

1 Cranial Architecture of Tube-snouted Gasterosteiformes (*Syngnathus rostellatus* and  
2 *Hippocampus capensis*)

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## 21 ABSTRACT

22 The long snout of pipefishes and seahorses (Syngnathidae, Gasterosteiformes) is formed as an  
23 elongation of the ethmoid region. This is in contrast to many other teleosts with elongate  
24 snouts (e.g. Butterflyfishes) in which the snout is formed as an extension of the jaws.  
25 Syngnathid fishes perform very fast suction feeding, accomplished by powerful neurocranial  
26 elevation and hyoid retraction. Clearly, suction through a long and narrow tube and its  
27 hydrodynamic implications can be expected to require certain adaptations in the cranium,  
28 especially in musculoskeletal elements of the feeding apparatus. Not much is known about  
29 which skeletal elements actually support the snout and what the effect of elongation is on  
30 related structures. Here, we give a detailed morphological description of the cartilaginous and  
31 bony feeding apparatus in both juvenile and adult *Syngnathus rostellatus* and *Hippocampus*  
32 *capensis*. Our results are compared to previous morphological studies of a generalized teleost,  
33 *Gasterosteus aculeatus*. We found that the ethmoid region is elongated early during  
34 development, with the ethmoid plate, the hyosymplectic and the basihyal cartilage being  
35 extended in the chondrocranium. In the juveniles of both species almost all bones are forming,  
36 although only as a very thin layer. The elongation of the vomeral, mesethmoid, quadrate,  
37 metapterygoid, symplectic and preopercular bones is already present. Probably because of the  
38 long and specialized parental care which releases advanced developmental stages from the  
39 brooding pouch, morphology of the feeding apparatus of juveniles is already very similar to  
40 that of adults. We describe morphological features related to snout elongation that may be  
41 considered adaptations for suction feeding; e.g. the peculiar shape of the interhyal bone and  
42 its saddle-shaped articulation with the posterior ceratohyal bone might aid in explosive hyoid  
43 retraction by reducing the risk of hyoid dislocation.

44 KEY WORDS: Syngnathidae, cranial morphology, snout elongation, suction feeding

45 The family Syngnathidae (Gasterosteiformes) encompasses the pipefishes and seahorses.  
46 Apart from the prehensile seahorse tail and the elongated pipefish body, syngnathids are  
47 characterized by their remarkably elongate snout (i.e., the part of the head in front of the  
48 eyes). Unlike other long snouted teleosts (e.g., butterflyfishes, Chaetodontidae), the tubular  
49 snout of syngnathids is not formed by the extension of the jaws, but by an elongation of the  
50 region between the autopalatine bone and the lateral ethmoid bone, namely the ethmoid  
51 region.

52 Pipefishes and seahorses approach their prey from below and a rapid neurocranial elevation  
53 positions the mouth close to the prey. Next, an explosive expansion of the snout followed by  
54 lower jaw depression, cause water to flow into the mouth aperture (Muller and Osse, 1984;  
55 Muller, 1987; de Lussanet and Muller, 2007; Roos et al., 2009). Suction feeding in pipefishes  
56 and seahorses is the fastest ever recorded in teleosts. Muller and Osse (1984) found that  
57 *Entelurus aequoreus* captured its prey in 5 ms, while Bergert and Wainwright (1997) recorded  
58 a time of 5.8 ms for *Hippocampus erectus* and 7.9 ms for *Syngnathus floridae*. De Lussanet  
59 and Muller (2007) recorded capture times of 6-8 ms for *S. acus* and Roos et al. (2009)  
60 recorded 5.77 ms for *H. reidi*. It was recently discovered that newborns are even faster (Van  
61 Wassenbergh et al., 2009). However, having a long and narrow snout is not without  
62 hydrodynamic costs. For example, by increasing the length of the snout the moment of inertia  
63 increases. Secondly, it implies that a large difference in pressure between the buccal cavity  
64 and the surrounding water must be created (Poiseuille's law). And finally, as the upper and  
65 lower jaws closing the mouth aperture are minute, the prey size is constrained. Hence, the  
66 hydrodynamic implications of suction feeding through a long, narrow tube can be expected to  
67 rely on special adaptations in the feeding apparatus, particularly of musculoskeletal  
68 components forming and acting upon the jaws and ethmoid region.

69 To understand to what degree structural specializations of the tubular snout can be related to  
70 this highly performant suction feeding, a detailed examination of the morphology is needed.  
71 Thus far, studies dealing with syngnathid morphology are scarce or lack great detail (Branch,  
72 1966; De Beer, 1937; Kadam, 1958; Kadam, 1961; McMurrich, 1883). To fill this gap in  
73 current knowledge, this study focuses on the detailed anatomy of the cranial skeletal system  
74 of *Syngnathus rostellatus* (Nilsson's pipefish) and *Hippocampus capensis* (Knysna seahorse).  
75 Special attention is paid to the snout morphology to understand which skeletal elements are in  
76 fact elongated and what the effect of this elongation may have on the cranial architecture. The  
77 study of juveniles is required for a better comprehension of interspecific differences, as well  
78 as the detailed anatomical nature of snout elongation. The highly derived syngnathid  
79 morphology is compared to that of a generalized teleost, namely *Gasterosteus aculeatus*  
80 (three spined stickleback), both percomorph representatives, based on the study of Anker  
81 (1974).

82

### 83 MATERIALS AND METHODS

84 Four adults and five juveniles of *Syngnathus rostellatus*, three adults and four juveniles of  
85 *Hippocampus capensis* and two adults and one juvenile of *H. reidi* were studied (Table 1).  
86 The specimens of *S. rostellatus* were caught on the Belgian continental shelf (North Sea),  
87 whereas the specimens of *H. capensis* and *H. reidi* were obtained from the breeding program  
88 of the Antwerp Zoo and from commercial trade, respectively. The age of the specimens of *S.*  
89 *rostellatus* could not be determined properly. Because the standard length of the sectioned  
90 juvenile of *S. rostellatus* was not measured, the ratio head length over standard length of the  
91 other specimens was used to estimate the standard length by interpolation, resulting in a  
92 length of 13.1 mm (Table 1). All specimens were catalogued in the collection of the  
93 Zoological Museum of the Ghent Universtity (UGMD).

94 The term juvenile instead of larva is conform with Balon (1975), because the fins are already  
95 differentiated. Newly released *H. kuda* resemble miniature adults and when they leave the  
96 pouch they are considered juveniles rather than larvae as in most marine teleosts (Choo and  
97 Liew, 2006). Besides that, growth allometries after release from the brood pouch reflect  
98 typical teleostean juvenile growth and not larval growth (Choo and Liew, 2006).

99 Adult as well as juvenile specimens of all species (with exception of a juvenile *H. reidi*) were  
100 cleared and stained with alizarin red S and alcian blue according to the protocol of Taylor and  
101 Van Dyke (1985). A stereoscopic microscope (Olympus SZX-7) equipped with a camera  
102 lucida was used to study and draw the bony and cartilaginous elements of the cranium. KOH  
103 5% was used to completely disarticulate the suspensorium of an adult specimen of all species,  
104 so all bones could be individually examined in detail. In the juveniles, bone staining was not  
105 very clear, so serial histological cross sections were used, which also enabled more precise  
106 detection of the skeletal elements. Prior to sectioning, specimens stored in ethanol 70% were  
107 decalcified with Decalc 25% (Histolab Products AB Gothenburg, Sweden), dehydrated  
108 through an alcohol series, and embedded in Technovit 7100 (Heraeus Kulzer Wehrheim,  
109 Germany). Semi-thin sections (5 µm) were cut using a sliding microtome equipped with a  
110 wolframcarbide coated knife (Leica Polycut SM 2500), stained with toluidine blue and  
111 mounted with DPX. Images of the sections were acquired using a digital camera (Colorview  
112 8, Soft Imaging System) mounted on a light microscope (Polyvar, Reichert, Jung), controlled  
113 by the software program analySIS 5.0 (Soft Imaging System GmbH Münster, Germany).

114 Graphical 3D-reconstructions of the chondrocranium of both *S. rostellatus* and *H. capensis*  
115 were generated, using Amira 3.1 (Template Graphics Software Mérignac, France) and  
116 Rhinoceros 3.0 software (McNeel Europe SL Barcelona, Spain). Sections were manually  
117 aligned, structures traced and surface models of the segmented structures were generated. The

118 specimen of *S. rostellatus* (13.1 mm SL) used for serial sectioning shows the hyoid in a  
119 resting position, whereas that of *H. capensis* (12.8 mm SL) had its hyoid depressed.

120

## 121 RESULTS

122 The terminology of the osteological components, for the most part, follows that of Lekander  
123 (1949) and Harrington (1955). The vomeral, circumorbital, parietal and postparietal bones  
124 follow the terminology of Schultze (2008).

125

### 126 *Juvenile cranium*

#### 127 *Syngnathus rostellatus*

128 The cartilaginous neurocranium consists of two parts which are separated by the eyes: the  
129 rostral ethmoid and the caudal otic capsule (Fig. 1). The ethmoid plate is long and narrow but  
130 becomes wider rostrally where it lies ventral to the rostral cartilage (Fig. 1A,B). More  
131 caudally the ethmoid plate bears a vertical ridge, i.e. the internasal septum, connected to the  
132 orbitonasal laminae, which enclose the orbitonasal foramina (Fig. 1A,B). Although the  
133 ethmoid plate and the septum are firmly fixed, histological differences among the  
134 cartilaginous elements suggests that the internasal septum is not formed as an outgrowth of  
135 the ethmoid plate. There is a clear difference in the size, shape and organization of their  
136 chondrocytes (Fig. 2D). The ethmoid plate is continuous with the trabecula communis, that  
137 lies medial to the orbits (Fig. 1B,C). Ventrally the otic capsule is provided with an articulation  
138 facet for the hyomandibular part of the hyosymplectic cartilage. Meckel's cartilage bears a  
139 ventral retroarticular process and articulates caudally with the pterygoquadrate part of the  
140 palatoquadrate cartilage, which is roughly L-shaped (Fig. 1A). The palatine part, which is  
141 completely separated from the pterygoquadrate part, lies lateral to the ethmoid plate (Fig. 1A).  
142 The largest cartilage element of the splanchnocranium is the hyosymplectic cartilage, which

143 consists of a long, horizontal symplectic part, and a shorter oblique hyomandibular part (Fig.  
144 1A,C). At the ventrocaudal margin of the hyosymplectic cartilage lies the interhyal cartilage,  
145 articulating ventrally with the ceratohyal cartilage (Fig. 1C). Medial of the two ceratohyal  
146 cartilages lies one long basihyal and two shorter hypohyal cartilages (Fig. 1C).

147 Juveniles of *S. rostellatus* show the onset of ossification in most places, however only a very  
148 thin layer of bone was observed (Fig. 2). Ventral to the ethmoid plate the dermal  
149 parasphenoid bone has already formed. This very long bone runs from the ethmoid region up  
150 to the posterior part of the otic region (Fig. 2D,F). Formation of the mesethmoid bone begins  
151 dorsal to the ethmoid plate and around the internasal septum (Fig. 2C). A thin bony sheet at  
152 the ventral end of the orbitonasal laminae is the precursor of the lateral ethmoid bone. Around  
153 the main part of Meckel's cartilage, the dentary bone is formed (whether this bone includes  
154 the mentomeckelian and splenial bones is uncertain due to the absence of canals; Fig. 2B).  
155 This bone bears a large ventral ridge and posteriorly encloses the anguloarticular bone (this  
156 could be fused with the splenial bones, but again no canals were observed), which is still  
157 poorly developed and only present on the lateral side of Meckel's cartilage (Fig. 2B). The  
158 retroarticular bone is visible as a small ossification of the ventrocaudal part of the Meckel's  
159 cartilage (Fig. 2B). In the upper jaw, both maxillary and premaxillary bones have appeared  
160 and are already fairly well developed. The former articulates with the rostral cartilage  
161 dorsally. The autopalatine bone is present but does not bear a clear maxillary or vomeral  
162 articulation facet yet (Fig. 2A). Ventral to the palatoquadrate cartilage the ectopterygoid bone  
163 is formed (Fig. 2A). This dermal bone shows a small horizontal part and a longer vertical one  
164 that meets the dorsal process of the quadrate bone. At the dorsal edge of the palatoquadrate  
165 cartilage, the small metapterygoid bone arises (Fig. 2C). The quadrate bone bears a dorsal  
166 process, as well as a ventromedial and ventrolateral wing. More caudally these wings enclose  
167 the cartilaginous hyosymplectic and the symplectic bone (Fig. 2C,E). The symplectic bone

168 consists of both the ossification around the rostral part of the hyosymplectic cartilage and a  
169 dorsal crest on top of the perichondral part (Fig. 2E). The hyomandibular bone is formed  
170 caudally around the hyosymplectic cartilage and bears dorsal articulations with the  
171 neurocranium and opercular bone that remain cartilaginous (Fig. 2F). The preopercular bone  
172 consists of both a short and long process, the long one covers the quadrate and symplectic  
173 bones rostrally, and is also provided with a large lateral process (Fig. 2E). Its shorter oblique  
174 bar covers the hyomandibular bone caudally (Fig. 2F). All other elements of the hyoid arch,  
175 i.e., basihyal, hypohyals, ceratohyals and interhyal cartilages, show the presence of a very thin  
176 sheet of bone (Fig. 2E,F). The hypohyal bones bear a ventrolateral and a ventromedial  
177 process, which surround the ceratohyal bones ventrally (Fig. 2E). Anterior and posterior  
178 ceratohyal bones are hard to distinguish from each other at this stage (Fig. 2E). Within the  
179 tendon of the sternohyoideus muscle, the urohyal bone has also arisen. The opercular bone is  
180 a thin but fairly large bony sheet, bearing a lateral process and articulating with the  
181 hyomandibular bone medially. None of the other opercular bones (interopercular,  
182 subopercular and suprapreopercular bones) and neither the branchiostegal rays are present yet.

183

#### 184 *Hippocampus capensis*

185 For the chondrocranium of *H. capensis* (Fig. 3), we report only those features which differ  
186 from *S. rostellatus*.

187 The ethmoid plate of the cartilaginous neurocranium in *H. capensis*, is shorter and rostrally  
188 narrower than that of *S. rostellatus* (Fig. 3A,B). Caudal to the olfactory organs, the ethmoid  
189 plate widens and meets the orbitonasal laminae (Fig. 3A,B, 4D). It is also continuous with the  
190 trabecula communis, but in the seahorse the latter is much shorter and more robust (Fig. 3C).  
191 The otic capsule has a distinct position compared to that in *S. rostellatus*, namely  
192 dorsocaudally of the orbits. Hence, it does not lie on the same level as the ethmoid plate, but



193 at an angle to the latter (otic capsule tilted about 34° up; Fig. 3A). At the ventral surface of the  
194 otic capsule, the articulation facet of the hyomandibular part of the hyosymplectic cartilage is  
195 much more prominent and it is laterally flanked by a spheno-pterotic ridge (Fig. 3A). The  
196 Meckel's cartilage is more tapered rostrally compared to that of *S. rostellatus* (Fig. 3A). The  
197 symplectic part of the hyosymplectic cartilage is somewhat shorter in *H. capensis*. The  
198 hyomandibular part, however, is longer and more vertically orientated compared to that of the  
199 pipefish (Fig. 3A). In the seahorse, the shorter basihyal cartilage lies in front of the ceratohyal  
200 cartilages, which may be due to the hyoid being retracted (Fig. 3A,C).

201 Almost all bones are present in the juvenile *H. capensis* studied, except for the circumorbital  
202 bones (Fig. 4). The vomeral bone lies ventral to the ethmoid plate and becomes covered by  
203 the parasphenoid bone more caudally (Fig. 4A,B,D). The latter bears two rather large lateral  
204 wings that reach the ventral surface of the otic capsule. The dentary bone rostrally bears a  
205 small lateral process and has a well developed coronoid process. The anguloarticular bone and  
206 retroarticular bone are prominent and there is a ligamentous connection between the  
207 retroarticular bone and the slender interopercular bone that continues to run up to the posterior  
208 ceratohyal bone (Fig. 4C). The dorsal crest of the symplectic bone is larger in *H. capensis*  
209 compared to *S. rostellatus* (Fig. 4E). There is a large spine on the lateral surface of the  
210 preopercular bone and the ascending bar is oriented vertically instead of obliquely as in the  
211 pipefish (Fig. 4F). The bony sheets around the hypohyal and ceratohyal cartilages are well  
212 developed (Fig. 4F). In addition, the anterior and posterior ceratohyal bones are distinct from  
213 each other. In the seahorse, the urohyal bone is much shorter. The opercular bone has a  
214 convex shape and bears a prominent lateral process. Also the subopercular bone and  
215 branchiostegal rays are fairly well developed in juvenile *H. capensis*.

216

217

#### *Adult cranium*

218 *Syngnathus rostellatus*

219 The most distinctive character of the skull of *Syngnathus rostellatus* is the highly extended  
220 tube snout (Fig. 5). It is formed by the elongation of the vomeral, mesethmoid and the  
221 circumorbital bones of the neurocranium and of the quadrate, metapterygoid, symplectic,  
222 preopercular and interopercular bones of the splanchnocranium (Fig. 5A).

223 Both the maxillary and premaxillary bones are relatively small and toothless (Fig. 5A,B,D,E).

224 The maxillary bone bears two cartilaginous processes dorsally: a rostral premaxillary one and  
225 a caudal one for the articulation with the vomeral bone. Below the latter process there is also a  
226 cartilaginous articulation surface for the autopalatine bone. The round rostral cartilage is  
227 situated mediocaudal of the maxillary bone and dorsally of the vomeral bone. Ventrally, the  
228 maxillary bone is triangularly shaped, covering the coronoid process of the dentary bone to  
229 which it is ligamentously connected. The slender premaxillary bone is rostrocaudally flattened  
230 and tapers ventrally. It is provided with a dorsocaudal cartilaginous articulation head for the  
231 maxillary bone.

232 The vomeral bone is a long and narrow bone that broadens anteriorly, forming an articulation  
233 with the autopalatine bone laterally and the maxillary bone rostrally (Fig. 5A,B,D,E). The  
234 hind part of the vomeral bone reaches the lateral ethmoid bones and is covered dorsally by the  
235 mesethmoid bone. More caudally, it is wedged in a fissure of the parasphenoid bone. The  
236 mesethmoid bone covers more than half the length of the snout and stretches out caudally, up  
237 to the parietal bones (Fig. 5A,B). The lateral ethmoid bone is a slim bone that separates the  
238 nasal opening from the orbits (Fig. 5A,B).

239 The parasphenoid bone is positioned rostrally between the dorsal mesethmoid bone and the  
240 ventral vomeral bone (Fig. 5A). It bears two lateral wings behind the orbits and fits into a  
241 wedge of the basioccipital bone caudally. In most specimens studied of *S. rostellatus* only two  
242 circumorbital bones are present, which seem to be homologous to an antorbitolacrimial and a

243 second infraorbital bone (see discussion). Only one specimen has just one bone on its right  
244 side. In the individuals with two circumorbital bones, the large antorbitolacrimal bone  
245 caudally reaches the front end of the nasal opening, and covers a large part of the quadrate  
246 bone (Fig. 5A,B). Ventrally, the antorbitolacrimal bone shows one or several small  
247 indentations. The second infraorbital bone is much smaller and borders the ventral side of the  
248 nasal opening, as well as the anterior side of the orbits (Fig. 5A,B,C).

249 The large dentary bone of the lower jaw has a well developed coronoid process (Fig.  
250 5A,C,D). Inside a cavity of the dentary bone, the smaller anguloarticular bone fits, which  
251 bears a distinctive cartilaginous articulation with the quadrate bone caudally (Fig. 5A,C,D).

252 The retroarticular bone is very small, with a strong mandibulo-interopercle ligament  
253 connecting it to the interopercular bone (Fig. 5A,C,D).

254 In the adult stage, the autopalatine bone carries a prominent cartilaginous maxillary process, a  
255 smaller articulation condyle for the vomeral bone and a slender cartilaginous process caudally  
256 (Fig. 5A,B,D,E). There is no separate dermopalatine bone and as in most extant teleosts, it is  
257 probably fused to the autopalatine bone (Arratia and Schultze, 1991). The ectopterygoid bone  
258 is roughly triangularly shaped, with a vertical part running along the ascending process of the  
259 quadrate bone and a horizontal part that is covered dorsally by the vomeral bone (Fig.  
260 5A,B,D,E). This dorsal part shows a gap into which the cartilaginous process of the  
261 autopalatine bone fits, with a firm connection linking both. Lateral to the vomeral bone and  
262 behind the ectopterygoid bone lies the metapterygoid bone which tapers posteriorly and is  
263 covered by the upper rostral margin of the lacrimal bone (Fig. 5A,B). The quadrate bone, a  
264 long perichondral bone that stretches out caudally, is mostly covered by the metapterygoid  
265 bone anteriorly and the two circumorbital bones posteriorly (Fig. 5A,B,C).

266 The hyomandibular bone articulates dorsally by a double condyle with the sphenotic and  
267 prootic bones, respectively, and bears a dorsocaudal opercular process. The symplectic bone

268 is almost completely covered by the preopercular and circumorbital bones and forms the  
269 ventral border of the orbits (Fig. 5A). It bifurcates anteriorly into two processes: a lower  
270 horizontal part that joins the quadrate bone, and a more dorsal oblique crest lying behind the  
271 upper margin of the second infraorbital bone.

272 The long horizontal process of the preopercular bone overlaps with the quadrate bone  
273 anteriorly where it tapers (Fig. 5A,C). Medially the preopercular bone has two ridges: one  
274 supporting the symplectic bone and one for insertion of the levator arcus palatini muscle,  
275 which continues to run along this ridge and more caudally in a groove of the hyomandibular  
276 bone. Ventrally the preopercular bone has a cartilaginous differentiation where the  
277 cartilaginous head of the interhyal bone articulates. There is no articulation between the  
278 interhyal bone and the hyomandibular bone. The interopercular bone is covered by the  
279 preopercular bone and the quadrate bone, with an interopercle-hyoid ligament connecting it to  
280 the posterior ceratohyal bone caudally (Fig. 5C). The interhyal bone, which is stout and small,  
281 is ventrally provided with a very firm, saddle-shaped joint for the posterior ceratohyal bone  
282 (Fig. 5A,C). The posterior ceratohyal bone has a small lateral process, close to the interhyal  
283 articulation (Fig. 5C). Onto this process, the interopercle-hyoid ligament attaches rostrally and  
284 at its caudal base, the two branchiostegal rays are connected. There is a firm interdigitation  
285 between the posterior and anterior ceratohyal bone. Distally, there is a small triangularly  
286 shaped gap between the left and right anterior ceratohyal bones, just below the very firm  
287 cartilaginous symphysis. The anterior ceratohyal bones are connected to the urohyal bone by a  
288 paired ceratohyal-urohyal ligament (Fig. 5C). The hypohyal bone is a small element that is  
289 firmly connected to the medial face of the anterior ceratohyal bone. Medial to the anterior  
290 ceratohyal bones and covered by the other elements of the hyoid lies the slender basihyal  
291 bone, which remains cartilaginous rostrally. The urohyal bone is a fairly long and slender

292 bone that broadens somewhat rostrally where the ceratohyal-urohyal ligaments attach (Fig.  
293 5C).

294 The opercular bone is large and has a convex lateral surface (Fig. 5A,B,C). There is just a tiny  
295 gill slit close to the cleithrum. The suprapreopercular bone is a small bone lying dorsorostrally  
296 to the opercular bone (Fig. 5A,B). The subopercular bone is sickle shaped, covered by the  
297 ventral edge of the opercular bone. The two branchiostegal rays, which are long and slender,  
298 join the caudal margin of the opercular bone and reach up to the gill slit (Fig. 5A,C). There  
299 are no canals for the lateral line system present in any of the bones studied.

300

### 301 *Hippocampus capensis*

302 The premaxillary and maxillary bones look very similar to those in *S. rostellatus* (Fig.  
303 6A,B,D,E). In *H. capensis*, however, they are more heavily built and the maxillary bone  
304 shows a more prominent convex curve when viewed rostrally. The rostral cartilage has a more  
305 elliptical shape instead of being round.

306 The dorsal part of the tube snout consists of the vomeral bone and the mesethmoid bone (Fig.  
307 6B). The latter has a slightly bifurcated rostral end and covers approximately half the snout  
308 length. The lateral ethmoid bone is very distinct and has quite a large lateral process (Fig.  
309 6A,B).

310 The parasphenoid bone stretches ventrally along the neurocranium and bends somewhat  
311 upwards in the otic region (Fig. 6A). The number of circumorbital bones in *H. capensis* is  
312 variable. In spite of this variability, some of them can be considered as homologous  
313 (antorbital, lacrimal and dermosphenotic bones) as indicated by Schultze (2008). The  
314 dermosphenotic bone is consistently present in all specimens observed. Variation was found  
315 at the level of all other circumorbital bones, including left right variation (e.g. one specimen,  
316 97.6 mm SL, has an additional fourth circumorbital bone on its right side of which the

317 homology is less obvious). Another specimen (99.0 mm SL) also seemed to have a fused  
318 antorbitolacrimal bone, whereas separate bones were observed in others. The most common  
319 pattern observed is where the antorbital bone is the smallest, covering the quadrate bone and  
320 the metapterygoid bone (Fig. 6A,B). The lacrimal bone also covers the quadrate bone and is  
321 provided with a dorsorostral gap into which the metapterygoid bone fits (Fig. 6A,B). Finally,  
322 the second infraorbital bone covers the quadrate, the preopercular and a large part of the  
323 symplectic bones (Fig. 6A,B,C). Of the circumorbital bones, the most anterior one covers the  
324 next at its caudal end, so the antorbital bone covers the lacrimal bone, which in turn covers  
325 the second infraorbital bone.

326 The dentary bone is a short but solid bone (Fig. 6A,C,D). Ventrocaudally, the anguloarticular  
327 bone bears two ventral processes in between which the small retroarticular bone fits (Fig.  
328 6A,C,D).

329 The autopalatine bone is a rather slender bone whereas the ectopterygoid bone is somewhat  
330 firmer compared to the one in *S. rostellatus* (Fig. 6A,B,D,E). The metapterygoid bone fits into  
331 a gap of the lacrimal bone posteriorly (Fig. 6A,B).

332 The two neurocranial condyles of the hyomandibular bone are larger and more distant from  
333 each other in the seahorse. In addition, the hyomandibular bone is provided with a lateral  
334 process that is firmly connected to the preopercular bone. The oblique fork of the symplectic  
335 bone present in the pipefish is larger in the seahorse and forms a dorsal plate upon the  
336 perichondral part. Only the caudal part, that borders the ventrorostral margin of the orbits, is  
337 visible in a lateral view (Fig. 6A). The preopercular bone has a short ascending process that  
338 forms the posterior margin of the orbits (Fig. 6A,C). The interopercular bone is much shorter  
339 compared to that in *S. rostellatus* (Fig. 6A,C). The interhyal, the anterior and posterior  
340 ceratohyal, the hypohyal and basihyal bones resemble those of *S. rostellatus* (Fig. 6A,C). The

341 urohyal bone, which is more robust, has a rostral bifurcation with both processes connected to  
342 the anterior ceratohyal bone by ceratohyal-urohyal ligaments (Fig. 6C).

343 The opercular bone is higher and has a less rounded dorsocaudal edge (Fig. 6A,B,C). The  
344 suprapreopercular bone is absent. The two very thin and slender branchiostegals reach up to  
345 the caudal edge of the opercular bone (Fig. 6A,B,C). As in *S. rostellatus* the canals for the  
346 lateral line are absent in all bones studied.

347

## 348 DISCUSSION

### 349 *Bone terminologies*

350 The dentary and anguloarticular bones in *Syngnathus rostellatus* and *Hippocampus capensis*  
351 could be a fusion of several bones. In most teleosts, the dentary bone comprises the  
352 perichondral mentomeckelian, the dermal splenial and the dermal dentary bones, and should  
353 thus be named ‘dento-splenio-mentomeckelium’ according to the nomenclature of Lekander  
354 (1949). The anguloarticular bone is then the fusion of the perichondral articular bone, the  
355 dermal splenial bones and the dermal angular bone; the ‘angulo-splenio-articulare’. However,  
356 whether this is also the case for syngnathids is not certain, because the absence of the  
357 preoperculo-mandibular canal may indicate the absence of the splenial bones. In the current  
358 deficiency of conclusive ontogenetic evidence to elucidate this, the terms ‘dentary bone’ and  
359 ‘anguloarticular bone’ are used here.

360 Kindred (1924) suggested there is a pterygoid bone in *S. fuscus*, which would be a fusion of  
361 the ectopterygoid and the endopterygoid bones. According to Kadam (1961) the ectopterygoid  
362 and the endopterygoid bones ossify separately in *Nerophis* (species not stated), *S. serratus*  
363 and *Hippocampus* (species not stated). Bergert and Wainwright (1997) found both, an  
364 ectopterygoid and an entopterygoid bone, in *S. floridae*, and solely an ectopterygoid bone in  
365 *H. erectus*. In *S. rostellatus* and *H. capensis* we found no indications of an endopterygoid

366 bone. As Kadam (1961) correctly pointed out, the bone that Kindred (1924) describes as the  
367 pterygoid bone consists as two separate elements and one of them is indeed the dermal  
368 ectopterygoid bone. However, he did not notice that the bone he called the endopterygoid  
369 bone is perichondral, and therefore homologous to a metapterygoid bone. Bergert and  
370 Wainwright (1997) followed Kindred (1924) in identifying the metapterygoid bone of *S.*  
371 *floridae* as the entopterygoid bone. In addition, they did not mention the presence of a similar  
372 bone in *H. erectus*. Swinnerton (1902) states that in *G. aculeatus* the pterygoid bone takes up  
373 the position of both entopterygoid and ectopterygoid bones, however, only one centre of  
374 ossification is found. According to De Beer (1937) *Gasterosteus aculeatus* is in the  
375 possession of both an ectopterygoid and an endopterygoid bone, fused to form what he calls a  
376 pterygoid bone. We could not exclude a fusion between the ecto- and endopterygoid bone in  
377 *S. rostellatus* and *H. capensis*. However, based on its topography, ventrolateral to the  
378 autopalatine and the metapterygoid bone, this bone is considered homologous to the  
379 ectopterygoid bone.

380 As Branch (1966) mentioned, the homology of the circumorbital bones has been unclear.  
381 Kindred (1924), and De Beer (1937), defined the metapterygoid bone of *S. fuscus* as “the  
382 intramembranous ossification dorsal to the quadrate, rostral to the symplectic and excluded  
383 from contact with the metapterygoid process of the palatoquadrate by the pterygoid”.  
384 However, Kadam (1961), Branch (1966) and Patterson (1977) pointed out this is not the  
385 metapterygoid bone, but the lacrimal bone. Jungersen (1910) identified the circumorbital  
386 bones as the posterior and anterior preorbital bones in *Syngnathus typhle* (which he called  
387 *Syphonostoma typhle*) because of their position lateral of the adductor mandibulae muscle.  
388 Gregory (1933) states that *Phyllopteryx* is in possession of “a row of antorbital plates on the  
389 side of the oral tube”, which he labels as two metapterygoid bones. As previously mentioned,  
390 Kindred (1924) and De Beer (1937) maintained that the lacrimal bone in *S. fuscus* is the



391 metapterygoid bone, although they correctly pointed out that the second infraorbital bone is a  
392 circumorbital bone. Kadam (1961) described the two bones of the suborbital chain in  
393 *Nerophis* as an anterior preorbital bone and a posterior suborbital bone and he remarked that  
394 in *Syngnathus* and *Hippocampus* there are two preorbital bones. The use of the terms  
395 preorbital and suborbital bones should be avoided as they only indicate the position of these  
396 bones relative to the orbit but don't say anything about their homology (Daget, 1964).  
397 Therefore we use the terms antorbital bone and infraorbital bones, as e.g. in Lekander (1949),  
398 Nelson (1969) and Schultze (2008). Occasionally, the term prevomer bone is used instead of  
399 vomer bone (Gregory, 1933; De Beer, 1937; Harrington, 1955), however because the  
400 homology with the vomer bone in sarcopterygians, the terminology of Schultze (2008) is  
401 followed here.

402

#### 403 *Aspects of snout elongation*

404 As shown in Table 1, even though size ranges are similar, there is a difference in  
405 developmental stage between the juveniles of *Syngnathus rostellatus* (11.0-14.5 mm SL) and  
406 *Hippocampus capensis* (12.8-14.0 mm SL). Due to the different developmental stages of our  
407 specimens (*S. rostellatus* specimens had not left the brood pouch), we cannot link the  
408 morphological differences between the two species to differences in their developmental rate.  
409 However, this poses no problem for the main goal of this study, i.e. to show the relation  
410 between snout elongation and cranial morphology in an early developmental stage. Therefore,  
411 we will focus on the differences between both species, irrespective of their different  
412 developmental stages.

413 Both *S. rostellatus* and *H. capensis* have an elongated snout compared to *Gasterosteus*  
414 *aculeatus*. This elongation is restricted to the ethmoid region (vomer, mesethmoid,  
415 circumorbital, quadrate, metapterygoid, preopercular, interopercular and symplectic bones). It

416 appears to occur early in development, as observed in several Syngnathidae (e.g. *H.*  
417 *antiquorum* (Ryder, 1881), *S. peckianus* (McMurrich, 1883), *S. fuscus* (Kindred, 1921),  
418 *Hippocampus* (Kadam, 1958) and *Nerophis* (Kadam, 1961)). In *H. antiquorum* and *S.*  
419 *peckianus*, the ethmoid region is even elongated before the yolk sac is fully absorbed (Ryder,  
420 1881; McMurrich, 1883).

421 A short comparison between some of these elements in syngnathids and the stickleback, as a  
422 generalized teleost representative without an elongated snout, is given here in order to  
423 understand the implications of snout elongation on cranial morphology in syngnathids (Fig.  
424 7).

425 The vomeral bone stretches up to the lateral ethmoid bone in *S. rostellatus* and *H. capensis*,  
426 but in *Nerophis* it does not reach the nasal region (Kadam, 1961). According to Kadam  
427 (1961), this is a difference between the Gasterophori (syngnathids with the brood pouch  
428 rostral to anal fin: e.g. *Nerophis*) and the Urophori (brood pouch caudal to anal fin: e.g.  
429 *Syngnathus* and *Hippocampus*). Rostrally the vomeral bone provides an articulation with the  
430 maxillary bone, but there is no mesethmoid-premaxilla articulation present as there is in  
431 primitive teleosts (Gregory, 1933).

432 In *S. rostellatus* and *H. capensis* the quadrate bone consists of a perichondral ascending  
433 process and a membranous horizontal process. Whether or not this horizontal process is  
434 homologous to the one considered a teleostean synapomorphy by Arratia and Schultze (1991),  
435 could not be confirmed here. The process is much smaller on the quadrate bone in *G.*  
436 *aculeatus*, which is triangularly shaped with its apex dorsally (Anker, 1974). The  
437 ventrorostral corner of the quadrate bone provides the articulation with the lower jaw and  
438 ventrocaudally it bears a cartilaginous extension that lies lateral to the symplectic bone  
439 (Anker, 1974).

440 The preopercular bone in *S. rostellatus* and *H. capensis* is L shaped. In the former the  
441 horizontal process is substantially longer than the vertical one, while in *H. capensis* the  
442 difference is less and in *G. aculeatus* the vertical process is the largest (Anker, 1974).  
443 Caudally, this vertical process meets the opercular bone in syngnathid species (Jungersen,  
444 1910; Kindred, 1924; Kadam, 1961; Branch, 1966), but in *G. aculeatus* they only join each  
445 other dorsally (ventrally they are separated by an ascending process of the subopercular bone;  
446 Swinnerton, 1902; Anker, 1974).

447 In *G. aculeatus* the interopercular bone covers the subopercular bone caudally (Anker, 1974),  
448 but both lie well separated from each other in *S. rostellatus* and *H. capensis*.

449 The occurrence of an antorbital bone and lacrimal bone, followed by six infraorbital bones  
450 bordering the orbit (the first, third and sixth being the lacrimal, jugal and dermosphenotic  
451 bones, respectively), is a primitive feature of most teleosts (Reno, 1966; Nelson, 1969;  
452 Schultze, 2008). In the suborder Syngnathoidei other circumorbital bones besides the lacrimal  
453 bone are usually absent (Nelson, 2006), however, in syngnathids there are usually two to three  
454 infraorbital bones, which develop late (Kadam, 1961). In *S. rostellatus* and *H. capensis* the  
455 circumorbital bones are positioned in front of the orbit instead of around it. There is, however,  
456 a difference between those two species, as most specimens of the seahorse studied have an  
457 antorbital bone, a lacrimal bone (= first infraorbital bone) and a second infraorbital bone,  
458 whereas there are only two circumorbital bones present in almost all *S. rostellatus* specimens  
459 studied. Here, the posterior one corresponds to the second infraorbital bone. The anterior one  
460 is the largest one and appears to be a fusion between the antorbital bone and the lacrimal  
461 bone. This hypothesis is supported by the absence of a separate antorbital bone, the bone  
462 being as large as and taking the place of both the antorbital bone and the lacrimal bone in *H.*  
463 *capensis*. In addition, there is a ventral indentation that could point out the incomplete fusion  
464 between the antorbital bone and the lacrimal bone. The formation of the antorbitolacrimal

465 bone could be a structural advantage to strengthen the elongated snout laterally. During the  
466 fast elevation of the snout, large, ventrally oriented forces are expected to be exerted onto the  
467 dorsal part of the snout. In the case of an unfused antorbital bone and lacrimal bone, a  
468 possible bending zone between the two bones exists. The formation of an antorbitolacrimal  
469 bone could reduce the risk of bending and still allows lateral expansion of the snout. In *G.*  
470 *aculeatus* there are three separate circumorbital bones present (Swinnerton, 1902; De Beer,  
471 1937; Anker, 1974).

472

#### 473 *Fast suction feeding adaptations*

474 Syngnathid fishes are known to capture prey by an unusual feeding strategy known as pipette  
475 feeding (de Lussanet and Muller 2007). They perform a rapid elevation of the head, which  
476 brings the mouth quickly close to the prey (Muller 1987). Then, expansion of their long snout  
477 generates a fast water flow that carries the prey into the mouth. This increase in buccal  
478 volume is mainly achieved by a lateral expansion, instead of ventral expansion typical for  
479 most suction feeding fish (Roos et al., in press). The hyoid is known to play an important role  
480 in suspensorium abduction as well as in depression of the lower jaw (Roos et al., in press).  
481 Seahorses and pipefishes are ambush predators, they sit and wait until a prey comes close to  
482 the mouth (Foster and Vincent, 2004). They are known to consume mainly small crustaceans  
483 such as amphipods and copepods (Foster and Vincent, 2004; Kendrick and Hyndes, 2005) and  
484 a recent study by Castro et al. (2008) showed that nematodes are also one of the main food  
485 items consumed in the wild. According to Kendrick and Hyndes (2005) the trophic  
486 specialization of these fishes can be explained by their extreme snout morphology (length and  
487 gape), their feeding behavior and in the case of seahorses, their low mobility.  
488 Syngnathids have a very small mouth aperture, severely limiting food particle size. The  
489 maxillary and premaxillary bones of *S. rostellatus* and *H. capensis* are rather small. Teeth,

490 both oral and pharyngeal, are absent and prey is swallowed whole (Lourie et al., 1999).  
491 *Gasterosteus aculeatus*, however, has a large, teeth bearing, premaxillary bone that is  
492 protrusible (De Beer, 1937; Alexander, 1967a; Anker, 1974; Motta, 1984; Nelson, 2006).  
493 Under the condition that a long ascending process of the premaxillary bone can be associated  
494 with a great amount of protrusion (Gosline, 1981; Motta, 1984; Westneat and Wainwright,  
495 1989; Westneat, 2004), the lack of an ascending process in *S. rostellatus* and *H. capensis*  
496 indicates there is no upper jaw protrusion (Branch, 1966; Bergert and Wainwright, 1997).  
497 They do have a small rostral cartilage, rostradorsally of the ethmoid plate and medially of the  
498 maxillary bones. This is not necessarily an adaptation to the powerful suction feeding but  
499 could rather be an ancestral feature also found in Percidae, Cichlidae, Atherinoidei,  
500 Gasterosteidae and others, where it assists in upper jaw protrusion (Alexander, 1967a; 1967b;  
501 Motta, 1984). Alternatively, the rostral cartilage in syngnathids could be involved in the fast  
502 rotation of the maxillary and premaxillary bones during mouth opening. Depression of the  
503 lower jaw induces a rostral swing of the maxillary bone, because of the firm primordial  
504 ligament running from the coronoid process to the maxillary bone. As a consequence of the  
505 connection between maxillary and premaxillary bones, both rotate anteriorly. The mouth  
506 aperture is then laterally enclosed, resulting in a more circular gape, hence, a more anteriorly  
507 directed water flow into the mouth might be generated as hypothesized by Lauder (1979;  
508 1985) and experimentally shown by Sanford et al. (2009). Kindred (1921) and Kadam (1961)  
509 also found a rostral cartilage in *S. fuscus* and *Nerophis*, which is connected to the palatine  
510 cartilage with dense connective tissue. Kadam (1958) further mentions a rostral cartilage  
511 articulating with the premaxillary and maxillary bones in *Hippocampus*.  
512 The lower jaw of *S. rostellatus* and *H. capensis* is similar to the one in *G. aculeatus*, but much  
513 shorter relative to their head length. The anguloarticular bone in the syngnathid species is  
514 more tightly fixed to the dentary bone, improving the rigidity of the lower jaw. This might

515 facilitate abduction of the left and right lower jaws, observed during manipulation of  
516 specimens (Roos et al., in press). In the stickleback there is no fusion between the angular  
517 bone and articular bone. The angular bone also fits into a cavity of the dentary bone, but with  
518 a potential pivoting zone in between them (Anker, 1974). There is a saddle-like joint between  
519 the articular bone and the quadrate bone, as in *S. rostellatus* and *H. capensis*.

520 The metapterygoid bone is a perichondral ossification of the metapterygoid process of the  
521 palatoquadrate cartilage (Arratia and Schultze, 1991). In *G. aculeatus*, as in other general  
522 teleosts, the quadrate and the hyomandibular bones are connected by means of the  
523 metapterygoid bone, forming the suspensorium (Gregory, 1933; Anker, 1974). This is not the  
524 case in *S. rostellatus* and *H. capensis*, where there is no connection between the short  
525 metapterygoid and the hyomandibular bones. Neither is there a connection between the very  
526 rudimentary metapterygoid process of the pterygoquadrate part of the palatoquadrate cartilage  
527 and the hyosymplectic cartilage in the pipefish and seahorse juveniles.

528 The symplectic part of the hyosymplectic cartilage in *S. rostellatus* juveniles is very long  
529 compared to the hyomandibular part, with the angle between these two parts being obtuse. In  
530 *H. capensis*, both parts are almost equally long and they are perpendicular to each other. This  
531 arrangement looks very much like the one in *G. aculeatus* (Swinnerton, 1902; Kindred, 1924).  
532 Kadam (1961) describes the symplectic bone in *Nerophis* as a chondromembranous bone with  
533 a perichondral part, namely the ossification of the anterior region of the hyosymplectic  
534 cartilage, and an intramembranous part, which rises up from the perichondral part. The  
535 vertical plate bears a dorsorostral process and decreases gradually in height more caudally.  
536 This is also found in *S. rostellatus* and *H. capensis*.

537 At the 6.3-9.0 mm SL stage of *G. aculeatus*, where there is no ossification of the cranial  
538 cartilage yet, the hyomandibular part of the hyosymplectic cartilage already has the two-  
539 headed articulation with the neurocranium as seen in adults (Swinnerton, 1902; Kindred,

540 1924; De Beer, 1937; Anker, 1974). The dorsorostral condyle articulates in a socket formed  
541 by the sphenotic bone, the dorsocaudal condyle fits in a socket of the pterotic bone (Anker,  
542 1974). In the juvenile syngnathids (*S. rostellatus*, *H. capensis* and *H. reidi*), there is only a  
543 single cartilaginous articulation. The hyomandibular bone in adult *S. rostellatus* and *H.*  
544 *capensis* is similar to the one in *G. aculeatus*; it also bears a double articular facet with the  
545 neurocranium, as in *H. reidi*. Dissection and manipulation of this double hyomandibular  
546 articulation in *S. rostellatus* and *H. capensis* proved that it is very firm. Strikingly, in *S. fuscus*  
547 (Kindred, 1924; De Beer, 1937), *Nerophis* (Kadam, 1961) and *S. acus* (Branch, 1966) only a  
548 single condyle is present, which is thought to increase the freedom of movement of the  
549 hyomandibular bone (Kindred, 1924; Branch, 1966).

550 The connection between the suspensorium and the hyoid arch is provided by the interhyal  
551 bone. The general teleost articulation is a ball-and-socket joint, with a rod-shaped interhyal  
552 bone bearing a rounded head that fits into a facet of the suspensorium, allowing the interhyal  
553 bone to rotate in every direction with respect to the suspensorium (Anker, 1989; Aerts, 1991).

554 The configuration in *G. aculeatus* is comparable (Anker, 1974). This is not true for *S.*  
555 *rostellatus* and *H. capensis*, where the interhyal bone articulates with the preopercular bone  
556 dorsally and bears two articulation heads ventrally, in between which the posterior ceratohyal  
557 bone articulates. In that way, movement is more restricted to one in a rostrocaudal direction,  
558 resulting in a hyoid retraction during the expansive phase of the suction feeding. The two  
559 heads of the hyomandibular bone in combination with the robust interhyal bone can be  
560 assumed to indirectly reduce the degrees of freedom between the hyoid and the neurocranium,  
561 hence contraction of the sternohyoideus muscle is expected to be translated in a more  
562 powerful hyoid depression. Fast hyoid rotation is thus possible with a reduced risk of  
563 disarticulation of the ceratohyal bone. In *S. peckianus* (McMurrich, 1883), *S. fuscus* (De Beer,  
564 1937), *Nerophis* (Kadam, 1961), *S. acus* (Branch, 1966), *S. floridae* and *H. erectus* (Bergert

565 and Wainwright, 1997) the interhyal bone is similar, but it is claimed to articulate with the  
566 hyomandibular bone instead of the preopercular bone.

567 Muller and Osse (1984) showed that high negative pressures will be reached in the gill cavity  
568 of the pipefish *Entelurus aequoreus* during prey capture. According to Osse and Muller  
569 (1980) the small gill slit and the strongly ossified gill cover are considered adaptations to the  
570 pipette type of feeding, characterized by a very fast neurocranial elevation (Muller and Osse,  
571 1984; Muller, 1987; de Lussanet and Muller, 2007). The pressure in the opercular cavities is  
572 considered to be higher with increasing snout length, and a comparison between different  
573 syngnathid species showed that increasing snout length also results in a structurally more  
574 robust opercular bone (e.g. more ridges, greater curvature and thicker; Osse and Muller, 1980;  
575 Muller and Osse, 1984). In both, *S. rostellatus* and *H. capensis*, the gill slits are nearly closed  
576 by a firm sheet of connective tissue covered with skin. Only at the dorsocaudal tip a small  
577 aperture is left. Their opercular bone is firm and thick and has a convex surface which will  
578 help in withstanding medially directed forces. Comparison between the two species reveals  
579 that the opercular bone in the pipefish, which has a more elongated snout, is smaller, thicker  
580 and has a greater curvature, as expected.

581 The branchiostegal rays support the branchiostegal membrane, which closes the gill cavity  
582 ventrally. Among teleosts there can be more than twenty branchiostegal rays, but  
583 acanthopterygians almost never have more than eight (Gosline, 1967; Arratia and Schultze,  
584 1990). In syngnathids the number of branchiostegal rays varies between one and three  
585 (McAllister, 1968). Here, in *S. rostellatus* and *H. capensis*, there are only two branchiostegal  
586 rays present on each side. As Gosline (1967) pointed out, the number of branchiostegal rays is  
587 related to the length of the hyoid bar. In syngnathids, the hyoid is relatively small, which  
588 might be associated with its lost function as a mouth bottom depressor (Roos et al., in press).  
589 A longer hyoid will have an increased moment of inertia resulting in hyoid depression at a



590 lower velocity. In addition, the angle between the working line of the sternohyoideus muscle  
591 and the hyoid will become less favorable as the hyoid length increases. Thus, the length of the  
592 hyoid bar is expected to be constrained and consequently, there will be less available space  
593 for attachment of the branchiostegal rays.

594 In both adult and juvenile *H. capensis* the braincase is tilted dorsally with respect to the  
595 ethmoid region so it is situated dorsocaudally to the orbita instead of caudally as in *S.*  
596 *rostellatus*, *S. fuscus* and *Nerophis* (all pipefishes; Kindred, 1921; Kadam, 1961). In the *H.*  
597 *reidi* juvenile (7.01 mm SL) this dorsal tilting of the otic capsule was also visible, although  
598 the tilt was less than the one in *H. capensis* juvenile (only about 20° up compared to 34° in  
599 the latter). In adult *H. capensis*, more or less the same tilt is observed (38° up). Kadam (1958)  
600 described the presence of a speno-pterotic ridge at the base of the taeniae marginales (which  
601 he calls postorbital processes) in *Hippocampus*, that appears to be missing in *Nerophis*  
602 (Kadam, 1961) and *S. fuscus* (Kindred, 1921). We also observed this ridge in *H. capensis* and  
603 *H. reidi*, but not in *S. rostellatus*. Apart from that, the hyosymplectic articulation socket  
604 mediocaudal to this ridge, is more distinct in the *Hippocampus* species studied.

605  
606 It is obvious that already at an early developmental age, the juvenile feeding apparatus  
607 resembles that of adult *S. rostellatus* and *H. capensis*. This might be the result of the  
608 specialized parental care that enables the postponing of release from the brooding pouch until  
609 an advanced developmental state is reached. In the seahorse brooding pouch, oxygen is  
610 supplied through surrounding capillaries and the male prolactin hormone is secreted, inducing  
611 breakdown of the chorion to produce a placental fluid (Lourie et al., 1999; Carcupino et al.,  
612 2002; Foster and Vincent, 2004). Lack of oxygen and endogenous energy is probably not  
613 longer a limiting factor and emergence from the pouch may be delayed, as in *Galeichthys*  
614 *feliceps*, an ariid mouth-brooder (Tilney and Hecht, 1993).

615

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