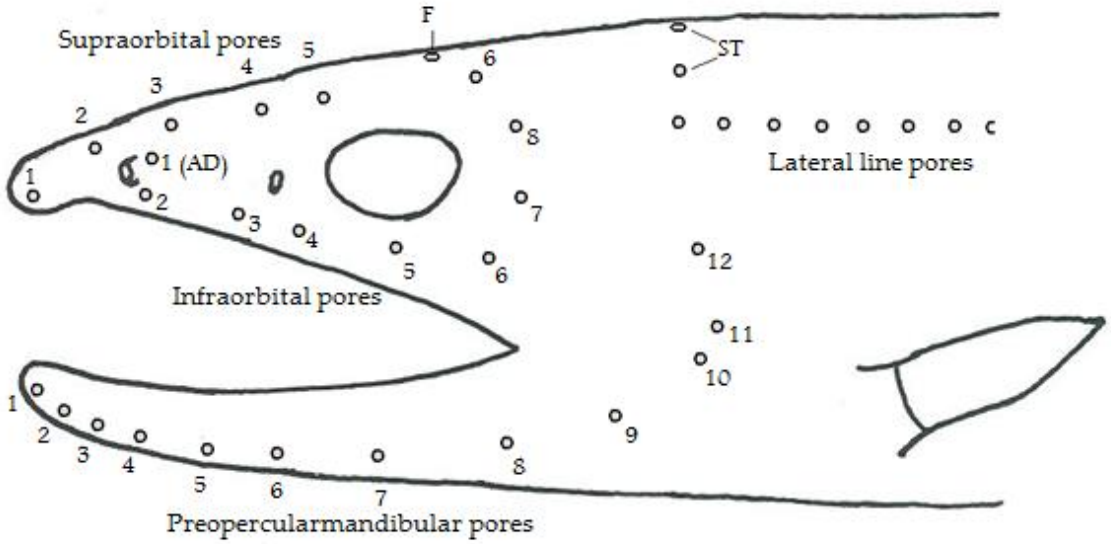

Figure 12: Schematic drawing of the cephalic lateral line pores. F denotes frontal pores, ST denotes supratemporal pores, AD denotes adnasal pores.

The number of specimens placed in the scale categories (figure 6) are listed in table 8. The examined area was close to the lateral line above the vent, but many of the specimens showed different scale shape and patterns on different areas of the body. This phenomenon was not investigated completely, but an example of the varying scale shape and pattern along the body is shown in figure 13. This specimen was placed in the b) category, but it shows a c)-type on the belly. The type specimen of *S. affinis* was placed in category b), and the type of *S. brevidorsalis* was placed in category c). Figure 14 shows a picture of the examined area of the specimen ME 17379-1.

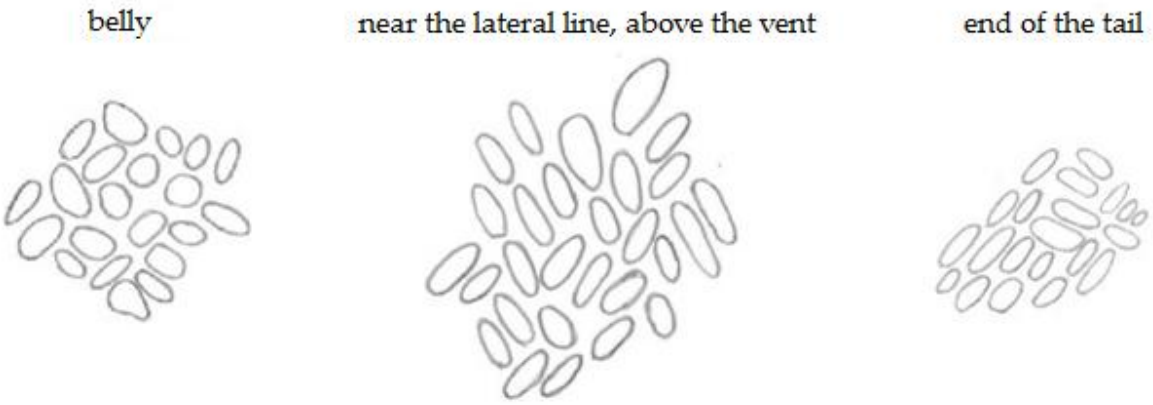

Figure 13: The scale shape and pattern of ME 12195-1, drawn from observation through a dissecting microscope.

Figure 14: Scales near the lateral line at the level of the vent. Picture taken of ME 17379-1, placed in category b).

The smaller, marginal teeth on the premaxillare-ethmoid complex (PME) showed no particular pattern, except that they were absent from the posteriormost area. Only six specimens showed some semblance of symmetry, and the number of marginal teeth varied from 4 to 14. The larger teeth seemed to be orientated along a median line in all specimens. The number of specimens with the different types of premaxillare-ethmoid dentition (figure 7) are listed in table 8. The most common pattern, found in 57 specimens, was a straight line along the middle of the PME. Some larger teeth could be found between the median line and margin, and some had a pair (one had two pairs) of larger teeth along the median line. The type specimen of *S. affinis* showed a type c) pattern with an uneven line along the middle of the PME. The type of *S. brevidorsalis* showed a unique pattern, h), with a median line with 2 larger teeth on both sides, symmetrically positioned. The number of large teeth varied from 2 to 8 (10 in *S.brevidorsalis*).

The dentition of the vomer was placed in three categories (fig 8) and the numbers of specimens placed in those categories are listed in table 8. The anteriormost teeth were sometimes a bit larger than the rest.

Table 8: Number of specimens placed in the categories of the characters scales, dentition of the premaxillare-ethmoid complex, and dentition of the vomer.

Character	Category	Number of specimens
Scales	a)	5
(categories, see fig. 6)	b)	103
	c)	5
Dentition of the premaxillare-ethmoid	a)	57
(categories, see fig. 7)	b)	16
	c)	11
	d)	10
	e)	2
	f)	1
	g)	1
	h)	1
Dentition of the vomer	a)	34
(categories, see fig. 8)	b)	22
	c)	56

3.1.2 Multivariate analyses

The longest gradient in the preliminary Detrended Correspondence Analysis (DCA) was 0.212, which is well below 3.0, so a linear method is appropriate (Leps and Smilauer 2003).

Figure 15 shows a biplot of the Principal Components Analysis (PCA) using the characters, predorsal length, lateral line pores in front of vent, vertebrae, and dorsal fin origin in relation to the vent. The eigenvalues for the first four axes are 0.399, 0.220, 0.204, and 0.171 respectively. The type specimens of *S. brevidorsalis* and *S. affinis* clearly stand out from the MAR-ECO specimens. They are both separated from the rest by their low number of vertebrae. The type of *S. affinis* is also separated by its long pectoral fin, while *S. brevidorsalis* is separated by predorsal length and dorsal fin origin in relation to the vent, in addition to the vertebrae.

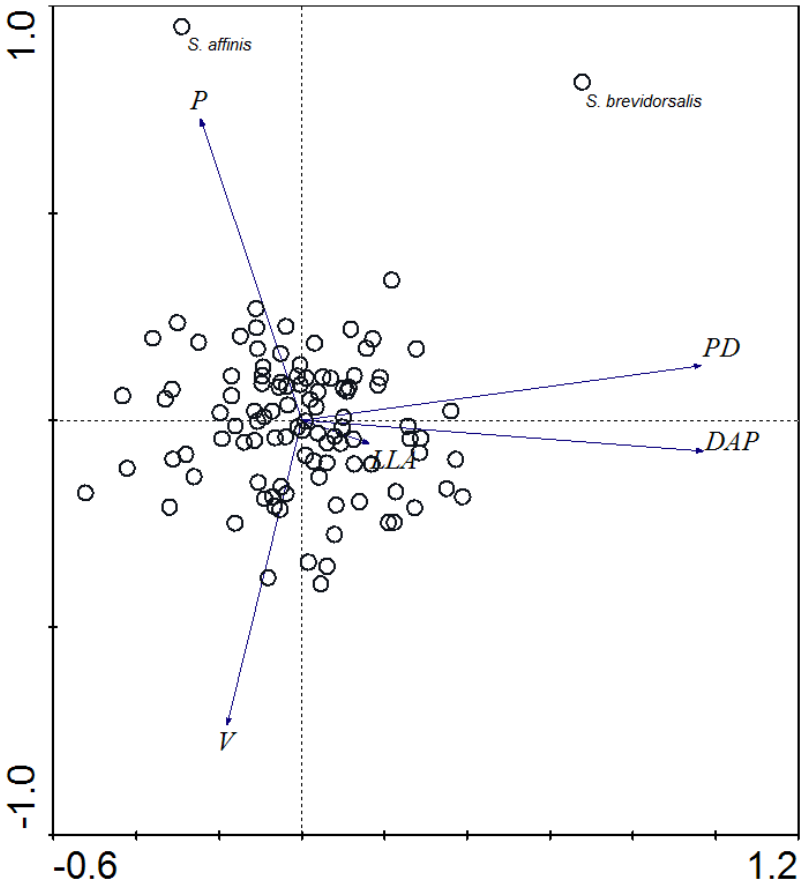

Figure 15: Ordination diagram of the Principal Components Analysis. The unmarked dots denote the MAR-ECO specimens. Abbreviations: Pectoral fin length (P), Predorsal length (PD), dorsal fin origin in relation to the vent (DAP), lateral line pores in front of vent (LLA), and vertebrae (V).

Figure 15 shows that predorsal length, dorsal fin origin in relation to the vent, and lateral line pores in front of the vent all show a positive correlation with the first axis. These characters are not correlated with vertebrae or pectoral fin length. Pectoral fin length and vertebrae are correlated with the second axis and negatively correlated with each other.

The MAR-ECO specimens, the type of *S. affinis*, and the type of *S. brevidorsalis* were viewed as three distinct entities in the Canonical Variate Analysis (CVA). The chosen critical p-value was 0.01 (Bonferroni-correction of 0.05). Vertebrae (V) came out as the best discriminating character (p-value 0.0010 after 999 permutations), explaining 0.647 of the total variation of 0.960. Pectoral fin length came out as second best (p-value 0.0020), explaining 0.117, followed by Predorsal length (p-value 0.0070), explaining 0.111, and dorsal fin origin in relation to the vent (p-value 0.0010), explaining 0.066 of the variation. These four characters together explain 0.928 of the total variation of 0.960. Lateral line pores in front of vent did not come out with discriminating power (p-value 0.032).

The CVA, done with only two distinct groups, *S. affinis* and the MAR-ECO specimens, gave two discriminating characters, using the Bonferroni-correction. Vertebrae explain the distinction best (p-value 0.008), accounting for 0.312 of the total variation of 0.442. Pectoral fin length is also a discriminating character (p-value 0.005), explaining 0.106 of the variation. Vertebrae and pectoral fin length together account for 0.418 of the total variation of 0.442.

3.2 Genetics

Most of the tissue samples examined were successfully extracted for genomic DNA and gave strong PCR products. Of 118 samples, only nine failed to yield any PCR product. Sixty specimens were sequenced for COI and sequences were trimmed to 652 basepairs (bp). The COI sequences are listed in Appendix VII. Two specimens were subsequently excluded from the analysis, namely ME 11502-10 and ME 4772-2. This was done because their sequences were shorter than the rest and their sequences showed no sign of constituting any unique haplotypes.

The morphological variations are very well covered by the molecular analysis. See table 9 for details. The premaxillare-ethmoid category h) is not covered, as only the syntype of *S. brevidorsalis* showed this type of dentition.

Table 9: The morphological variation covered by the molecular sequences, compared to the total morphological variation of all the MAR-ECO specimens. Bold font shows the extrema or categories not covered by the molecular analysis. Abbreviations: total length (TL) and pectoral fin length (P).

Character	Range covered by genetics	Range of all MAR-ECO specimens
Total length	206 – 693 mm	206 – 693 mm
Standard length	97.6 – 99.0 % TL	97.6 – 99.0 % TL
Predorsal length	27.6 – 43.2 % TL	27.6 – 43.2 % TL
Preanal length	25.3 – 30.6 % TL	25.3 – 30.6 % TL
Head length	11.5 – 14.6 % TL	11.5 – 14.6 % TL
Upper jaw length	6.9 – 9.0 % TL	6.9 – 9.0 % TL
Lower jaw length	6.8 – 8.8 % TL	6.8 – 8.8 % TL
Snout length	3.5 – 4.7 % TL	3.5 – **4.8** % TL
Eye diameter	1.3 – 2.3 % TL	1.3 – 2.3 % TL
Nostril to Eye	0.3 – 0.7 % TL	0.3 – **0.8** % TL
Nose length	1.4 – 2.2 % TL	1.4 – 2.2 % TL
Vent to Anal fin	0.7 – 1.9 % TL	0.7 – 1.9 % TL
Pectoral fin length	4.2 – 5.8 % TL	4.2 – 5.8 % TL
Body depth	3.5 – 8.9 % TL	**3.1** – 8.9 % TL
Gill slit length	1.1 – 2.2 % TL	1.1 – 2.2 % TL
Interorbital width	1.0 – 2.1 % TL	1.0 – **2.2** % TL
Lateral line pores	131 – 153	131 – 153
Lateral line pores in front of vent	29 – 34	29 – 34
Supraorbital pores	6 – 7	6 – 7
Infraorbital pores	7 – 9	7 – 9
Preopercularmandibular pores	10 – 13	10 – 13
Vertebrae	145 – 151	145 – **152**
Preanal vertebrae	29 – 34	29 – 34
Predorsal vertebrae	32 – 33	32 – 33
Dorsal fin rays	325 – 360	325 – 360
Anal fin rays	270 – 325	270 – 325
DAP	0.0 – 3.1 number of P	0.0 – 3.1 number of P
Scales	Categories a), b), c)	Categories a), b), c)
Vomerine dentition	Categories a), b), c)	Categories a), b), c)
Premaxillary-ethmoid dentition	Categories a), b), c), d), e)	Categories a), b), c), d), e), **f), g)**

Twenty-five different COI haplotypes were found in the 60 MAR-ECO specimens examined. Of the four GenBank sequences from the North Atlantic, one additional haplotype was found, giving a total of 26 haplotypes recovered for the North Atlantic. Most of the

haplotypes were represented by a single specimen; only four were represented by several specimens. The most common haplotype was found in 29 specimens. Single representatives of each of the four shared haplotypes were included in further molecular analyses, and these haplotypes were reffered to as groups A, B, C, and D. Table 10 lists the specimens included in these groups.

Table 10: Specimens with shared haplotype, listed in groups.

	No.	Specimens
Group A	7	ME 1196, ME 4756-6, ME 10799-2, ME 12195-5, ME 12195-23, ME 12263-2, EU148344.
Group B	29	ME 4756-5, ME 4756-8, ME 4758-3, ME 4758-4, ME 4758-5, ME 4758-6, ME 4758-10, ME 4772-5, ME 4772-8, ME 4774-3, ME 4774-7, ME 4816-3, ME 4816-4, ME 4816-5, ME 10799-11, ME 10799-12, ME 11502-1, ME 11502-8, ME 11502-17, ME 12195-1, ME 12195-2, ME 12195-6, ME 12195-10, ME 12263-1, ME 12263-4, ME 12263-7, ME 17379-1, ME 20793-2, EU148342.
Group C	2	ME 4758-8, ME 4772-9
Group D	2	ME 20793-3, EU148341

The neighbor-joining tree constructed from the obtained sequences and outgroups shows a clear grouping of the North Atlantic specimens (see figure 16). All North Atlantic specimens group together in a clade that shows an average within group K2P difference of 0.5 % (see distance matrix in Appendix VIII). Closest to this group is the NC005805 *S. kaupii* sequence retrieved from GenBank. The voucher specimen for this sequence is from Japan. The average distance between this sequence and the North Atlantic group is 8.7 %. The next branch consists of a single sequence from *Diastobranchus capensis*, a species in the same subfamily as *Synaphobranchus*, and the average distance between this and the North Atlantic specimens is 15.6 %. The two sequences of *Ilyophis brunneus*, a species from the same family, but different subfamily, constitute the last branch, and have an average distance of 19.8 % to the North Atlantic specimens. All the main branches have 100 % bootstrap support.

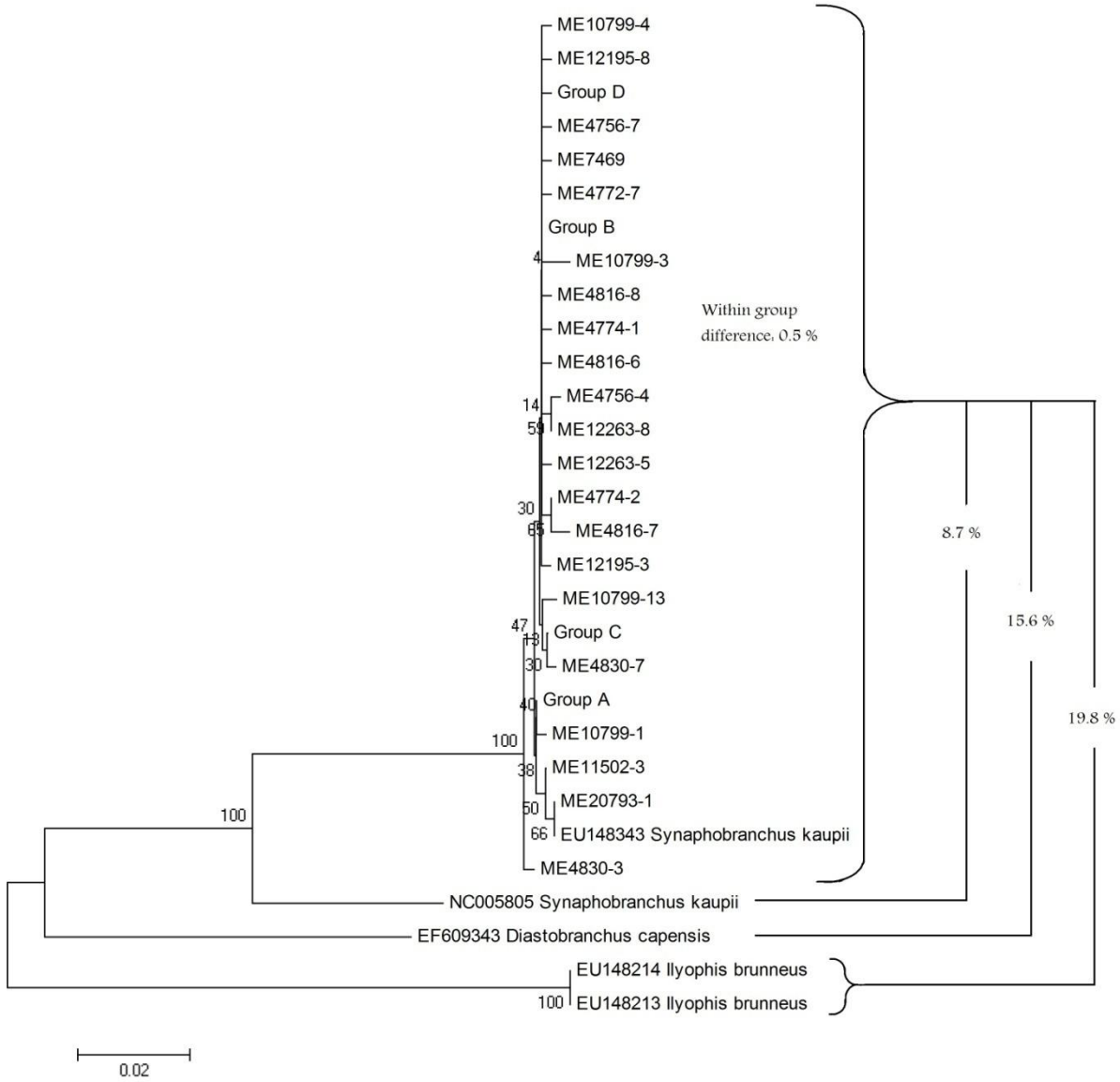

Figure 16: Neighbor-Joining tree of COI haplotypes, showing the branching and average distances of the examined sequences. GenBank sequences are indicated by accession numbers and full species names (three GenBank specimens are included in the groups, see table 10).

4 Discussion

Supported by both the morphological and molecular analyses, this study indicates that the MAR-ECO specimens constitute a single species. Their accordance with Johnson`s (1862) description and their high number of vertebrae show that they belong to the species *Synaphobranchus kaupii*. The comparison of the MAR-ECO specimens with a syntype of *Synaphobranchus affinis*, shows that the previously used diagnostic characters, dorsal fin origin in relation to the vent, predorsal length, scales, and dentition of vomer and the premaxillare-ethmoid complex (Almeida and Biscoito 2007, Bruun 1937, Castle 1964, Jordan and Snyder 1901, Matsubara and Ochiai 1951, Melo 2007, Okamura 1995, Robins 1971, Robins and Robins 1989, Sulak and Shcherbachev 1997), cannot be considered diagnostic between the two species. However, the present study suggests that *S. affinis* might constitute a distinct species, separable from *S. kaupii* by the total number of vertebrae. The analysis of the morphometric character variation in relation to the ontogeny shows a relation in 11 of the 16 examined characters, and thus caution should be used when comparing different size classes of these fish.

4.1 Morphological analyses

4.1.1 Diagnostic inconsistencies

Predorsal length, dorsal fin origin in relation to the vent, dentition, scale shape and pattern, total number of vertebrae, lateral line pores in front of the vent, lateral line pores in front of the origin of the dorsal fin, and number of rays in the median fins have been used as diagnostic characters between *S. kaupii* and *S. affinis* in taxonomic studies and identification literature (Almeida and Biscoito 2007, Bruun 1937, Castle 1964, Castle 1986, Jordan and Snyder 1901, Masuda et al. 1984, Matsubara and Ochiai 1951, Melo 2007, Norman and Trewavas 1939, Okamura and Machida 1987, Robins 1971, Robins and Robins 1989, Smith 2002, Sulak and Shcherbachev 1997). Lateral line pores in front of the origin of the dorsal fin is only used by Melo (2007), where he shows no overlap between the two species. This character is related to the highly variable dorsal fin origin, and is not considered in this study.

The literature study revealed many inconsistencies concerning some of the diagnostic characters. The number of lateral line pores in front of the vent is mentioned in the identification key in Sulak and Shcherbachev`s (1997) article, but with overlap (*S. kaupii* 27 – 33, *S. affinis* 25 – 29). This recognized overlap and data from the present study (where the type of *S. affinis* falls within the MAR-ECO range) show that this character is unsuitable as diagnostic between the two species. The predorsal lengths given by the various authors are shown in figure 17, and all authors show some degree of overlap. The total number of vertebrae is used to discriminate *S. kaupii* and *S. affinis* in several studies, and most of them claim that there is no overlap in this character (Matsubara and Ochiai 1951, Norman and Trewavas 1939, Robins 1971, Robins and Robins 1989). Two studies show that *S. affinis* has a greater range of number of vertebrae and overlaps the range of *S. kaupii* (Almeida and Biscoito 2007, Sulak and Shcherbachev 1997). This is shown in figure 18. The descriptions of the squamation of the species *S. kaupii* and *S. affinis* vary from author to author and from figure to figure (i.e. Castle 1961, Castle 1964, Matsubara and Ochiai 1951, Norman and Trewavas 1939, Robins 1971, Robins and Robins 1989, Sulak and Shcherbachev 1997), the general opinion in the literature is that the scales of *S. kaupii* are more elongate than the oval *S. affinis* scales (Matsubara and Ochiai 1951, Okamura and Machida 1987, Robins 1971, Robins and Robins 1989, Sulak and Shcherbachev 1997).

4.1.2 Ontogenetic change

The analyses of morphometric characters` relation to total length indicate that 11 of the 16 examined characters show ontogenetic change. An example of this can be seen in figure 1, where two specimens of different size are shown. The difference in body depth is clearly visible. Vaillant (1888), thought that Johnson (1862) might have made a spelling mistake when describing the body depth of *S. kaupii*. Johnson`s example was of a specimen of 813 mm total length and Vaillants specimen was 600 mm total length. The regression line in figure 11 m) explains the difference. This means that size is an important factor when comparing morphometrics in these fish. Only predorsal length, distance between the posterior nostril and the eye, distance between vent and anal fin, gill slit length, and interorbital length, are morphometric characters that can be compared across size classes.

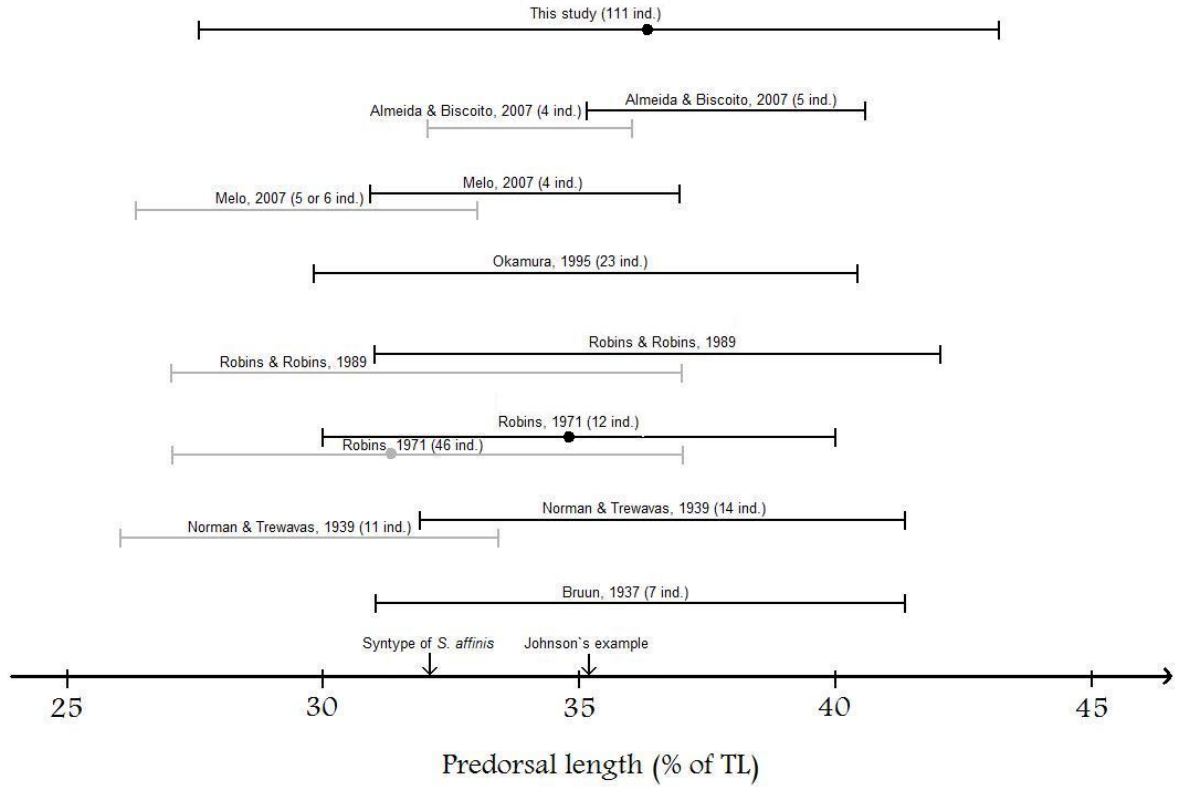

Figure 17: Predorsal length range from this study and previous studies. Dark lines indicate the range for *S.kaupii* and grey lines indicate the range for *S.affinis.* Dots mark the mean value, if available. The distribution of PD from this study is normally distributed. The exact number of individuals in Robins & Robins (1989) is unknown. "Johnson`s example" is from the measurement shown in the description of *S. kaupii* (Johnson, 1862).

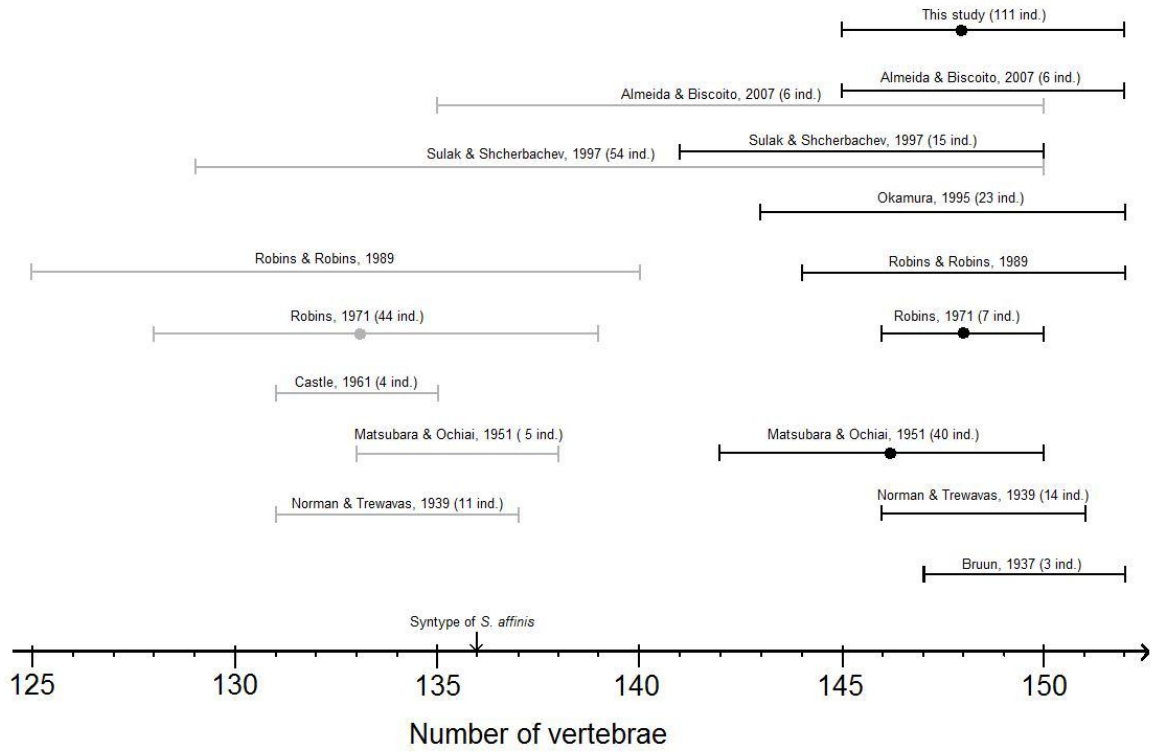

Figure 18: Vertebrae range from this and previous studies. Dark lines indicate the range for *S. kaupii* and grey lines indicate the range for *S. affinis*. Dots mark the average value, if available. The exact number of individuals in Robins & Robins (1989) is unknown.

4.1.3 Univariate analyses

The great variation in predorsal length in this group of fish has caused confusion among taxonomists over the years (see taxonomic history and figure 17), and this is understandable considering the taxonomic importance this character has in other groups of eels. Dorsal fin origin is viewed as a family character of Congridae, and a generic character in the Muraenidae (Castle 1964). The predorsal length recorded in this study shows a large range of 15.6 % of total length between the extrema, and the character is normally distributed. The character shows no relation to total length, and is therefore comparable between size classes. The predorsal length of the type of *S. affinis* falls well within the range of the MAR-ECO specimens, as is shown by the test for outliers. This clearly shows that this character cannot be used as diagnostic between *S. kaupii* and *S. affinis*. Robins (1971) showed a difference in the average value of predorsal length between *S. kaupii* and *S. affinis*, but the overlap is so extensive that it is of no use in individual identification.

The character dorsal fin origin in relation to the vent also shows a large, normally distributed variation of 3.1 pectoral fin lengths between the extrema. This is a character that changes during ontogeny, so a comparison of different size classes should be made with caution. As the predorsal length is not affected by ontogeny, this change must be viewed as a result of the change in preanal length during ontogeny only. For dorsal fin in relation to the vent, the syntype specimen of *S. affinis* falls within the MAR-ECO population, considering the range, the test for outliers, and total length. Therefore, this character cannot be considered as diagnostic between the species *S. kaupii* and *S. affinis*. The reason for this great variation in predorsal length and dorsal fin origin in relation to the vent is peculiar, considering the origin of the dorsal fin`s diagnostic importance in related taxa (see Castle 1964). I do not attempt to account for this, but some information may be added. In the leptocephali of *S. kaupii*, the position of the dorsal fin origin is 12-19 myomeres in front of the vent, and is reduced during the metamorphosis to fit the description of the adults, with dorsal fin origin behind the level of the vent (Bruun 1937). Robins and Robins (1989) state that all synaphobranchines swim with their head and body angled downwards about 30°, and that the anal fin is expanded and helps the undulating swimming mode. They argue that the forward position of the vent and anal fin, and the reduction of the height of the dorsal fin may be adaptive for this swimming mode. They also argue that the variation found in the origin of the dorsal fin may

reflect a lack of selection pressure. They state that they know no other type of eel with such variation in this character. I have not seen this description of the swimming mode in any other of the several behavioral studies conducted on *S. kaupii* (i.e. Heger et al. 2007, Bailey et al. 2005, Pakhorukov 1999, Uiblein et al. 2002, Uiblein et al. 2003).

The syntype of *S. affinis* falls outside of the range of the MAR-ECO specimens concerning the pectoral fin length. The test for outliers also excludes it from the MAR-ECO population. The pectoral fin is exposed to wear and tear, and especially the thin tip is lost in many specimens, so this might be considered a rather poor morphometric character. However, I did not find the pectoral fin of the *S. affinis* type to be in a noticeable better shape than the rest of the examined pectoral fins. This suggests that pectoral fin length might have some separating value. The type of *S. affinis* has a total length of 371 mm, and this puts it in the lower end of the MAR-ECO size range. Figure 11 l) shows that the pectoral fin length decreases with increased size. Considering this, the difference between the *S. affinis* type and the MAR-ECO specimens may be due to chance. More *S. affinis* specimens must be examined before a proper conclusion can be drawn of the pectoral fin`s distinguishing value.

Böhlke (1982), claims that vertebrae counts are useful for the identification of eels where other characters are problematic, and that many species have unique numbers of vertebrae. Several authors discriminate *S. kaupii* and *S. affinis* by their number of vertebrae (see figure 18). However, Sulak and Shcherbachev (1997) and Almeida and Biscoito (2007) show overlap in this character. It seems that these authors have weighted the character, origin of the dorsal fin in relation to the vent, most heavily. As noted above, this is not useful as a discriminating character between these species. Subsequent counting of vertebrae will naturally blur the two groups found based on number of vertebrae. A possible explanation for the grouping caused by the number of vertebrae is sexual dimorphism. Castle and Böhlke (1976) found sexual dimorphism in the number of vertebrae in the moringuid eel *Moringua edwardsi*. Males of this species have 109-117 (mean 112.6) and females have 116-123 (mean 119.4) vertebrae. However, Robins (1971), found both females and males in their samples of both *S. kaupii* and *S. affinis*. Another possible explanation for the difference in vertebrae number is the fact that number of vertebrae in fish may be affected by environmental factors, especially temperature. This is shown in several studies of different fish families (Tåning 1952, Swain and Foote 1999, Gabriel 1944, Itazawa 1959, Tåning 1950). The plastic

period for the vertebrae is early in the ontogeny, long before hatching, and an experiment showed a difference of 3.2 vertebrae in *Salmo trutta* between groups exposed to different temperatures in the sensitive period (Tåning 1950, Tåning 1952). Geographic variation in vertebrae and other characters, due to genetical or environmental factors, could be expected in species with a wide distribution, like the *Synaphobranhcus* species. This could seem a likely explanation for the difference found between the MAR-ECO specimens and the *S. affinis* type. However, Robins (1971) found *S. kaupii* and *S. affinis* together in the Atlantic, and Matsubara and Ochiai (1951) found *S. kaupii* and *S. affinis* together in the Pacific. Considering the above, there is a possibility that *S. kaupii* and *S. affinis* constitute two cryptic species, separable by the number of vertebrae. The total number of vertebrae is an impractical character as it is obtained through x-rays or dissection. One pore and one vertebra develop from each myomer in the leptocephalus larva, so the number of lateral line pores corresponds to the number of vertebrae in most eels (Böhlke 1989). This is unfortunately not applicable to the *Synaphobranhus* eels. The lateral line does not reach the very end of the tail, and it is often not continuous in the far posterior part (observed in 24 of 80 specimens). The fact that I counted 139 lateral line pores and 136 vertebrae in the type of *S. affinis*, also shows that this cannot be trusted.

Predorsal vertebrae, dorsal fin rays, and anal fin rays are other meristic characters where the type of *S. affinis* stands out from the MAR-ECO specimens. Predorsal vertebrae and dorsal fin rays are not commented on further here because of the low number of specimens examined for these characters. The number of anal fin rays in the type of *S. affinis* is lower than in the MAR-ECO specimens, and it is possible that this is a character that can be used as diagnostic between *S. kaupii* and *S. affinis*. Fin ray counts may have systematic value in eels, even though these characters are generally viewed to be of less value in eels than in other teleosts (Castle 1961).

The distribution of the morphometric characters of the MAR-ECO specimens did not show or suggest any distinct groups. Thirteen of the 16 morphometric characters came out as normally distributed by the Shapiro-Wilk test. The three non-normal distributed characters are standard length, the length between the posterior nostril and the anterior margin of the

eye, and eye diameter. The one specimen with the outlying eye diameter (fig 9 h)) also stands out with its short total length. The regression line in figure 11 h) may explain its large eye diameter.

Regarding the meristic characters, only the total number of lateral line pores and number of anal fin rays come out as normally distributed by the Shapiro-Wilk test. The bar-plot of the number of lateral line pores shows some multimodality, and one specimen stands out by having 153 pores. Included in the count of this specimen were a few extra irregular pores along the lateral line, positioned between the regularly arranged pores.

The cephalic lateral line pores are presented as species specific and figures of the pore positions of the different species are shown in Sulak and Shcherbachev (1997). None of the specimens examined in the present study fits to any of these figures. The type specimen of *S. affinis* showed the most common pattern observed in the present study (figure 12). This shows that the position of the cephalic lateral line pores cannot be used a diagnostic character between these species. Robins (1971) described the same pattern as seen in this study, although she had denoted some of the pores to other canals.

The present study shows that the shape and pattern of the scales of the MAR-ECO specimens varies along the body. Although not examined specifically, the scales on the belly and along the median line of the dorsum tend to be more rounded, some almost circular, compared to the scales on the sides of the body. The scales also seem to become more elongate towards the posterior. The examined area should therefore be defined strictly, if comparisons between specimens are to be made. The type specimen of *S. affinis* was placed in category b) together with 102 of the MAR-ECO specimens. No obvious difference was found in neither scale shape nor pattern. This shows that the scale shape or pattern near the lateral line at the level of the vent cannot be used as a diagnostic character between *S. kaupii* and *S. affinis*.

The distribution and size of teeth are good systematic characters within the apodes (eels) (Bruun 1937). The dentition of the vomer has been used as a diagnostic character between *S. kaupii* and *S. affinis*. Matsubara and Ochiai (1951) claim that *S. affinis* has a longer series of

vomerine teeth than *S. kaupii*. Sulak and Shcherbachev (1997) present a figure in which the vomerine teeth of *S. affinis* are shown to be arranged in a uniserial line, and those of *S. kaupii* with some teeth in a biserial series. Robins and Robins (1989) claim that both species have uniserial vomerine teeth, but that they zig-zag anteriorly in *S. kaupii*. The present study shows that the vomerine dentition of the MAR-ECO specimens may be a straight uniserial line, an uneven uniserial line, or a biserial series (see table 8). The syntype of *S. affinis* had a straight uniserial line. This shows that the dentition on vomer is not useful as a diagnostic character between the MAR-ECO specimens and the *S. affinis* type.

The dentition on the premaxillare-ethmoid complex is a diagnostic character between *S. kaupii* and *S. affinis* according to Sulak and Shcherbachev (1997). They state, illustrated by a figure, that *S. kaupii* has a median series of large teeth, while the teeth of *S. affinis* are more irregularly arranged. Present study shows that there is some variation in the MAR-ECO specimens concerning the position of the larger teeth on the premaxillary-ethmoid complex (see table 8), but the general pattern is that they are oriented against a median line. The type of *S. affinis* had an uneven median line of the largest teeth (together with 10 of the MAR-ECO specimens), but the median orientation was clear. This shows that the dentition of the premaxillary-ethmoid complex is not usful as a diagnostic character between the MAR-ECO specimens and *S. affinis*. The dentition of the examined specimens could appear somewhat irregular at times, because the teeth pointed a bit here and there, but the bases of the teeth always showed an orientation along a median line. This irregularity might be explained by the fact that *S. kaupii* has a very flexible collagenous area at the attachments of the teeth (Fink 1981). Fink found *S. kaupii* to have the most depressable teeth of a non-euteleost in his study.

4.1.4 Multivariate analyses

The ordination diagram of the Principal Components Analysis (figure 15) shows the MAR-ECO specimens separated from the syntype of *S. affinis* and the syntype of *S. brevidorsalis*. The eigenvalue of the first axis is 0.399 and thus it explains about 40 % of the variation found in the dataset. The very variable characters, predorsal length and dorsal fin origin in relation to the vent, show a strong correlation with the first axis. The second axis should be

considered with caution. Its eigenvalue is only 0.220, explaining 22 % of the variation. The sum of all eigenvalues in a Principal Components Analysis is 1.0. Using five variables in the analysis, five different axes are produced, and each of these could explain about 1/5 (20 %) by pure chance. This PCA analysis is perhaps most valuable in showing the correlation between the variables. Predorsal length and dorsal fin origin in relation to the vent show no correlation with the total number of vertebrae. This shows that predorsal length or origin of dorsal fin length are of no use to discriminate between the specimens with high and low total number of vertebrae.

The Canonical Variate Analysis confirms that the total number of vertebrae is the best discriminating character between the MAR-ECO specimens and the type of *S. affinis*. Pectoral fin length also came out with discriminating power, but as noted above, this character should be used with caution in a diagnostic sense because of its ontogentic change. The p-values listed for the characters in this test should also be considered with caution because *S. affinis* and *S. brevidorsalis* are only represented by one specimen.

4.1.5 *Synaphobranchus brevidorsalis*

The test for outliers finds it highly unlikely that the *S. brevidorsalis* type specimen could be a part of the MAR-ECO population in nine of the 16 morphometric characters, and in six of the ten meristic characters examined. Its values differ from the range of the MAR-ECO specimens in four morphometric characters and six meristic characters. The total number of vertebrae (127) is much lower than in even the *S. affinis* type. The numbers of dorsal and anal fin rays are also clearly lower. Even though this study shows a great variation in predorsal length, this specimen has the greatest predorsal length recorded. The interorbital width is greater than in the MAR-ECO specimens and the *S. affinis* type. In addition, my subjective impression during the examination of this species was that it clearly stood out from all the other examined specimens, and that the broader head and round scales were the most prominent characters that separated it.

4.2 Molecular analysis

The range of morphological variation observed in the MAR-ECO specimens is well covered in the molecular analysis, as is shown in table 9. The average within-group Kimura two parameter (K2P) distance of the COI sequences retrieved from the MAR-ECO specimens and four other sequences of *S. kaupii*, retrieved from GenBank, is 0.5 %. Although there is no generally applicable percentage divergence that separates species, numerous studies involving COI give an idea of the utility of this gene to discriminate between species. In the insect order Lepidoptera, the divergence values for COI are generally more than 3 % between species (Hebert et al. 2003). Studies of vertebrates show an average within-species K2P distance of 0.60 % in Neotropical bats (Clare et al. 2007), and 0.39 % in fish (Ward et al. 2005). A comparison of the DNA barcode region for widely distributed fishes between the North Atlantic and Australasia was carried out by Ward et al. (2008). In that study, two species showed no difference between the two areas, nine species had a 0 – 1 % variation, two species showed a variation of 1 – 2 %, and two species had a difference of more than 2 %. The authors suggested further taxonomic studies of the latter two species. Comparing the results of these studies, especially those of fishes, with the present study supports the assertion that the MAR-ECO specimens belong to a single species.

The average K2P-distance between congeneric species has been found to be 7.80 % in Neotropical bats (Clare et al. 2007), 9.93 % in fishes (Ward et al. 2005), and 9.54 % in another study of fishes (Ward and Holmes 2007). The average within-family distance in fish increases to 15.5 % (Ward et al. 2005). The COI sequence of a specimen of *S. kaupii* from Japan, retrieved from GenBank, had an average distance of 8.7 % from the MAR-ECO specimens. Considering the above, this strongly suggests that this Japanese specimen belongs to a different species than the MAR-ECO specimens, but it is likely that it belongs to the same genus. Unfortunately, I have not been able to examine the voucher specimen morphologically. It is likely that the Japanese specimen is misidentified or belongs to a cryptic species that strongly resembles *S. kaupii* morphologically. This example also shows the importance of correct identification when dealing with DNA sequencing of species, and the importance of maintaining available voucher specimens.

The possibility of hybridization is a potential problem when interpreting mitochondrial DNA sequences (Rees et al. 2002, Ward et al. 2005). Hybridization might have been suspected if the morphological examination had revealed morphologically intermediate specimens, in between the species *S. kaupii* and *S. affinis*. No such phenomenon was observed and, in addition, molecular data did not indicate any deep divergences within North Atlantic *Synaphobranchus,* which may have suggested the presence of hybridization or morphologically cryptic species.

Nine of 118 specimens failed to yield any PCR product. There is a possibility that these had COI haplotypes that were so different from the others that the primers did not work on them. However, there is nothing in the morphological analyses that suggest any major genetic difference, so I believe that the failure to yield a PCR product is due to some other technical problem (e.g. contact with formalin or suboptimal storage).

4.3 Discussion of the materials and methods

4.3.1 Materials

This study covers the North Atlantic specimens with a high number of vertebrae well. To fully investigate the species complex, we would have needed more specimens. Atlantic specimens with a low number of vertebrae, and a better collection of the Pacific and other areas are needed. The type specimen of *S. kaupii* was also unavailable for the present study. One specimen is listed as a syntype of *S. kaupii* with the museum number BMNH 1862.11.9.49 in "Catalog of Fishes electronic version" (Eschmeyer and Fricke 2008). In CLOFNAM (Blache et al. 1973), CLOFETA (Smith and Castle 1990), and Robins and Robins (1989), the type of *S. kaupii* is listed with the number BMNH 1862.11.9.79. Both of these numbers were requested from the British Museum, but they were unable to provide any type specimens of *S. kaupii*. It seems that these have been lost or misplaced. *S. affinis* is listed in "Catalog of Fishes electronic version" as syntypes BMNH 1887.12.7.250, with 11 specimens. Upon request we received only one specimen, and the others seem to be missing from the collection. The type of *S. brevidorsalis* is listed as syntypes with "?2" specimens in the same catalog. Upon request we only received one specimen, and the possible second

seems to be missing. The voucher specimen (CBM-ZF 10302) of the full mitochondrial DNA sequence of *S. kaupii* from Japan, available at GenBank, was also very interesting for this study. A request was sent to the Natural History Musem & Institute, Chiba, Japan, but they have not been able to provide me with the specimen. Requests for specimens of *S. affinis* from the North Atlantic have also been made to several institutions, but all available specimens are preserved in formalin, or tissue samples are missing.

A major problem of this study is the narrow geographic distribution of the specimens examined. Both *S. kaupii* and *S. affinis* are reported with an almost circumglobal distribution (e.g. Sulak and Shcherbachev 1997). To get a better view of the morphological and molecular variation of these species, more specimens from other areas need to be examined.

4.3.2 Methods

All measurements in this study are expressed as % of total length in this study. Characters of the head are commonly presented as % of head length. Bruun (1937) states that presenting all measures in % of total length gives a better view of the variation, and that the use of fractions with varying reference may cloud the differences between species. As shown in this study, the head length is itself a variable character of these fishes, so I conform to Bruun`s view of this matter.

Some of the examined characters present inherent problems. The caudal fin and pectoral fins are exposed to wear and tear, and thus some of the observed variation may be due to this. The caudal fin seemed generally to be in good condition, but the pectoral fins were often worn, especially the thin tips of the pectoral fins, which were often missing. Jaw length is also difficult to define in these fish. The corner of the mouth ends in a cutanous crease of varying length, and this makes it difficult to define an exact measuring point. The gill slit length was measured in its natural position, without stretching the slit to its maximum length. Stretching the slit would give larger measurements, and this is a possible explanation for the longer gill slit length presented in Johnson`s description (Johnson 1862).

The color of the fish may vary due to several factors, such as type of substrate, condition of the fish, fixation-, and storage methods (Böhlke 1989). Color is therefore not considered a good character for these fish and was not investigated. Figure 1 and 2 are good examples of

some of the variation in color observed. The type of *S. affinis* (figure 2) has been stored for more than 130 years and has lost all of its pigmentation.

Eels have fewer reference points for measurements than most fish, and I believe most sensible measurements have been taken. In hindsight I would also have tried to measure the height of the median fins. The dorsal fin of the *S. affinis* type seemed more prominent anteriorly than my impression from the MAR-ECO specimens, but this was not investigated further. The pectoral fin rays were difficult to count, even by the use of dissection microscope and x-rays, so this character was not investigated.

The characters used for the multivariate analyses were selected on the basis of previously used diagnostic characters. Many characters could have been added, but the fact that most of the characters usable for identification varied with total length made their value questionable. CANOCO (ter Braak and Smilauer 2002) is a program that does not allow empty spaces in the data set, and thus several characters could not be used.

4.4 Conclusions and suggestions for future work

4.4.1 Conclusions

No groupings within the MAR-ECO specimens were found, considering both the morphological and molecular analyses. This indicates that they all belong to a single species, and they are identifiable as *Synaphobranchus kaupii* Johnson, 1862.

The type specimen of *Synaphobranchus affinis* Günther, 1877, may represent a member of a cryptic species that closely resembles *S. kaupii*, separable by the total number of vertebrae and median fin rays.

The previously used diagnostic characters predorsal length, dorsal fin origin in relation to the vent, shape and pattern of the scales, dentition of the vomer, and dentition of the premaxillare-ethmoid complex, cannot be used as diagnostic between the species *S. kaupii* and *S. affins*.

The total length of the examined specimens must be considered when comparing morphometric characters of these eels.

4.4.2 Suggestions for future work

Several questions about the taxonomy of the *Synaphobranchus* remain unanswered. There is a possibility that we are dealing with cryptic species in this group and the use of DNA sequences will thus prove a helpful tool. A morphological and molecular study of these species on a wider geographic scale is necessary. The two groups of vertebrae number found in the Atlantic and the Pacific should also be investigated.

The fate of the *S. kaupii* syntype(s) and the rest of the syntypes of *S. affinis* and *S. brevidorsalis* should be investigated. The complex taxonomy of these species shows the importance of type specimens. If the syntypes of *S. kaupii* are truly lost, a neotype should be established. There are specimens available from the type locality, Madeira. A re-description of *S. kaupii* that includes the morphological variation and DNA barcode sequences should accompany the establishment of a neotype. If future investigations should reveal *S. affinis* to be truly distinct from *S. kaupii*, a re-description of *S. affinis* will also be necessary. The inconsistencies between authors and the ontogenetic analysis of the present study (which exclude several characters) justify these re-descriptions. Re-descriptions necessitates the examination of all the valid *Synaphobranchus* species.

The leptocephali are not considered in this study, but several authors describe taxonomic problems concerning the larvae, especially the connection between adults and larvae (Bruun 1937, Castle 1965, Lea 1913, Smith 1979, Smith 1989). Comparison of DNA sequences from leptocephali and adults should easily solve this problem.

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Appendix I: Systematic position of *Synaphobranchus*

Systematic placement following Nelson (2006):

Phylum Chordata: Pharyngeal gill slits, notochord, and a postanal tail present at least in some stage of the life history; bilaterally symmetrical; complete gut (Brusca and Brusca 2003).

Subphylum Craniata: The notochord does not extend in front of the brain; cranium always present, vertebrae present in most cases; cartilage and/or bone tissue present; heart divided into chambers; blood usually with red blood corpuscles; well developed brain with 10 – 12 pairs of cranial nerves; epidermis consist of several cell layers; sensory capsules and neural crest formation present.

Superclass Gnathostomata: Vertebrates with jaws derived from modified gill arches; endochondral bone and three semicircular canals present; usually with paired limbs; the gills are directed externally and covered with ectoderm; the gill arches are not fused with the neurocranium; nerve fibers myelinized.

Grade Teleostomi: Thought to form a monophyletic group of the three classes Acanthodii†, Actionpterygii, and Sarcopterygii.

Class Actinopterygii: Fins with rays; scales ganoid, cycloid, ctenoid, or absent; spiracle and gular plate usually absent; branchiostegal rays and interopercle usually present; none with internal nostrils.

Subclass Neopterygii: The number of fin rays equal their supports in dorsal and anal fins; internal process of premaxilla lines the anterior part of the nasal pit; spermatozoa without acrosome.

Division Teleostei: Elongated ural neural arches; unpaired basibranchial toothplates; mobile premaxilla; urohyal distinctive, formed from the tendon of the sternohyoideus muscle as an unpaired ossification.

Subdivision Elopomorpha: Ribbonlike larva called leptocephalus; ear not connected with the swim bladder; *recessus lateralis* absent; usually more than 15 branchiostegal rays.

Order Anguilliformes: Pelvic fins and their supporting skeleton absent; pectoral fins absent in some; dorsal fin and anal fin confluent with the caudal fin in most (some lack caudal fin); scales absent or cycloid, embedded in the skin; very elongate body; usually narrow gill openings; posteriorly displaced gills; gill rakers and pyloric ceca absent; premaxillae, vomer and ethmoid usually fused to a single bone; teeth on maxilla; swim bladder; no oviducts; several bones (opisthotic, orbitosphenoid, mesocoracoid, gular plate, posttemporal, postcleithra, supramaxilla, and extrascapular bones) absent; hyomandibular fused with quadrate. 15 families, 141 genera, and more than 700 species.

Suborder Congroidei: Fused frontal bones. 9 families, 112 genera, and more than 500 species.

Family Synaphobranchidae: Gill openings positioned low on the body; 110-205 vertebrae; leptocephali with elongated eyes and lens at the anterodorsal end of eye. 10 genera and more than 30 species.

Subfamily Synaphobranchinae: The lower jaw is longer than the upper jaw; scales present; pointed head shape; small, pointed teeth; gill openings confluent or slightly separated.

Genus *Synaphobranchus*: Gill openings united ventrally, as a single external opening divided internally (Johnson 1862). Note: The gill openings can be viewed as a single opening, but more often it looks like two parallel longitudinal slits, only slightly separated. 6 species.

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Appendix II: Studied species

Synaphobranchus kaupii Johnson, 1862

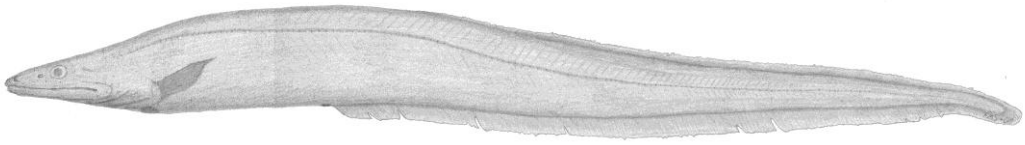

Figure AII1: *Synaphobranchus kaupii*

Etymology

Genus: from synaphes, Greek; united, and branchia, Greek; gills. Masculine noun. Refers to the ventrally united gill slits.

Species: after Dr. Johann Jakob Kaup of Darmstadt, who did major work on apodes. Masculine noun, genitive case.

Synonyms (adults)

Synaphobranchus kaupi – common misspelling

Synaphobranchus pinnatus (not Gronow) Günther, 1870

Nettophichthys retropinnatus Holt, 1891

Synaphobranchus iraconis Jordan & Snyder, 1901

Synaphobranchus pinnatus var. *brevidorsalis* Lloyd, 1909

Synaphobranchus pinnatus var. *parvipinnis* Roule, 1916

Common names

English: northern cutthroat eel, Kaup`s arrowtooth eel, slatjaw cutthroat eel, one-slit eel, and cut-throat eel. Danish: spidssnudet dybhavsål. Japanese: irako-anago. Portuguese: congrinho and moreão.

Behavior

Synaphobranchus kaupii is a benthic (Blache et al. 1973, Moore et al. 2003, Robins and Robins 1989, Smith and Castle 1990) or demersal/benthopelagic (Partridge et al. 1989, Saldanha and Bauchot 1986, Wagner 2002) species that inhabits the continental upper slope to upper rise (Wagner 2002). It is a common and abundant fish (Blache et al. 1973, Merrett and Domanski 1985, Bailey et al. 2005, Haedrich and Merrett 1988, Haedrich et al. 1975, Heger et al. 2007, Merrett et al. 1986, Merrett and Marshall 1981, Moore et al. 2003, Robins and Robins 1989, Suetsugu and Ohta 2005)that is reported as dominant in many areas at slope depths (Gillibrand et al. 2007, Gordon and Mauchline 1996, Markle and Musick 1974, Priede et al. 1994, Sedberry and Musick 1978)

Usually active swimmers (Pakhorukov 1999, Bailey et al. 2005, Uiblein et al. 2002, Uiblein et al. 2003), but can also be stationary in the water in any angle (head up or down) (Merrett and Marshall 1981) or lay still on the bottom (Pakhorukov 1999, Uiblein et al. 2003). Robins and Robins (1989) claims that all Synaphobranchines swim with their head and body angled downwards about 30° with the anal fin expanded to assist the undulating swimming mode, but none of the other authors have mentioned this feature. As mentioned above, they are demersal fish, but they are registered in small numbers, most young individuals, 3 – 60 m above the sea floor (Merrett et al. 1986), and some specimens from the present study are caught in pelagic trawls (see table 2 in the materials and methods section).

A study by Wagner (2002) suggest that *S. kaupii* primarily uses olfaction for finding food. He calls them “swimming noses” because of their great olfactory capabilities. The olfactory bulb of the brain is more than twice as large as the average for eels. They arrive at baits in greater numbers and before other scavengers (Bailey et al. 2005).

Distribution

S.kaupii is distributed in all the major ocean basins; the Atlantic, the Indian Ocean, and the Pacific Ocean. In the western North Atlantic Ocean from the Davis Strait in the north to the Caribbean in the south. Central North Atlantic from south of Iceland and southwards along the mid-Atlantic ridge. Eastern North Atlantic from west of the Faroe slope to the coast of northwest-Africa. In the South Atlantic it is recorded from off Brazil and along the African west coast. In the Indian Ocean it is recorded from the east coast of Africa and off Madagascar. In the Pacific it has been recorded from off Japan and the East China Sea through the Indo-Pacific and south to south of Australia. *S. kaupii* has not been recorded from the Mediterranean or the northeastern Pacific (Sulak and Shcherbachev 1997). The species has also been recorded from off Hawaii (Bruun 1937, Smith and Castle 1990), the northern coast of Chile (Pequeño 1997), and the Arabian Sea (Lloyd 1909).

The vertical distribution of adult fish is wide, from 131 m (Robins and Robins 1989) to 4800 m depth (Saldanha and Bauchot 1986), but is most common in depths between 400 and 2200 m (Sulak and Shcherbachev 1997). The leptocephali are pelagic and are recorded from depths of less than 10 meters to 350 m. All the records of leptocephali from shallower than 100 m are collected at night, and this suggests some kind of diel vertical migration (Bruun 1937).

S. kaupii has been recorded in a wide temperature range, from -1.1° C (Sulak and Shcherbachev 1997) to 10.39° C (Uiblein et al. 2002). It lives on or above both soft (Koefoed 1927, Uiblein et al. 2002, Uiblein et al. 2003, Vaillant 1888) and hard (Uiblein et al. 2003, Vaillant 1888) substrate.

Diet

The diet is mainly pelagic crustaceans, fish and cephalopods (Chambers and Dick 2005, Merrett and Domanski 1985, Gordon and Duncan 1987, Gordon and Mauchline 1996, Houston and Haedrich 1986, Marques 1998, Merrett and Marshall 1981, Saldanha 1980, Saldanha and Bauchot 1986, Sedberry and Musick 1978). Pieces of large fish in the stomach and arrival at baited cameras suggest a role as a scavenger (Gillibrand et al. 2007, Gordon

and Mauchline 1996, Heger et al. 2007, Marques 1998, Merrett and Marshall 1981, Sedberry and Musick 1978, Wagner 2002). One specimen examined in this study had a large piece of fish in its stomach. At its narrowest the piece was wider than the specimen`s skull! Some studies show a change of diet with increasing size. Marques (1998) states that smaller eels eat mainly carideans, and that larger eels eat more fish and other decapods, including large crabs. Houston and Haedrich (1986) report a shift from benthic to pelagic prey with increasing size. Gordon and Mauchline (1996) report that larger fish seems to have a less diverse diet than smaller fish. However, Saldanha (1980), did not observe any qualitative eating preference related to size.

Life history

Elvers and adults are recorded with sizes from 91 mm standard length (Merrett and Marshall 1981) to 998 mm total length (Belloc 1949). The leptocephali larvae are recorded with lengths of 20 to 131 mm (Bruun 1937). An increase in size with increasing depth, deeper-bigger, has been shown in some studies (Gordon and Duncan 1987, Merrett and Domanski 1985, Bailey et al. 2005, Gordon and Mauchline 1996, Priede et al. 1994), but Snelgrove and Haedrich (1985) did not find this trend off Newfoundland. There is a trend that females grow larger than males (Gordon and Mauchline 1996, Merrett and Domanski 1985, Robins 1971).

There are some evidence that *S. kaupii* in the North Atlantic spawn outside of the southeast coast of North America and that the larvae drift pelagically for a period of up to two years towards the northeast Atlantic, similar to that of the species *Anguilla anguilla* (Bruun 1937, Murray and Hjort 1912). They are sexually mature from about 430 mm, and the highest amount of reproductively active individuals occur in February and April, but mature eels are recorded in all months except May, June, December and January (Robins and Robins 1989). Karmovskaya and Merrett (1998) claim that the species is semelparous. The largest fish may be 8 years old (Merrett and Domanski 1985).

Synaphobranchus affinis Günther, 1877

Figure AII2: Syntype of *S.affinis*.

Etymology

Genus: from synaphes, Greek; united, and branchia, Greek; gills. Masculine noun. Refers to the ventrally united gill slits.

Species: affinis, Latin; related to, part of. Adjective.

Synonyms

Synaphobranchus pinnatus (not Gronow) Günther, 1887

Synaphobranchus brachysomus Gilbert 1905

Synaphobranchus taketae Tanaka, 1916

Synaphobranchus indicus Bruun, 1937

Synaphobranchus indicus occidentalis Bruun, 1937

Common names

English: grey cutthroat. Gilbert`s synaphobranchid eel has been used for its junior synonym *S. brachysomus* Gilbert, 1905. Japanese: hora-anago.

Behavior

S. affinis is a benthic (Moore et al. 2003, Smith and Castle 1990) inhabitant of the continental slope (Mecklenburg et al. 2002, Moore et al. 2003, Smith and Castle 1990, Sulak and Shcherbachev 1997). It is reported as “not rare” in the west Pacific, from Japan to the Philippines by Jordan and Snyder (1901).

Distribution

S. affinis has a wide distribution, and is reported from the Atlantic, Pacific, and the Indian Ocean. In the western Atlantic from Nova Scotia to the Caribbean. Eastern Atlantic from west of Gibraltar to the west coast of Africa and off South-Africa. In the Indian Ocean along the east coast of Africa, off the Reunion Islands, and the east coast of Australia. In the Pacific it is recorded from off Japan, Indo-Pacific, off Australia, off New Zealand, off Hawaii, and the South East Pacific. One individual has been recorded in the Bering Sea (Sulak and Shcherbachev 1997). It is also recorded from the mid-Atlantic ridge in the North Atlantic (Bergstad et al. 2007), near the Azores (Almeida and Biscoito 2007), and off Brazil (Melo 2007).

Its depth distribution is reported from 290 m (Parin et al. 1997, Sulak and Shcherbachev 1997) to 2334 m (Sulak and Shcherbachev 1997), but most occur between 500 and 1500 m (Sulak and Shcherbachev 1997). One possible leptocephalus of *S.affinis* was collected at a depth of less than 25 meters (Castle 1965).

Known temperature range is 2.4 – 11.3° C (Sulak and Shcherbachev 1997).

Diet

Parin et al. (1997) report the diet to be 80 % pelagic and 20 % benthic, and that micronecton dominates. Robins and Robins (1989) report the diet to be crustaceans and small fish.

Life history

Adults and elvers are recorded with total lengths from 11.9 cm (Shinohara et al. 1996) to 1600 mm (Sulak and Shcherbachev 1997), the second longest registration is 840 mm (Biscoito 2004).

One leptocephalus, that is possibly *S. affinis,* is recorded from off Sydney, Australia, with a total length of 17.8 mm. The small size suggests spawning near Sydney (Castle 1965). Little is reported about the reproduction or life history, but Smith (1989) reports 89 elvers (72-105 mm total length) from outside of North Carolina in late April. They had probably gone through the metamorphosis recently.

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Appendix III: Morphometric and meristic data of the studied specimens

Abbreviations: ID – identification number, TL – total length, SL – standard length, PD – predorsal length, PA – preanal length, HL – head length, J – upper jaw length, LJ – lower jaw length, S – snout length, E – eye diameter, NE – nostril to eye, N – nose length, AA – vent to anal fin, P – pectoral fin length, DA – body depth, GS – gill slit length, IW – interorbital width, DAP – dorsal fin origin in relation to the vent, LL – total number of lateral line pores, LLA – lateral line pores in front of vent, SO – supraorbital pores, IO – infraorbital pores, POM – preopercularmandibular pores, VPA – preanal vertebrae, VPD – predorsal vertebrae, V – total number of vertebrae, DR – dorsal fin rays, AR – anal fin rays.

Total length has mm as measuring unit. The other morphometric characters are expressed as % of total length, except DAP which has number of pectoral fin lengths as unit.

ID	TL	SL	PD	PA	HL	J	LJ	S	E	NE	N	AA	P	DA	GS	IW	DAP	LL	LLA	SO	IO	POM	VPA	VPD	V	DR	AR
ME10799-2	477	98,1	37,9	28,3	13,2	8,7	8,6	4,1	1,6	0,5	1,6	0,9	5,4	5,6	1,4	1,8	1,8	142	30	6	8	12	32	NA	150	NA	NA
ME10799-1	521	98,7	30,7	27,6	12,6	7,7	7,5	4,1	1,5	0,5	1,8	0,9	5,3	5,0	1,6	1,6	0,6	139	32	6	8	12	32	NA	147	NA	NA
ME10799-3	545	98,5	38,2	27,9	13,1	8,1	7,9	4,1	1,7	0,5	1,9	1,0	5,3	6,8	1,5	1,8	1,9	137	31	6	8	12	33	NA	150	NA	309
ME10799-4	644	98,4	43,2	28,7	13,3	8,2	8,1	4,1	1,4	0,7	1,8	1,1	5,2	7,9	1,3	1,8	2,8	141	32	6	8	13	32	NA	148	NA	NA
ME12263-4	483	98,6	38,7	28,8	13,1	8,5	8,4	4,2	1,7	0,6	1,8	1,1	5,5	6,3	1,4	2,0	1,8	143	32	6	8	12	NA	NA	148	NA	NA
ME12263-7	462	98,7	39,0	29,0	14,3	8,6	8,4	4,6	1,7	0,6	2,2	1,1	5,3	6,4	1,6	2,1	1,9	143	32	6	8	12	32	NA	147	NA	294
ME12263-8	527	98,9	34,3	29,2	13,7	8,4	8,3	4,3	1,8	0,6	1,9	1,5	5,4	5,6	2,1	2,0	0,9	146	33	6	9	12	33	NA	148	NA	NA
ME12263-1	541	98,7	42,9	28,3	13,2	8,2	8,1	4,0	1,6	0,5	1,7	1,1	5,0	6,0	1,7	1,6	2,9	146	31	6	8	12	32	NA	151	NA	NA
ME12263-3	547	98,7	38,4	28,9	13,2	7,6	7,4	3,9	1,5	0,5	1,8	1,5	5,1	5,6	1,7	1,9	1,9	141	32	6	8	NA	NA	NA	147	NA	NA
ME12263-6	461	98,5	37,1	28,9	12,6	8,1	8,0	4,2	1,5	0,6	1,9	1,1	4,8	5,9	1,7	1,8	1,7	139	32	6	8	12	NA	NA	147	NA	NA
ME12263-5	507	98,8	29,2	27,8	13,4	8,2	7,9	4,2	1,5	0,6	1,8	1,2	5,1	6,6	1,7	2,1	0,3	NA	30	6	8	12	30	NA	146	NA	NA
ME12263-2	473	98,5	31,5	28,3	13,2	8,2	8,1	4,7	1,6	0,6	2,2	1,1	5,7	7,0	1,5	2,1	0,6	137	30	NA	8	12	30	33	147	325	270
ME4774-8	439	98,9	32,8	29,2	13,3	8,0	7,9	4,1	1,6	0,5	1,8	1,1	5,4	3,9	1,7	1,3	0,7	136	32	6	8	12	33	NA	145	NA	NA
ME4774-9	380	98,7	37,6	28,4	13,3	8,3	8,1	4,5	1,7	0,7	2,0	1,3	5,8	3,5	1,8	1,6	1,6	146	32	6	8	12	32	NA	151	NA	NA
ME4774-10	411	98,3	38,4	27,5	12,8	7,5	7,4	4,0	1,6	0,5	2,1	1,7	5,1	4,2	1,8	1,6	2,2	139	29	6	8	12	32	NA	148	NA	NA
ME10729-1	364	98,4	33,5	28,0	13,2	7,8	7,3	4,1	1,8	0,5	2,0	1,1	5,3	3,1	1,5	1,6	1,0	NA	31	6	8	NA	33	NA	148	NA	NA
ME7469	484	98,6	36,6	29,3	12,9	7,9	7,7	4,5	1,5	0,7	1,9	0,9	5,6	5,7	2,2	1,9	1,3	145	33	6	8	12	32	NA	150	NA	NA

ID	TL	SL	PD	PA	HL	J	LJ	S	E	NE	N	AA	P	DA	GS	IW	DAP	LL	LLA	SO	IO	POM	VPA	VPD	V	DR	AR
ME4756-12	396	98,2	36,9	27,3	13,1	8,1	7,9	4,4	1,7	0,5	2,1	1,3	5,7	4,3	1,4	NA	1,7	141	30	6	8	12	33	NA	147	NA	300
ME4756-11	357	97,8	38,1	29,7	13,4	8,6	8,4	4,5	1,7	0,6	2,0	1,1	5,6	4,2	1,7	1,5	1,5	147	32	6	8	12	34	NA	149	NA	NA
ME4756-10	482	98,5	33,4	26,8	13,3	7,9	7,8	4,1	1,4	0,6	2,1	1,2	5,2	3,9	1,8	NA	1,3	142	29	6	8	13	31	NA	149	NA	NA
ME20793-1	404	98,8	35,4	28,5	12,7	7,7	7,5	4,5	1,6	0,6	2,1	1,4	5,6	4,4	1,8	1,7	1,2	NA	32	6	8	11	32	NA	146	NA	NA
ME20793-2	398	98,2	40,2	28,1	13,7	8,1	7,9	4,3	1,8	0,6	2,0	1,4	5,7	5,2	2,2	1,3	2,1	140	33	6	8	13	32	NA	147	NA	NA
ME20793-3	436	98,2	34,6	26,6	13,1	7,7	7,7	4,1	1,5	0,7	1,7	1,5	5,8	5,1	1,5	1,6	1,4	NA	31	6	8	13	32	NA	148	NA	NA
ME4830-2	598	98,8	39,8	27,9	12,3	7,6	7,4	4,0	1,7	0,6	2,0	1,2	4,5	6,3	1,7	1,4	2,6	139	31	6	8	12	NA	NA	145	NA	NA
ME4830-4	586	98,6	35,3	28,5	12,6	7,7	7,5	3,7	1,5	0,6	1,8	1,0	4,7	6,0	1,8	1,7	1,5	145	30	6	8	12	31	NA	145	NA	NA
ME4830-7	484	98,3	36,4	28,5	13,7	8,6	8,4	4,1	1,7	0,5	1,9	1,3	5,6	5,6	1,8	1,7	1,4	140	30	6	8	12	32	NA	149	NA	NA
ME4830-6	594	98,7	37,0	29,1	13,2	8,5	8,3	4,0	1,6	0,6	1,8	1,0	5,1	5,3	1,7	1,7	1,6	137	32	6	8	13	33	NA	146	NA	NA
ME4830-8	530	98,5	37,0	27,4	12,8	7,8	7,7	3,7	1,6	0,5	1,8	1,3	5,4	5,2	1,5	1,6	1,8	141	30	6	8	12	30	NA	147	NA	310
ME4830-9	563	98,4	38,0	29,5	13,4	8,1	7,8	4,3	1,7	0,7	2,0	1,5	5,5	4,8	1,5	1,6	1,6	141	32	6	8	13	NA	NA	148	NA	NA
ME4830-1	577	98,6	36,7	28,4	14,0	7,9	7,8	4,0	1,8	0,4	1,8	1,1	5,6	5,3	1,8	1,5	1,5	139	32	6	8	12	32	NA	149	NA	NA
ME4816-5	548	98,9	41,2	28,8	13,1	7,6	7,4	3,7	1,4	0,5	1,8	1,3	5,3	5,7	2,0	1,7	2,3	153	34	6	8	12	33	NA	145	NA	NA
ME4816-7	561	98,4	35,8	27,3	12,1	7,8	7,6	3,9	1,5	0,6	1,7	1,2	4,8	NA	1,7	1,7	1,8	142	32	6	8	12	32	NA	147	NA	NA
ME4816-4	551	98,7	31,0	28,7	13,1	7,9	7,7	3,9	1,7	0,5	2,0	1,4	5,0	6,1	1,5	1,6	0,5	138	33	6	8	13	34	NA	148	NA	NA
ME4816-2	577	98,4	34,5	29,3	13,9	8,8	8,7	4,3	1,7	0,6	2,1	1,2	5,4	6,4	1,7	1,5	1,0	140	32	6	8	11	33	NA	147	NA	300
ME4816-6	546	98,5	36,3	26,4	13,0	7,8	7,6	3,8	1,5	0,5	1,7	1,6	4,5	NA	1,6	1,6	2,2	140	30	6	8	12	31	NA	148	NA	NA
ME4772-10	529	98,5	34,6	28,2	13,0	8,0	7,8	4,1	1,6	0,6	2,0	1,7	5,0	NA	1,4	1,6	1,3	136	31	6	8	13	32	NA	147	NA	NA
ME4772-7	596	98,5	36,7	27,2	12,3	8,1	7,9	3,9	1,7	0,6	2,0	1,6	5,8	6,6	1,5	1,5	1,6	147	31	6	8	13	31	NA	149	NA	NA
ME4772-3	571	98,6	35,4	27,7	12,9	8,1	7,8	4,0	1,7	0,4	2,0	1,2	5,1	5,9	1,6	1,5	1,5	143	32	6	8	13	31	NA	146	NA	NA
ME4772-9	565	98,6	41,9	29,2	12,5	8,3	8,1	4,4	1,4	0,7	2,1	1,4	5,2	4,4	1,7	1,4	2,5	144	33	6	8	11	NA	NA	149	NA	NA
ME4772-4	594	98,7	40,4	29,0	12,4	7,8	7,6	3,8	1,4	0,5	1,9	1,3	4,8	6,9	1,6	1,6	2,4	145	32	6	8	12	33	NA	151	NA	NA
ME4772-1	611	98,5	37,6	27,0	12,3	7,6	7,5	3,9	1,5	0,5	1,9	1,4	4,8	5,6	2,0	1,8	2,2	141	32	6	8	13	32	NA	149	NA	NA
ME4772-6	527	98,3	35,3	27,3	13,5	8,5	8,3	4,3	1,7	0,6	2,0	1,4	5,4	6,7	1,7	1,6	1,5	141	31	6	8	12	31	NA	149	NA	NA
ME4772-5	521	98,5	30,9	28,0	13,6	8,6	8,3	4,0	1,6	0,5	2,0	1,5	5,1	6,7	1,7	1,7	0,6	139	31	6	8	13	30	NA	145	NA	NA
ME4772-8	522	98,5	40,8	28,0	13,4	8,7	8,6	4,1	1,6	0,5	2,0	1,7	5,5	5,7	1,4	1,7	2,3	146	31	6	8	13	32	NA	149	NA	NA
ME4772-2	641	98,6	41,0	28,5	11,6	7,3	7,2	3,8	1,4	0,5	1,7	1,5	5,1	NA	1,8	NA	2,4	139	32	6	7	13	33	NA	148	NA	277
ME4774-4	492	98,4	35,4	28,3	13,1	8,9	8,8	4,3	1,5	0,6	2,0	1,1	4,9	4,5	1,2	1,4	1,5	147	32	6	8	12	NA	NA	150	NA	NA

ID	TL	SL	PD	PA	HL	J	LJ	S	E	NE	N	AA	P	DA	GS	IW	DAP	LL	LLA	SO	IO	POM	VPA	VPD	V	DR	AR
ME4774-3	592	98,8	38,7	25,3	11,9	6,9	6,8	3,5	1,5	0,5	1,7	1,3	4,8	NA	1,3	1,4	2,8	141	29	6	8	NA	29	NA	148	NA	313
ME4774-6	505	98,4	35,0	29,1	13,4	7,7	7,5	4,1	1,6	0,6	1,9	1,4	5,1	4,6	1,6	1,5	1,2	141	33	6	8	12	34	NA	150	NA	NA
ME4774-2	654	98,8	33,8	27,4	12,1	7,8	7,6	3,5	1,5	0,5	1,7	1,8	4,4	4,9	1,2	1,0	1,5	147	31	6	8	12	32	NA	150	NA	NA
ME4774-5	461	98,0	36,9	28,9	13,0	8,2	8,1	4,2	1,6	0,6	2,0	1,5	5,3	5,7	1,8	1,2	1,5	142	33	6	8	13	34	NA	149	NA	NA
ME4758-8	525	98,5	38,7	28,2	13,1	8,1	8,1	4,1	1,7	0,6	1,9	1,5	5,3	5,2	1,6	1,4	2,0	145	32	6	8	12	32	NA	150	NA	304
ME4758-9	561	98,6	37,8	28,3	12,7	8,0	8,1	3,9	1,4	0,5	1,9	1,2	4,9	NA	1,8	1,8	1,9	137	31	6	8	12	32	NA	148	NA	NA
ME4758-2	590	98,5	36,4	27,8	12,8	7,7	7,5	3,8	1,4	0,6	1,7	1,5	4,6	4,7	1,5	1,5	1,9	148	32	6	8	11	33	NA	152	NA	NA
ME4758-1	557	98,7	38,2	28,0	13,5	8,2	8,0	4,1	1,7	0,5	1,9	1,6	5,0	6,8	1,6	1,6	2,1	133	30	6	8	12	31	NA	145	NA	NA
ME4758-10	501	98,4	36,1	29,3	13,1	8,6	8,4	4,2	1,7	0,6	2,0	1,3	5,4	6,2	1,8	1,5	1,3	140	31	6	8	11	32	NA	147	NA	NA
ME4758-3	504	98,4	36,1	30,6	12,9	8,3	8,2	4,1	1,5	0,5	1,9	1,2	5,1	4,0	1,7	1,6	1,1	143	34	6	9	12	34	NA	148	NA	NA
ME4758-6	529	98,9	37,1	28,4	13,2	8,6	8,4	4,3	1,6	0,7	1,9	1,3	5,0	NA	1,5	1,4	1,7	147	32	6	8	13	32	NA	148	NA	NA
ME4758-5	512	98,8	32,8	28,5	13,5	8,4	8,3	4,0	1,6	0,5	2,1	1,2	5,8	4,8	1,5	1,4	0,7	139	30	6	8	12	32	NA	147	NA	NA
ME4758-4	566	98,6	36,0	27,7	12,5	7,6	7,3	3,7	1,5	0,5	1,8	1,4	4,6	4,9	1,9	1,6	1,8	142	31	6	8	13	32	NA	151	NA	NA
ME4758-7	576	98,6	29,7	26,9	12,2	7,9	7,6	3,9	1,5	0,5	2,0	1,2	4,5	6,0	2,0	1,8	0,6	143	31	6	8	12	30	NA	147	NA	NA
ME4756-8	515	98,4	40,0	27,8	13,7	9,0	8,8	4,1	1,7	0,7	2,1	1,7	5,8	6,2	1,9	1,5	2,1	148	31	6	8	12	31	NA	148	NA	NA
ME4756-5	550	98,5	34,9	26,7	13,0	7,9	7,8	4,0	1,7	0,7	2,0	1,7	4,8	6,6	1,6	1,7	1,7	135	31	6	8	12	31	NA	149	NA	NA
ME4756-3	595	98,8	33,9	27,4	12,5	8,1	7,8	3,9	1,5	0,6	1,9	1,1	5,2	6,0	1,3	1,4	1,3	139	33	6	NA	12	31	NA	147	NA	NA
ME4756-1	611	98,7	36,2	27,0	12,1	7,8	7,7	3,8	1,5	0,5	1,8	1,5	4,6	5,3	1,8	1,5	2,0	141	32	6	8	12	33	NA	151	NA	265
ME4756-4	554	98,6	35,2	28,3	12,7	7,9	7,9	4,0	1,5	0,5	2,0	1,6	5,3	5,7	1,7	1,2	1,3	131	30	6	8	12	31	NA	145	NA	NA
ME4756-7	596	98,7	35,9	26,8	11,6	7,9	7,9	3,5	1,4	0,5	1,9	1,3	5,0	6,2	1,5	1,4	1,8	138	31	6	8	12	31	NA	148	NA	NA
ME4756-6	522	98,7	35,8	27,8	13,4	8,1	8,0	3,7	1,6	0,4	2,0	1,9	5,3	6,4	1,9	1,5	1,5	139	31	6	8	13	32	NA	147	NA	NA
ME4774-1	611	98,2	36,3	28,3	12,7	7,8	7,5	3,8	1,5	0,5	NA	1,9	4,5	7,1	1,6	1,5	1,8	138	30	NA	NA	13	31	NA	146	NA	NA
ME4774-7	474	98,7	35,4	27,2	14,0	8,5	8,5	4,3	1,8	0,5	2,1	1,9	5,7	5,9	1,4	1,6	1,4	136	30	6	8	11	31	NA	146	NA	NA
ME4816-8	568	98,2	36,4	27,5	13,1	8,0	7,8	4,0	1,4	0,6	2,2	1,4	4,9	5,3	1,7	1,7	1,8	140	31	6	8	13	31	NA	148	NA	325
ME4816-3	498	98,4	40,6	29,9	13,3	8,5	8,4	4,0	1,6	0,4	2,2	1,2	5,4	6,1	1,7	1,5	2,0	139	34	6	8	12	33	NA	147	NA	NA
ME4816-1	582	98,6	37,8	25,9	12,5	8,3	8,0	4,0	1,7	0,6	2,0	1,7	5,3	8,7	1,4	1,5	2,2	134	30	6	8	11	30	NA	147	NA	NA
ME4830-3	555	98,7	37,3	29,4	13,9	8,8	8,6	4,2	1,6	0,5	2,0	1,4	5,0	6,2	1,9	1,7	1,6	144	32	6	8	13	34	NA	146	NA	NA
ME4830-5	536	98,5	39,7	27,6	12,6	8,3	8,1	3,7	1,5	0,5	2,1	1,2	5,0	4,3	1,7	1,4	2,4	137	33	6	8	12	34	NA	150	NA	NA
ME4756-9	506	98,4	40,1	28,5	13,7	8,6	8,5	4,3	1,7	0,6	2,2	1,6	5,4	5,5	1,5	1,3	2,2	135	30	6	8	12	31	NA	146	NA	295

ID	TL	SL	PD	PA	HL	J	LJ	S	E	NE	N	AA	P	DA	GS	IW	DAP	LL	LLA	SO	IO	POM	VPA	VPD	V	DR	AR
ME4756-2	557	98,6	40,9	27,3	12,9	8,4	8,1	4,0	1,6	0,5	2,0	1,4	5,8	4,8	1,8	1,5	2,4	143	32	6	8	13	NA	NA	145	NA	NA
ME1196	206	97,6	35,3	27,1	13,3	7,9	7,7	4,5	2,3	0,3	2,0	0,7	5,6	3,5	1,4	1,3	1,5	NA	32	6	8	NA	NA	NA	151	NA	NA
ME10799-13	540	98,7	33,3	25,7	11,5	7,1	7,1	3,6	1,6	0,5	1,4	1,2	4,9	6,1	1,1	1,5	1,6	NA	32	6	NA	NA	33	NA	149	NA	NA
ME10799-11	621	98,7	35,4	28,7	12,9	8,0	7,8	4,0	1,6	0,6	1,9	1,5	4,9	7,9	2,0	1,7	1,4	149	32	7	8	13	33	NA	150	NA	NA
ME10799-10	659	98,9	42,2	28,5	12,6	7,8	7,5	3,9	1,4	0,6	1,8	1,5	4,7	7,2	1,8	1,8	2,9	137	31	6	8	12	32	NA	147	NA	276
ME10799-14	539	98,9	34,1	27,5	13,1	7,6	7,2	3,9	1,5	0,5	1,7	1,3	4,6	6,3	1,4	1,8	1,4	NA	32	6	8	12	32	NA	148	NA	NA
ME10799-12	660	98,8	42,3	27,7	13,1	7,7	7,6	4,2	1,4	0,7	1,9	1,4	4,7	6,6	1,6	1,5	3,1	NA	31	6	8	12	32	NA	149	NA	NA
ME12195-10	555	98,7	37,8	30,3	13,0	8,2	8,1	4,4	1,6	0,6	1,9	1,4	5,4	8,9	1,5	1,6	1,4	NA	34	6	8	11	34	NA	150	NA	NA
ME12195-13	523	98,9	37,7	27,2	12,9	7,4	7,2	3,9	1,6	0,5	1,8	1,3	5,0	5,9	1,5	1,4	2,1	NA	31	6	8	13	32	NA	151	NA	303
ME12195-12	551	98,7	37,9	28,1	13,8	8,5	8,2	4,8	1,7	0,7	2,2	1,1	5,4	6,8	1,5	1,7	1,8	NA	31	6	8	13	32	NA	147	NA	NA
ME12195-14	544	98,7	39,3	26,8	12,5	7,9	7,8	4,0	1,6	0,5	1,8	1,2	5,1	6,4	1,5	1,3	2,4	NA	30	6	8	12	31	NA	150	NA	NA
ME12195-11	553	98,6	32,7	28,6	13,5	8,6	8,5	4,2	1,7	0,6	1,7	1,1	5,2	6,2	1,4	1,5	0,8	NA	32	6	8	11	33	NA	151	NA	NA
ME12195-7	595	98,7	37,3	29,2	12,9	8,0	7,9	4,1	1,4	0,6	1,8	1,1	5,0	6,7	1,4	1,7	1,6	NA	32	6	7	12	32	NA	147	NA	NA
ME12195-23	468	98,5	35,9	28,0	12,9	8,6	8,2	4,6	1,5	0,6	1,8	1,2	5,5	6,6	1,4	1,8	1,4	NA	30	6	8	12	31	NA	148	NA	NA
ME12195-22	461	98,7	34,7	28,9	13,8	8,6	8,3	4,4	1,5	0,5	1,9	1,1	5,3	5,9	1,5	1,7	1,1	NA	31	6	8	12	32	NA	149	NA	NA
ME12195-9	578	98,8	33,9	26,8	13,2	7,8	7,6	4,1	1,6	0,6	1,8	1,1	5,2	5,8	1,3	1,6	1,4	NA	31	6	8	12	32	NA	149	NA	NA
ME12195-24	440	98,4	34,3	28,4	12,5	7,9	7,7	4,1	1,7	0,6	1,8	1,3	5,2	NA	1,2	1,5	1,1	NA	30	6	8	12	NA	NA	150	NA	NA
ME12195-6	603	98,8	28,7	27,5	12,3	7,6	7,4	3,9	1,6	0,5	1,7	1,3	4,8	6,7	1,4	1,7	0,2	NA	31	6	8	12	32	32	147	360	292
ME12195-3	644	98,9	33,1	27,2	12,7	7,9	7,7	3,7	1,5	0,6	1,6	1,4	4,8	6,1	1,2	2,0	1,2	NA	31	6	8	12	30	NA	150	NA	NA
ME12195-2	643	98,9	39,2	26,9	13,1	8,2	8,1	4,0	1,7	0,7	1,5	1,7	4,9	5,8	1,4	1,6	2,5	NA	32	6	8	13	33	NA	151	NA	NA
ME12195-1	668	99,0	36,1	27,2	13,2	7,9	7,8	4,2	1,4	0,7	1,7	1,4	4,2	7,0	1,5	1,7	2,1	138	29	6	9	12	30	NA	147	NA	NA
ME12195-5	621	98,7	38,3	28,8	13,4	8,2	7,9	3,9	1,5	0,7	1,6	1,0	4,9	4,8	1,6	1,7	1,9	NA	33	6	8	11	33	NA	148	NA	NA
ME12195-4	626	99,0	38,0	28,0	13,2	7,5	7,3	4,3	1,5	0,8	1,5	1,7	4,8	5,5	1,4	1,7	2,1	NA	30	6	8	11	30	NA	146	NA	NA
ME12195-8	591	98,8	40,8	28,6	14,6	8,5	8,3	4,3	1,6	0,7	1,9	1,3	4,9	6,2	1,9	1,7	2,5	NA	31	6	8	12	32	NA	147	NA	NA
ME11502-8	547	98,5	27,6	27,6	13,1	9,0	8,8	4,3	1,8	0,7	1,7	1,2	5,0	5,6	1,7	1,5	0,0	NA	31	6	8	13	31	NA	150	NA	NA
ME11502-14	464	98,7	32,1	29,3	13,5	8,5	8,3	4,3	1,7	0,5	1,9	1,3	5,0	4,6	1,3	1,8	0,6	NA	32	6	8	13	33	NA	148	NA	NA
ME11502-6	599	99,0	40,2	28,0	12,9	8,3	8,0	4,3	1,5	0,7	1,9	1,1	4,9	5,9	1,5	1,5	2,5	NA	31	6	8	12	31	NA	146	NA	NA
ME11502-16	417	98,1	35,3	29,5	13,0	7,9	7,8	4,1	1,7	0,6	1,9	1,4	5,2	4,8	1,6	2,2	1,1	NA	33	6	8	12	33	NA	149	NA	NA
ME11502-4	574	98,6	37,8	28,6	12,6	7,4	7,1	4,1	1,5	0,5	2,0	1,4	4,9	6,1	1,6	1,7	1,9	NA	31	6	8	13	31	NA	147	NA	NA

ID	TL	SL	PD	PA	HL	J	LJ	S	E	NE	N	AA	P	DA	GS	IW	DAP	LL	LLA	SO	IO	POM	VPA	VPD	V	DR	AR
ME11502-17	439	98,4	38,3	27,3	13,5	8,6	8,4	4,5	1,7	0,6	2,1	1,1	5,5	3,9	1,5	1,5	2,0	NA	29	6	8	10	30	NA	149	NA	NA
ME11502-2	689	99,0	35,0	28,2	12,3	7,4	7,3	3,8	1,5	0,6	1,7	1,1	4,8	5,8	1,2	2,0	1,4	139	32	6	8	12	32	NA	148	NA	NA
ME11502-3	595	98,7	39,7	28,2	13,6	8,2	8,1	4,5	1,3	0,7	1,8	1,3	4,4	6,1	1,6	2,0	2,6	142	31	6	8	11	31	NA	147	NA	285
ME11502-1	693	99,0	38,0	28,1	12,4	8,2	8,1	4,0	1,5	0,6	1,7	1,6	4,7	7,3	1,5	1,6	2,1	NA	33	6	8	12	32	NA	146	NA	NA
ME11502-15	447	98,7	39,1	29,1	14,0	8,7	8,6	4,3	1,7	0,6	1,8	1,2	5,2	4,4	1,3	1,7	1,9	NA	32	6	8	12	32	NA	146	NA	NA
ME17379-1	617	98,7	37,0	27,1	13,0	7,9	7,7	4,0	1,4	0,6	1,6	1,1	5,4	7,2	1,4	1,7	1,8	139	30	6	8	12	31	NA	148	NA	NA
ME17379-2	490	98,6	38,2	30,0	13,2	8,4	8,2	4,2	1,7	0,7	1,8	1,0	5,5	5,1	1,4	1,7	1,5	142	33	6	8	12	34	NA	146	NA	NA
Syntype *S. affinis*	371	97,8	32,1	27,0	14,3	7,7	7,4	4,0	1,8	0,5	1,5	0,9	6,4	6,4	NA	NA	0,8	139	30	6	8	12	30	35	136	272	241
Syntype *S. brevidorsalis*	593	97,1	46,7	32,2	13,5	7,0	6,9	3,5	1,8	0,4	1,5	1,5	4,7	6,3	1,8	2,4	3,1	125	33	6	9	12	35	50	127	228	212

Appendix IV: Commands and calculations executed in R

The examples are from the analyses of the character preanal length (PA).

Importing data from excel:

```
> syn<-read.table("clipboard",dec=",",header=T)
> attach(syn)
```

Range, mean, standard deviation, and n:

```
> summary(PA)
   Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
  25.34   27.38   28.16   28.11   28.75   30.56
> sd(PA,na.rm=T)
[1] 0.9511391
> length(PA)
[1] 111
```

Shapiro-Wilk test:

```
> shapiro.test(PA)

        Shapiro-Wilk normality test

data:  PA
W = 0.9945, p-value = 0.9437
```

Histogram of the distribution:

```
> hist(PA,las=1,cex.lab=1.5,main="Distribution of Preanal
length",xlab="PA (% of TL)")
```

→ shows the histogram.

Regressions:

```
> pamod0<-lm(PA~1)
> pamod1<-lm(PA~TL)
> anova(pamod0,pamod1,test="F")

Analysis of Variance Table
Model 1: PA ~ 1
Model 2: PA ~ TL
  Res.Df    RSS  Df Sum of Sq   F  Pr(>F)
1    109 98.466
2    108 93.447   1     5.018 5.8 0.01772 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

> pamod1

Call:
lm(formula = PA ~ TL)

Coefficients:
(Intercept)           TL
  29.739476    -0.003011

> plot(TL,PA,las=1,cex.lab=1.5,xlab="TL (mm)",ylab="PA (% of TL)")
> abline(pamod1)
```

→ shows the plot and the regression line.

Appendix V: Morphometric characters expressed as % of head length.

Table AV1: Measured characters expressed as % of head length. The bold font show where the syntypes fall outside of the MAR-ECO range. “Range” denotes the range observed in the MAR-ECO specimens and “n” denotes the number of examined specimens. “SD” means standard deviation.

Character	Range	Mean	SD	n	Syntype *S. affinis*	Syntype *S. brevidorsalis*
Upper jaw length	56.8-68.4	62.12	2.48	111	**53.8**	**52.1**
Lower jaw length	55.4-68.2	60.77	2.60	111	**51.7**	**51.3**
Snout length	27.4-35.3	31.35	1.53	111	28.3	**25.9**
Eye diameter	9.8-17.1	12.18	0.91	111	12.3	13.2
Nostril to eye	2.6-5.7	4.36	0.62	111	3.6	3.1
Nose length	11.5-16.7	14.49	1.17	110	**10.2**	**11.3**
Pectoral fin length	31.9-47.3	39.45	2.61	111	45.1	35.0
Gill slit length	8.8-16.8	12.27	1.71	111	-	13.3
Interorbital length	8.1-16.8	12.44	1.56	108	-	**18.1**

Appendix VI: Results of the dissection of ME 12195-1

Elongate oval scales covers the head, body and tail, more rounded on abdomen. The nose cavity is large and covers most of the volume in the snout.

Dark peritoneum. Some nematodes were present in the body cavity. The liver was rather small and had only one lobe. The stomach was large, it stretched far posterior of the vent. The intestine started at the anterior end of the stomach. Pyloric ceca lacking. The first part of the intestine was straight and rather thick with a rich supply of blood vessels. The end part of the intestine was thinner with some twists. The intestine lay on the right hand side of the stomach. Figure AVI1 shows drawings of the digestive system. The length of the body cavity was about ½ of TL. Very long swimbladder, ending 85 mm from the end of caudal fin, stretching about 75 % of TL. Female, in a maturing state, with medium sized gonads

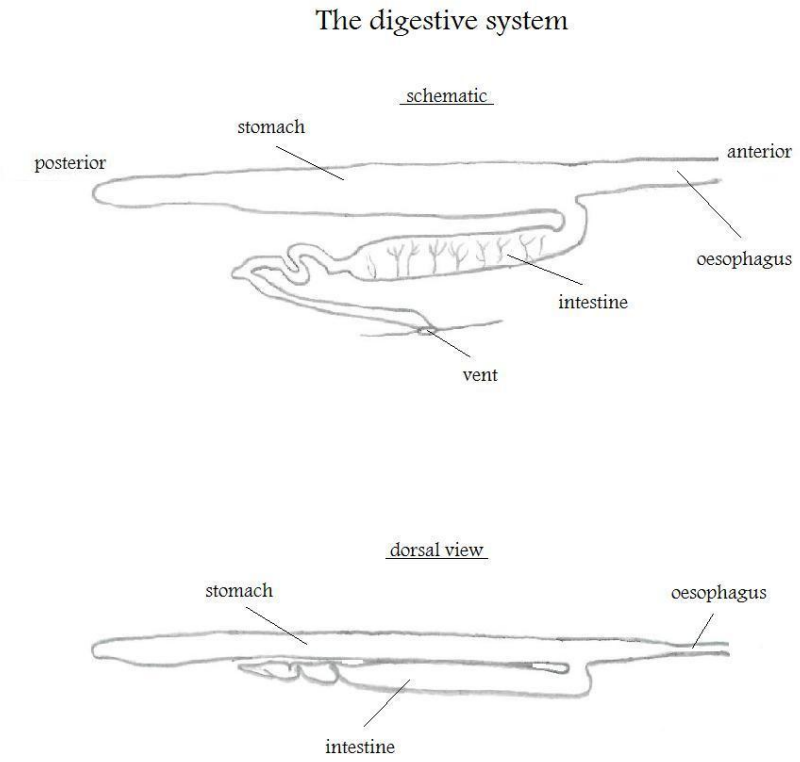

Figure AVI1: The digestive system of ME 12195-1.

Appendix VII: COI sequences

NC005805 is from the Japanese specimen retrieved from GenBank. EU148343 is from a North Atlantic *S. kaupii*, also retrieved from GenBank. The sequence of the most common haplotype (Group B) is listed at the top. Only differing bases are shown in the other sequences.

Bases 1 - 78

```
Group B     CCTATATTTAGTATTTGGTGCTTGAGCTGGCATGGTGGGCACCGCGCTCAGCCTGCTTATCCGAGCCGAACTAAGCCA
Group A     ..............................................................................
Group C     ..............................................................................
Group D     ..............................................................................
ME4756-4    ..............................................................................
ME4756-7    ..............................................................................
ME4772-7    ..............................................................................
ME4774-1    ..............................................................................
ME4774-2    ..................................................A...........................
ME4816-6    ..............................................................................
ME4816-7    .................................C.................A...........................
ME4816-8    ..............................................................................
ME4830-3    ..............................................................................
ME4830-7    ..............................................................................
ME7469      ..............................................................................
ME10799-1   ..............................................................................
ME10799-3   ------------------------------------------.....................................
ME10799-4   ..............................................................................
ME10799-13  ..............................................................................
ME11502-3   ............G.....................................................................
ME12195-3   ..............................................................................
ME12195-8   ..............................................................................
ME12263-5   ..............................................T...............................
ME12263-8   ..............................................................................
ME20793-1   ..............................................................................
NC005805    ...G...C.....................................................A..........G..T.....
EU148343    ............T.............................................?.................
```

Bases 79 - 156

```
Group B    GCCCGGAGCCCTACTTGGAGATGACCAAATCTATAATGTTATTGTTACAGCACATGCCTTCGTGATAATCTTCTTTAT
Group A    ........................................................................
Group C    ........................................................................
Group D    ........................................................................
ME4756-4   ........................................................................
ME4756-7   ........................................................................
ME4772-7   ........................................................................
ME4774-1   ........................................................................
ME4774-2   ........................................................................
ME4816-6   ........................................................................
ME4816-7   ........................................................................
ME4816-8   ........................................................................
ME4830-3   ........................................................................
ME4830-7   ........................................................................
ME7469     ........................................................................
ME10799-1  ........................................................................
ME10799-3  ........................................................................
ME10799-4  ........................................................................
ME10799-13 ........................................................................
ME11502-3  ........................................................................
ME12195-3  ........................................................................
ME12195-8  ..............C.........................................................
ME12263-5  ........................................................................
ME12263-8  ........................................................................
ME20793-1  ........................................................................
NC005805   A.................C.................C.................A..G...........
EU148343   ........................................................................
```

Bases 157 - 234

```
Group B     AGTAATACCCGTGATAATCGGGGGATTTGGCAATTGATTAGTCCCCCTAATAATTGGCGCCCCAGATATAGCATTCCC
Group A     ........................................................................
Group C     ........................................................................
Group D     ........................................................................
ME4756-4    ........................................................................
ME4756-7    ........................................................................
ME4772-7    ............A...........................................................
ME4774-1    ........................................................................
ME4774-2    ........................................................................
ME4816-6    ........................................T...............................
ME4816-7    ........................................................................
ME4816-8    ........................................................................
ME4830-3    ......G.................................................................
ME4830-7    ........................................................................
ME7469      ........................................................................
ME10799-1   ........................................................................
ME10799-3   ........................................................................
ME10799-4   ........................................................................
ME10799-13  ........................................................................
ME11502-3   ........................................................................
ME12195-3   ........................................................................
ME12195-8   ........................................................................
ME12263-5   ........................................................................
ME12263-8   ........................................................................
ME20793-1   ........................................................................
NC005805    ....................................G..A.............G....................
EU148343    ........................................................................
```

Bases 235 - 312

```
Group B     TCGAATAAATAACATAAGCTTCTGACTCCTCCCCCCATCATTTCTTCTATTATTAGCCTCATCTGGAGTAGAAGCTGG
Group A     ............................................................G...........
Group C     ........................................................................
Group D     ........................................................................
ME4756-4    ........................................................................
ME4756-7    ........................................................................
ME4772-7    ........................................................................
ME4774-1    ..............................................G.........................
ME4774-2    ........................................................................
ME4816-6    ........................................................................
ME4816-7    ...............................................C........................
ME4816-8    ........................................................................
ME4830-3    ...........................................................G.....G..........
ME4830-7    ........................................................................
ME7469      ...........................................................C............
ME10799-1   ...........................................................G..........
ME10799-3   ........................................................................
ME10799-4   ........................................................................
ME10799-13  ........................................................................
ME11502-3   ...........................................................G..T........
ME12195-3   ........................................................................
ME12195-8   ........................................................................
ME12263-5   ........................................................................
ME12263-8   ........................................................................
ME20793-1   ...........................................................G..T........
NC005805    A..........................................C.........G.....G..........
EU148343    ..................?.....................................G..T........
```

Bases 313 - 390

```
Group B     TGCAGGGACAGGATGAACAGTTTATCCCCCTCTTGCTGGGAATCTGGCTCACGCCGGGGCCTCCGTAGACTTAACCAT
Group A     ........................................................................
Group C     ........................................................................
Group D     ........................................................................
ME4756-4    ........................................................................
ME4756-7    C.......................................................................
ME4772-7    ........................................................................
ME4774-1    ........................................................................
ME4774-2    ........................................................................
ME4816-6    ........................................................................
ME4816-7    ........................................................................
ME4816-8    ........................................................................
ME4830-3    ........................................................................
ME4830-7    ........................................................................
ME7469      ........................................................................
ME10799-1   ........................................................................
ME10799-3   .......................................................................A..
ME10799-4   ........................................................................
ME10799-13  ......................C.................................................
ME11502-3   ........................................................................
ME12195-3   ....................................A...................................
ME12195-8   ........................................................................
ME12263-5   ........................................................................
ME12263-8   ........................................................................
ME20793-1   ........................................................................
NC005805    ...G.............C..C..G..C........C..C.....C.........................
EU148343    ........................................................................
```

Bases 391 - 468

```
Group B     TTTTTCCCTCCATCTCGCAGGAATCTCGTCTATTCTTGGAGCCATTAACTTTATTACTACAATTATTAATATAAAACC
Group A     ........................................................................
Group C     ........................................................................
Group D     ........................................................................
ME4756-4    ........................................................................
ME4756-7    ........................................................................
ME4772-7    ........................................................................
ME4774-1    ........................................................................
ME4774-2    ........................................................................
ME4816-6    ........................................................................
ME4816-7    ........................................................................
ME4816-8    ........................................................................
ME4830-3    ........................................................................
ME4830-7    ........................................................................
ME7469      ........................................................................
ME10799-1   ........................................................................
ME10799-3   ........................................................................
ME10799-4   .........T..............................................................
ME10799-13  ........................................................................
ME11502-3   ........................................................................
ME12195-3   ........................................................................
ME12195-8   ........................................................................
ME12263-5   ........................................................................
ME12263-8   ........................................................................
ME20793-1   ........................................................................
NC005805    ...C.................G...........C.....G.............C.....................
EU148343    ........................................................................
```

Bases 469 - 546

```
Group B     CCCTGCCATCTCACAGTACCAGACTCCCCTATTTGTTTGGGCCGTTTTAGTAACAGCAGTCCTCCTACTATTATCGCT
Group A     ...............................................................................
Group C     ..............A................................................................
Group D     ............................T..................................................
ME4756-4    ...............................................................................
ME4756-7    ...............................................................................
ME4772-7    ...............................................................................
ME4774-1    ...............................................................................
ME4774-2    ...............................................................................
ME4816-6    ...............................................................................
ME4816-7    ..............................................................................A..
ME4816-8    ....................................C..........................................
ME4830-3    ...............................................................................
ME4830-7    ..............A.....................................................C.......
ME7469      ...............................................................................
ME10799-1   ........................................T......................................
ME10799-3   ...................................................G...........................
ME10799-4   ...............................................................................
ME10799-13  ..............................................................C.......
ME11502-3   ...............................................................................
ME12195-3   ...............................................................................
ME12195-8   ...............................................................................
ME12263-5   ...............................................................................
ME12263-8   ...............................................................................
ME20793-1   ...................................................G...........................
NC005805    ..............A.....A..C..A...........A.....CC.G.............T......C....C..
EU148343    ...................................................G...........................
```

Bases 547 - 624

```
Group B     GCCAGTTCTTGCCGCAGGAATTACCATACTCCTTACCGACCGAAACTTAAACACAACCTTCTTTGACCCGGCAGGAGG
Group A     ................................................................................
Group C     ................................................................................
Group D     ................................................................................
ME4756-4    ..................G.............................................A........
ME4756-7    ................................................................................
ME4772-7    ................................................................................
ME4774-1    ................................................................................
ME4774-2    ................................................................................
ME4816-6    ................................................................................
ME4816-7    ................................................................................
ME4816-8    ................................................................................
ME4830-3    ................................................................................
ME4830-7    ................................................................................
ME7469      ................................................................................
ME10799-1   ................................................................................
ME10799-3   ...............................................................T............
ME10799-4   ................................................................................
ME10799-13  ................................................................................
ME11502-3   ................................................................................
ME12195-3   ................................................................................
ME12195-8   ................................................................................
ME12263-5   ................................................................................
ME12263-8   ..................G.............................................................
ME20793-1   ................................................................................
NC005805    ..................T..C.....G........T.........C....T.................A.....G..
EU148343    ................................................................................
```

Bases 625 - 652

Group B	GGGGGATCCTATTTTATACCAACACTTA
Group A	.....
Group C	.....
Group D	.....
ME4756-4	.....
ME4756-7	.....
ME4772-7	.....
ME4774-1	.....
ME4774-2	.....
ME4816-6	.....
ME4816-7	.....
ME4816-8	.....
ME4830-3	.....
ME4830-7	.....
ME7469	.....
ME10799-1	.....
ME10799-3	.....
ME10799-4	.....
ME10799-13	.....
ME11502-3	.....
ME12195-3	.....
ME12195-8	.....
ME12263-5	.....
ME12263-8	.....
ME20793-1	.....
NC005805	A.....C.....
EU148343	.....

Appendix VIII: Kimura 2-parameter distance matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
[1] Group A																														
[2] ME4756-4	0.005																													
[3] Group B	0.002	0.003																												
[4] ME4756-7	0.003	0.005	0.002																											
[5] Group C	0.003	0.005	0.002	0.003																										
[6] ME4772-7	0.003	0.005	0.002	0.003	0.003																									
[7] ME4774-1	0.003	0.005	0.002	0.003	0.003	0.003																								
[8] ME4774-2	0.003	0.005	0.002	0.003	0.003	0.003	0.003																							
[9] ME4816-6	0.003	0.005	0.002	0.003	0.003	0.003	0.003	0.003																						
[10]ME4816-7	0.007	0.008	0.005	0.007	0.007	0.007	0.007	0.003	0.007																					
[11]ME4816-8	0.003	0.005	0.002	0.003	0.003	0.003	0.003	0.003	0.003	0.007																				
[12]ME4830-3	0.003	0.008	0.005	0.007	0.007	0.007	0.007	0.007	0.007	0.010	0.007																			
[13]ME4830-7	0.005	0.007	0.003	0.005	0.002	0.005	0.005	0.005	0.005	0.008	0.005	0.008																		
[14]ME7469	0.003	0.005	0.002	0.003	0.003	0.003	0.003	0.003	0.003	0.007	0.003	0.007	0.005																	
[15]ME10799-1	0.002	0.007	0.003	0.005	0.005	0.005	0.005	0.005	0.005	0.008	0.005	0.005	0.007	0.005																
[16]ME10799-3	0.007	0.008	0.005	0.007	0.007	0.007	0.007	0.007	0.007	0.010	0.007	0.010	0.008	0.007	0.008															
[17]ME10799-4	0.003	0.005	0.002	0.003	0.003	0.003	0.003	0.003	0.003	0.007	0.003	0.007	0.005	0.003	0.005	0.007														
[18]ME10799-13	0.005	0.007	0.003	0.005	0.005	0.005	0.005	0.005	0.005	0.008	0.005	0.008	0.003	0.005	0.007	0.008	0.005													
[19]ME11502-3	0.002	0.007	0.003	0.005	0.005	0.005	0.005	0.005	0.005	0.008	0.005	0.005	0.007	0.005	0.003	0.008	0.005	0.007												
[20]ME12195-3	0.003	0.005	0.002	0.003	0.003	0.003	0.003	0.003	0.003	0.007	0.003	0.007	0.005	0.003	0.005	0.007	0.003	0.005	0.005											
[21]ME12195-8	0.003	0.005	0.002	0.003	0.003	0.003	0.003	0.003	0.003	0.007	0.003	0.007	0.005	0.003	0.005	0.007	0.003	0.005	0.005	0.003										
[22]ME12263-5	0.003	0.005	0.002	0.003	0.003	0.003	0.003	0.003	0.003	0.007	0.003	0.007	0.005	0.003	0.005	0.007	0.003	0.005	0.005	0.003	0.003									
[23]ME12263-8	0.003	0.002	0.002	0.003	0.003	0.003	0.003	0.003	0.003	0.007	0.003	0.007	0.005	0.003	0.005	0.007	0.003	0.005	0.005	0.003	0.003	0.003								
[24]ME20793-1	0.003	0.008	0.005	0.007	0.007	0.007	0.007	0.007	0.007	0.010	0.007	0.007	0.008	0.007	0.005	0.007	0.007	0.008	0.002	0.007	0.007	0.007	0.007							
[25]Group_D	0.003	0.005	0.002	0.003	0.003	0.003	0.003	0.003	0.003	0.007	0.003	0.007	0.005	0.003	0.005	0.007	0.003	0.005	0.005	0.003	0.003	0.003	0.003	0.007						
[26]EU148343	0.003	0.008	0.005	0.007	0.007	0.007	0.007	0.007	0.007	0.010	0.007	0.007	0.008	0.007	0.005	0.007	0.007	0.008	0.002	0.007	0.007	0.007	0.007	0.000	0.007					
[27]NC005805	0.085	0.085	0.087	0.089	0.085	0.089	0.089	0.089	0.087	0.091	0.089	0.085	0.083	0.089	0.087	0.092	0.089	0.083	0.087	0.087	0.089	0.089	0.087	0.089	0.089	0.089				
[28]*D. capensis*	0.154	0.158	0.156	0.156	0.154	0.158	0.154	0.158	0.156	0.156	0.154	0.152	0.156	0.156	0.156	0.160	0.158	0.156	0.154	0.156	0.158	0.154	0.158	0.156	0.154	0.156	0.141			
[29]*I. brunneus*	0.197	0.200	0.197	0.197	0.195	0.195	0.197	0.195	0.197	0.197	0.197	0.195	0.197	0.197	0.200	0.202	0.197	0.202	0.199	0.195	0.200	0.195	0.200	0.199	0.200	0.199	0.174	0.173		
[30]*I. brunneus*	0.197	0.200	0.197	0.197	0.195	0.195	0.197	0.195	0.197	0.197	0.197	0.195	0.197	0.197	0.200	0.202	0.197	0.202	0.199	0.195	0.200	0.195	0.200	0.199	0.200	0.199	0.174	0.173	0.000	

Appendix IX: Some nominal issues

Synaphobranchus kaupi Johnson, 1862 is a commonly used spelling of *Synaphobranchus kaupii* Johnson, 1862. Johnson spelled the species name as *kaupii,* and this is the spelling that should be used. Article 33.4 of the International Code of Zoological Nomenclature (The International Commission on Zoological Nomenclature, 2000) states that "the use of the genitive ending *-i* in a subsequent spelling of a species-group name that is a genitive based upon a personal name in which the correct original spelling ends with *-ii*, or vice versa, is deemed to be an incorrect subsequent spelling, even if the change in spelling is deliberate".

The Synaphobranchidae and its members have, to my knowledge, not been given any Norwegian names. Member(s) of the family have been caught in Norwegian waters. There are no recorded *Synaphobranchus* species in Norwegian waters, but I find it very possible that they will appear some day. *S. kaupii* is common west of the Faroe Islands and the British Isles, and the Faroe-Shetland Channel should not provide any geological boundary for this deep-sea species. I suggest the name "dyphavsåler" as the Norwegian name for the family Synaphobranchidae. The family is most commonly referred to as "deep-sea eels" in English, and the common name in Danish is "dybhavsåler". "Deep-sea eels" is a proper name for this family as all of its known members are defined as part of the deep sea fauna. I suggest the name "samspaltede dyphavsåler" as the Norwegian name for the genus *Synaphobranchus*. This name refers to the united gill slits of these eels, a feature that defines the genus.

Many articles have been published concerning various aspects of the ecology of *S. kaupii*. The study of the ecology of these fishes is interesting, but I will urge caution concerning the species identification. Taxonomical experts are having trouble with the identification of this species in laboratories. So I would say that the field identifications made by ecologists are questionable, especially *in situ* observations from manned submersibles or Remotely Operated Vehicles (ROV).

Reference

THE INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE (2000) *The International Code of Zoological Nomenclature*.