DINOPERCIDAE, A NEW FAMILY FOR THE PERCOID MARINE FISH GENERA
DINOPERCA BOULENGER AND CENTRARCHOPS FOWLER (PISCES: PERCIFORMES)

by

P.C. Heemstra and T. Hecht
ABSTRACT


The Genus Dinoperca was erected by Boulenger (1895) for the Northern Indian Ocean species Hapalogenys petersi Day and assigned to the Family Serranidae. Boulenger (1903) described a second species, D. queketti, from South Africa. Most subsequent authors have accepted the placement of Dinoperca in the Serranidae, but Johnson (1983) removed it from the Serranidae to the taxonomic limbo of "Incertae sedis". Centrarchops Fowler (1923), with a single west African species, was originally assigned to the Serranidae and has been treated by subsequent authors in the Serranidae. The osteology, myology and the otolith (sagitta) of D. petersi reveal no characters that would relate Dinoperca to any particular family of percoids. Furthermore, the presence or absence of certain characters preclude Dinoperca and Centrarchops from the Family Serranidae, and the superfamilies Haemuloidea, Lutjanoidea and Sparoidea. Two features appear to be uniquely derived characters (synapomorphies) justifying a separate family for Dinoperca and Centrarchops: (1) Frontal bones bearing a high median crest that articulates posteriorly with the supraoccipital crest and is cleft dorsally by a narrow median sulcus extending ventrally to the roof of the brain cavity. (2) Large swim-bladder with three pairs of large intrinsic muscles.

CONTENTS

Introduction ................................................................. 1
Methods ....................................................................... 1
Dinoperca petersi (Day, 1875) ................................ 1
Osteology ................................................................... 3
Otoliths .................................................................. 12
Swim-Bladder ............................................................ 13
Myology .................................................................. 13
Centrarchops chapini Fowler, 1923 ....................... 14
Discussion ................................................................ 15
Unusual features and comparison of Dinoperca and Centrarchops ........................................ 18
Dinopercidae fam. n. .................................................. 19
Acknowledgements .................................................... 19
References ............................................................... 20

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P.C. Heemstra¹ and T. Hecht²

INTRODUCTION

The percoid fish Genus Dinoperca Boulenger, 1895 comprises two nominal species: D. petersi (Day, 1875) and D. queketti Boulenger, 1903. The type species, originally described as Hapalogenys petersi from Pakistan and the Mekran coast of Iran, was considered a synonym of D. queketti by Smith (1949).

Boulenger (1895) created Dinoperca as a new genus for Hapalogenys petersi Day, because "it is quite certain that it is by no means related to Hapalogenys ...". Boulenger assigned his new genus to the Family Serranidae (from which Hapalogenys was excluded), since "its affinities appear to be with Sterolepis, from which it is distinguished by the longer soft dorsal". Barnard (1927) and Smith (1949) also included Dinoperca in the Serranidae. Fowler (1931) obviously (and uncharacteristically) overlooked the existence of Dinoperca in his treatment of Hapalogenys petersi in the Family Pomadasyidae, but he later (1934) treated D. queketti in the Serranidae. Johnson (1983) removed Dinoperca from the Serranidae to the taxonomic limbo of "Incertae sedis".


Our investigation of the osteology, myology and the otolith (sagitta) of D. petersi revealed no characters that would relate Dinoperca to any particular family of percoids. Furthermore, the presence or absence of certain characters preclude Dinoperca from the Serranidae as well as from any of the families assigned by Johnson (1980) to the superfamilies Haemuloidea, Lutjanoidea and Sparoidea. We have found, however, two features that appear to be shared derived characters (synapomorphies) which justify a separate family for Dinoperca and Centrarchops: (1) Frontal bones bearing a high median crest that articulates posteriorly with the supraoccipital crest and is cleft dorsally by a deep median sulcus extending ventrally to the roof of the brain cavity. (2) Large swim-bladder with three pairs of intrinsic muscles. The unique configuration of the sagittal otolith of Dinoperca may be another synapomorphy of this family, but we were not able to establish the otolith configuration of Centrarchops, because the otolith had disintegrated in the single preserved specimen from which removal of the otolith was attempted.

The purpose of the present paper is to establish a new family for the genera Dinoperca and Centrarchops. In support of the validity of this new taxon, we give descriptions of D. petersi and C. chapini; and we describe in detail the osteology, cheek muscles, sagittal otolith and swim-bladder of D. petersi. Although our examination of C. chapini has been limited to superficial dissection and radiography, we have found evidence (see below) to exclude it from the Serranidae and relate it to Dinoperca petersi.

METHODS

Five specimens of Dinoperca petersi were used to examine skeletal features. Two specimens (113 and 126 mm SL) from the collection of the J.L.B. Smith Institute of Ichthyology were cleared and stained with alizarin. Another 113 mm SL specimen (USNM 269543) was kindly made available by G. David Johnson of the U.S. National Museum of Natural History. This specimen was cleared with the enzyme technique of Taylor (1967) and stained for cartilage as well as bone. A dried skeletal preparation of a 417 mm SL specimen was loaned by Camm Swift of the Los Angeles County Museum of Natural History. A 268 mm SL fish was skeletonized with hot water. Twenty specimens were dissected to examine the swim-bladder. Sagittal otoliths were removed from 26 specimens, ranging in size from 165 to 622 mm total length.

Terminology of the caudal fin skeleton follows the paradigm of Nybelin (1963) with the modifications of Patterson (1968) and Monod (1968). In recent publications dealing with the caudal skeleton of percoid fishes, the terminal vertebral element and its bilaterally-paired, pointed, distal processes are often incorrectly designated as the "urostyle". Monod (1968: 50) has pointed out that the term "urostyle" was originally proposed by Huxley for the ossified sheath of the notochord as seen in Gasterosteus aculeatus. This hollow median structure is also seen in some elopomorphs (e.g., Elops lacerta) and clupeomorphs (e.g., Clupea harengus): Monod, 1968: Figs. 29 & 120.

The middle element of the trisegmental dorsal and anal fin pterygiophores is here called a "middle radial", rather than a "medial radial". In anatomical works, the term "medial" is usually used as the antonym of "lateral", and it seems likely to lead to confusion if "medial" is also used to refer to the middle element in a series of 3 elements. Eaton (1945) was the first author to use this terminology; Potthoff (1980) also uses "middle radial". The formula used to express the positions of predorsal bones, anterior dorsal fin pterygiophores and anterior neural spines is that devised by Ahlstrom et al. (1976).

Dinoperca petersi (Day, 1875)

Hapalogenys petersi Day, 1875: 77, Pl. 20, Fig. 3 (Sind and Mekran coast).


Dinoperca queketti Boulenger, 1903: 63, Pl. 2 (Natal); Barnard, 1927: 490; Fowler, 1934: 427, Fig. 11; Morgans, 1982: 30.

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DESCRIPTION: (Based on 17 specimens, 103-412 mm SL; morphometric data are given in Table 1.) A moderately large species attaining 62 cm and 5 kg. Dorsal-fin rays IX-XI, 18-20; dorsal-fin margin notched before the soft-rayed portion; soft dorsal fin high anteriorly, the 3rd to 8th rays longer than the others and more than twice length of longest dorsal spines; interspinous membranes deeply incised, their rear edge joined to the lateral surface of each spine. Anal fin rays III, 12-14; anal spines slender, their relative lengths in the ratio 1:2:3. Caudal fin truncate, with 9+8 principal rays and 8+7 branched rays; 11 or 12 dorsal procurent caudal rays, of which the last 5 are segmented; 11 ventral procurent caudal rays, of which the last 4 are segmented. Pelvic fins with 1 spine and 5 branched soft-rays. Pectoral fin with 17 or 18 rays, with usually the dorsalmost 2 rays unbranched and the rest branched; the ventralmost ray may or may not be branched.

Body oblong-oval, moderately compressed; greatest depth 2.3-2.5 in SL; greatest body width 2.4-2.7 in body depth. Head length 2.7-3.0 in SL. Eye large, its horizontal diameter 2.9-4.2 in head length.

Head, body and fins covered with small ctenoid scales; maxilla, preorbital and lower jaw also scaly; snout scaly except for a triangular patch of skin that covers the ascending processes of the premaxillae. Lips and lower jaw covered with minute (microscopic) villi, giving the lips and lower jaw a velvet-like feel and appearance. Branchiostegal membrane and rays naked. Spinous dorsal fin naked distally but with scales at the base and running up the leading edge of each spine. Lateral line curving slightly dorsally from head to caudal peduncle, then running straight along midlateral part of peduncle and along middle caudal rays to the rear edge of the fin. Lateral-line scales of anterior part of body mostly hidden by adjacent scales; 53-63 tubed scales from head to base of caudal fin. No enlarged auxiliary scale or scaly process at base of pelvic fins. No scaly flap of skin at upper end of pectoral-fin base.

Rear edge of opercle with 2 flat points. Preopercle serrate, the serrae at the “angle” enlarged. Subopercle and interopercle smooth. Maxilla mostly exposed when mouth is closed; posterior edge of maxilla slightly concave; supra-maxilla long and slender.

TABLE 1. Measurements of *Dinoperca petersi* (17 specimens, 103-412 mm SL) and *Centrarchops chapini* (2 specimens, 213-225 mm SL), in % SL or % head length (*).

<table>
<thead>
<tr>
<th></th>
<th><em>D. petersi</em></th>
<th><em>C. chapini</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Greatest body depth</td>
<td>39-44</td>
<td>50-53</td>
</tr>
<tr>
<td>Body depth at dorsal fin origin</td>
<td>37-42</td>
<td>48-49</td>
</tr>
<tr>
<td>Distance snout to dorsal fin origin</td>
<td>40-42</td>
<td>41-42</td>
</tr>
<tr>
<td>Distance from snout to anus</td>
<td>57-65</td>
<td>61-63</td>
</tr>
<tr>
<td>Distance from snout to anal fin</td>
<td>62-70</td>
<td>73-77</td>
</tr>
<tr>
<td>Pectoral fin length</td>
<td>23-26</td>
<td>27-28</td>
</tr>
<tr>
<td>Length of caudal peduncle</td>
<td>18-21</td>
<td>11-15</td>
</tr>
<tr>
<td>Depth of caudal peduncle</td>
<td>13-15</td>
<td>12-12</td>
</tr>
<tr>
<td>Anal fin length</td>
<td>25-32</td>
<td>31-36</td>
</tr>
<tr>
<td>First anal spine length</td>
<td>1.9-5.3</td>
<td>8-9</td>
</tr>
<tr>
<td>Second anal spine length</td>
<td>5.4-11</td>
<td>16-17</td>
</tr>
<tr>
<td>Third anal spine length</td>
<td>7.2-14</td>
<td>12-14</td>
</tr>
<tr>
<td>Third dorsal spine</td>
<td>6.7-11</td>
<td>14-16</td>
</tr>
<tr>
<td>Head length</td>
<td>34-37</td>
<td>38-39</td>
</tr>
<tr>
<td>Snout length*</td>
<td>27-30</td>
<td>24-26</td>
</tr>
<tr>
<td>Orbit diameter*</td>
<td>21-35</td>
<td>24-24</td>
</tr>
<tr>
<td>Interorbital*</td>
<td>21-27</td>
<td>22-24</td>
</tr>
<tr>
<td>Postorbital*</td>
<td>44-52</td>
<td>52-53</td>
</tr>
<tr>
<td>Upper jaw length*</td>
<td>44-48</td>
<td>37-38</td>
</tr>
<tr>
<td>Maxilla width*</td>
<td>13-17</td>
<td>11-14</td>
</tr>
</tbody>
</table>
Nostrils distinct, oval, subequal and close together; anterior nostril with a skinny rim prolonged into a rounded flap posteriorly. Olfactory organ elongate-oval with 20 lamellae on lateral side of rachis and 18 on the medial side of a specimen 29 cm SL.

Premaxillae slightly protrusile, with a band of short, curved, conical, depressible teeth; the band is 5 or 6 teeth wide anteriorly in fish 15-20 cm SL, increasing to about 15 teeth wide in a fish 30 cm SL; and narrows to 2 rows of teeth at the posterior end; outer edge of premaxilla with a series of 15-20 larger, well-spaced, stout, fixed canines. Lower jaw with a narrow band of 1-3 rows of short, curved, conical, depressible teeth and an outer series of 12-17 larger, well-spaced, stout, fixed canines. Vomer with a chevron-shaped band of short, sharp, conical teeth. Palatines with an elongate band of similar teeth, the band 6 or 7 teeth wide at its widest point, in fish 15-20 cm SL, increasing to 13-15 teeth wide in a fish 30 cm SL. Large adults have a distinct, elongate patch of villiform teeth on the medial side of the middle part of the ectopterygoids. This tooth patch first appears at about 19 cm SL and is well developed on a specimen of 29 cm SL. Tongue wide, broadly rounded and edentate. No teeth on endoptygoids.

Branchiostegal rays 7. Gill 4, with a slit behind the last gill. Pseudobranch large, with about 60 filaments. Gill-rakers (13-18)+(23-28); usually 1 or 2 rudimentary rakers at proximal end of epi- and hypobranchials; the longest raker on the first arch slightly longer than the longest gill filaments.

DISTRIBUTION: D. petersi is common in Pakistan waters and off Natal; it has also been reported from Kenya (Morgans, 1982). We have examined 1 specimen, USNM 204457, from Zavori Zavala, Mozambique. In South Africa it occurs from Natal to Algoa Bay.

REMARKS: Although Smith (1949) did not examine any specimens from the northern Indian Ocean, he seems to have been correct in synonymizing the South African Dino­perca queketti with its northern counterpart D. petersi. We examined two specimens of D. petersi from the coast of Pakistan (355 & 412 mm SL, Los Angeles County Museum of Natural History Catalogue No. 38294-1) and found only a slight difference from South African specimens in the number of lower-limb gill-rakers: the two Pakistan fish have 23 and 25 rakers, versus 26 to 28 rakers for South African fish. This slight difference may be due to the small size of the sample from Pakistan or to a latitudinal cline in the number of gill-rakers. But we lack sufficient data to demonstrate a clinal variation in the number of gill-rakers. The lateral-line scale count of “ca. 100” given for D. petersi in the original description (Day, 1875: 77) is apparently erroneous. The two specimens from Pakistan that we examined have 56 and 61 lateral-line scales, well within the range of 53-63 for South African specimens. In view of the great similarity of the Pakistan and South African specimens in colour pattern and various meristic and morphometric data (see above and Table 1), we agree with Smith and regard these two nominal species as synonyms.

OSTEOLOGY

CRANIUM (Fig. 2): The broad vomer has direct osseous articulations with the supraethmoid dorsally, the lateral ethmoids posteriorly, and the parasphehoid posteriorly. The ventral surface of the head of the vomer is covered with a chevron-shaped patch of teeth. The median dorsal ridge of the vomer bears an elongate cartilaginous segment (ethmoid) that extends into the median dorsal ridge of the supraethmoid. There is another small cartilaginous piece of the ethmoid visible on each lateral side of the vomer at the junction of the supraethmoid and lateral ethmoid. The lateral surfaces of the vomer are bound by a strong, thick ligament to the anterior end of the palatines.

The supraethmoid articulates posteriorly with the frontals and the lateral ethmoids. Posteriorly, it bears a strong, crescentic, transverse ridge that is partly covered by the anterior ends of the frontal bones. The lateral ends of this transverse ridge are the sites of attachment for the large ethmo-maxillary ligaments and for the nasal bones.

The large, wing-like lateral ethmoids articulate dorsally with the frontals and ventrally with the parasphehoid. Ventrally they bear two facets for articulation with the palatines. The anterior facet is round and located at the end of a distinct lateral protuberance; the posterior facet is a narrow surface along the ventromedial part of the lateral wing-like edge of the bone. Along the ventrolateral edge is a narrow facet for articulation of the preorbital. The large olfactory foramen is located near the medial edge of the bone. The medial part of the lateral ethmoids is excavated to form the anterior myodome, which opens laterally via the olfactory foramen. The cartilaginous ethmoid forms the median roof of the myodome and posteriorly gives rise to a thin, median, septal cartilage that separates the two halves of the anterior myodome and the medial edges of the ventral part of the lateral ethmoids. This septal cartilage continues ventrally to serve as the cartilaginous articulation between the posterior part of the lateral ethmoids and the parasphehoid. A strong ligament runs from the upper end of the lateral ethmoids to the anterior end of the endoptygoids.

The thin tubular nasals are dermal bones that lie on either side of the median supraethmoid bone and medial to the anterior nostrils. They receive a branch of the laterosen­sory canal system from the anterior end of the frontals.

The dorsal surface of the orbits comprises mainly the frontals. Posteriorly the frontals join (via sutures) the supraoccipital, parietals, pterotics, sphenotics and (ventromedially) the pterosphehoids. Dorsally, the frontals bear a median crest that is deeply excavated dorsally to form a narrow median frontal sulcus, which continues posteriorly almost to the supraoccipital and ventrally to the base of the crest and roof of the brain cavity, where it communicates with the median commissure of the laterosensory canal system (Fig. 3). The median crest of the frontals merges posteriorly with the well-developed supraoccipital crest. Posteriorly, between the median frontal crest and the lateral edge of the bone, is a large oblique crest that articulates with the parietal crest.

The pterosphehoids occupy the lateral edges of the orbital entrance to the brain cavity. They are separated dorsally by a wide gap where they articulate with a low flange on each frontal. The pterosphehoids articulate posteriorly with the sphenotics and prootics, and ventrally with the two arms of the basisphenoid. The posterior region of the pterosphehoids is pierced by a small foramen that communicates with the brain cavity.

The sphenotics bear a prominent, lateral, wing-like process that articulates via connective tissue with the 5th infrorbital bone. On the dorsal surface of this lateral process is a folded tubular canal (= dermosphenotic; see description of infraorbital bones below) that communicates with the flattened channel of the frontal overlying the sphenotic
Figure 2. *D. petersi*, 268 mm SL, cranium in dorsal, lateral and ventral views.
and with the infraorbital canal. This wide laterosensory channel also communicates posteriorly with that of the pterotics. The anterior face of the sphenotics bears two contiguous recesses. Posteriorly, the sphenotics articulate with the pterotics and ventrally with the prootics. The posterolateral region of the sphenotics is deeply excavated to form the dorsal part of the deep, round fossa for articulation with the anterior condyle of the hyomandibula; the ventral portion of this socket being contributed by the prootic.

The pterotics articulate with the prootics, intercalars, exoccipitals, and (dorsolaterally) with the ventral extrascapulas; anteriorly the pterotics join the sphenotics, frontals and parietals. Each pterotic forms the lateral edge of a large cartilaginous fenestra (interosseus space) that is also bounded by the parietal, epioccipital and exoccipital, and which forms the floor to the posttemporal fossa. In a dorsal view of the cranium, this fenestra is hidden by the parietal crest and epiotic bone. The lateral edge of the pterotic is excavated to form a channel for the laterosensory canal, which branches dorsally into the ventral extrascapula and ventrally into the dorsal end of the preopercle.

The extrascapulas (Fig. 4) are thin, tubular, dermal bones that carry the dorsal branch of the laterosensory canal. The ventral bone resembles an inverted ‘‘T’’, connecting anteriorly with the pterotic, posteriorly with the posttemporal, and dorsally with the dorsal extrascapula. The dorsal extrascapula lies lateral to the edge of the parietal crest.

The U-shaped parietals bear a prominent oblique crest that is continuous with the posterolateral crest of the frontals and continues posteriorly to join the raised articular process of the epioccipitals. A small foramen that communicates with the brain cavity is located on the medial side of the crest near its base and in the middle of the dorsal aspect of the bone.

The epioccipitals are shaped rather like a three-sided pyramid with the large articular facet for the posttemporal at the apex of the pyramid. The articulation with the supraoccipital is a sartorial joint. The connection with the exoccipital is a synchondrosis, except for the suture of the vertical strut supporting the posttemporal facet. Anteriorly, the epioccipital joins the parietal via the suture along the rear edge of the parietal crest. The lateral edge of the base of the epioccipital is bounded by the cartilaginous fenestra previously described.

The supraoccipital bears a high, thin, median crest which is continuous with that of the frontals. Posteriorly, the crest is strengthened by two oblique ridges arising from near the epioccipital suture. The suture between the frontals and the supraoccipital is continuous with the parietal and epioccipital sutures. Posteriorly, the crest descends to the dorsal edges of the exoccipitals, which form the dorsal vault of the foramen magnum. The suture between the supra- and exoccipitals runs forward and then laterally
through the middle of an oblique ridge at the medial end of the epioccipital-exoccipital synchondrosis.

The exoccipitals are joined dorsally and ventrally by median sutures to form the margins of the foramen magnum. The posterior ends of the exoccipitals form two, contiguous, irregularly ovoid, large condyles for articulation with the first centrum. The exoccipitals form the postero-dorsal component of the otic bullae, where they join, via sutures, to the basioccipital and prootics; the junction of the three bones being the site of a small, triangular, cartilaginous fontanelle. Dorsolaterally, the exoccipitals articulate, via suture, to the intercalars. The epioccipital-exoccipital suture runs anteromesiod from the posttemporal facet of the intercalar bones. There is a round fossa in the exoccipitals just posterior to the aforementioned cartilaginous fenestra. The foramen for the vagus nerve (X) is located in the anterior region of the exoccipitals just ventral and medial to the posterior suture of the intercalars. This foramen is immediately preceded by a short, raised, flattened ridge.

The intercalars are subhorizontal, plate-like bones that lie anterolaterally to the exoccipitals and just dorsal to the otic bullae. Anteriorly, the intercalars are joined, via suture, to the prootics. On their posterolateral edge, the intercalars bear a stepped facet for articulation with the ventral arm of the posttemporals.

The basioccipital is completely covered dorsally by the exoccipitals. Ventrally, it joins, via suture, the flattened, bifurcate, rear end of the parasphenoid which, together with the midventral sulcus of the basioccipital, forms the posterior opening of the posterior myodome. The plane of the articular facet for the first centrum is oblique to the horizontal axis of the basioccipital. Anteriorly, the basioccipital joins the prootic via a narrow synchondrosis. Baulelot’s ligament attaches in a shallow lateral fossa at the rear end of the basioccipital.

The prootics are complex bones that provide the anterior portion of the otic bullae, the anterior roof of the myodome, and the anterior floor of the brain cavity. The dorsoanterior region of the prootics (including the medial wall of the pars jugularis) is perforated by 5 or 6 (5 in the left prootic, 6 in the right) foramina. In the 113 mm SL specimens, both prootics have 6 foramina through the medial wall of the pars jugularis. These foramina are relatively larger in the smaller fish. The lateral wall (lateral commissure) of the pars jugularis is a narrow shaft of bone. Medially the prootics unite to form the vaulted roof of the myodome. This connection seems to be a partly open suture which terminates anteriorly at the oval hypophysial fenestra immediately posterior to the crotch of the basioccipital. The dorsal end of each limb of the basisphenoid is joined suturally to the anteromedial edge of the prootics. The lateral surface of the prootics is suturally articulated to the postero-lateral flange of the parasphenoid. Inside the cranial cavity, the prootics bear a posteriorly directed flange or shelf that runs across the front of the floor of the brain cavity and is continuous laterally with a similar lamina on the internal surface of the sphenotics. The width of this prootic shelf is greatest medial to the pars jugularis and decreases towards the median suture where it disappears. There is a short, small, oval canal (for the internal carotid artery) running obliquely into the anterior part of the myodome at about the middle of the prootic-parasphenoid suture.

The parasphenoid bears a thin, median, dorsal ridge, to which the basisphenoid is suturally joined; the rear end of the ridge being continuous with the rear edge of the ventral part of the basisphenoid. After a short interruption immediately posterior to the basisphenoid, the median ridge arises again on the anterior floor of the myodome and gradually diminishes posteriorly. Anteriorly, the median dorsal ridge runs into the median septal cartilage at the anterior face of the orbits. Ventral to the prootics, the parasphenoid bears a shallow median sulcus.

The basisphenoid is well developed; its two dorsal arms articulate with the parasphenoids and prootics.

INFRAORBITAL BONES (Fig. 5): The elongate preorbital (= lacrimal) articulates anteriorly with the lateral ethmoid and posteriorly with the second infraorbital. Along its dorsal edge, the preorbital bears a medial flange which ends anteriorly in a transverse (medio-lateral) condyle for articulation with the lateral ethmoid. The preorbital does not overlap the posterior half of the maxilla when the mouth is closed. The lateral surface is partly roofed over to form a channel for the infraorbital branch of the laterosensory system. The second infraorbital is as deep as it is long. The third infraorbital appears, in lateral view, to be an elongate tubular bone; but it bears a large wing-like subocular shelf on its medial side. The fourth and fifth infraorbitals are subequal in length to the third.

The sixth infraorbital (dermosphenotic) lies in a trough of the sphenotic. In the 113 and 126 mm specimens, the dermosphenotics are tightly bound to their sphenotics but they can, with difficulty, be pulled off. In the 268 mm specimen the dermosphenotics are fused with their sphenotics and cannot be distinguished as separate bones. The laterosensory channel for the dermosphenotics communicates dorsally with that of the frontals.

![Figure 5. Infraorbital bones of D. petersi, 113 mm SL, lateral view (above); dorsal view (below) of 2nd through 5th infraorbitals: D - dermosphenotic (= 6th infraorbital), P - preorbital (=1st infraorbital), SS - subocular shelf.](image-url)
The antero-dorsal margin of the hyomandibula bears a round condyle for articulation with the socket on the ventral edge of the sphenotic. The second cranial facet of the hyomandibula is a narrow articular surface along the dorsal edge of the bone; this elongate facet articulates with the pterotic bone. The round condyle that articulates with the socket on the opercle is located on the posterior edge of the hyomandibula. The large foramen for the hyomandibular trunk of the facial nerve is located on the posterior edge of the hyomandibula, the suture line being difficult to discern.

Figure 6. D. petersi, 113 mm SL, medial view (above) and lateral view (below) of left suspensorium and palatine arch: EC - ectopterygoid, EN - endopterygoid, H - hyomandibula, M - metapterygoid, ML - metapterygoid lamina, P - palatine, POP - preopercle, Q - quadrate, S - symplectic.

The metapterygoid bears the usual posterior lamina that is present in most percoid fishes. The lamina articulates (synchondrosis) with the anterolateral edge of the hyomandibula's ventral arm. The dorsal end of the metapterygoid is firmly sutured to the hyomandibula. (In the 113 mm SL specimen, the metapterygoid seems almost fused to the hyomandibula, the suture line being difficult to discern.) The vertically oriented, rounded flange that projects posteriorly from the posteromedial edge of the metapterygoid to overlap the medial side of the hyomandibula - which Johnson (1980: 31) says is characteristic of "all haemuloids" - is absent in Dinoperca petersi. The lower edge of the metapterygoid articulates, via cartilage, with the quadrate and symplectic. The anterior margin of the metapterygoid overlaps (direct osseous articulation) the posteroventral margin of the endopterygoid.

The ventral half of the rod-shaped symplectic lies along the shallow channel that runs along the mesial side of the posteroventral margin of the quadrate. The dorsal end of the symplectic articulates, via cartilaginous condyles, with the lower end of the hyomandibula and the dorsal end of the interhyal.

At the ventral end of the quadrate is a double-headed (flanged spool) condyle that articulates with the concave facet of the articular. The anterior edge of the quadrate is overlapped by the posterior margin of the medial lamina of the ectopterygoid and abuts the posterior edge of the lateral lamina of the ectopterygoid. The articulations of the quadrate with the ectopterygoid and preopercle are synarthrotic joints. There is no contact between the endopterygoid and the quadrate.

The large endopterygoid projects dorsomedially from the plane of the palatine arch as a thin sheet of bone. The posterolateral edge overlaps (medially) the anterior edge of the lower part of the metapterygoid. The lateral edge of the endopterygoid forms a long synarthrosis with the dorsal edge of the ectopterygoid. The anterior tip of the endopterygoid overlaps the flap that projects posteroventrally from the middle of the palatine bone, the entire articulation being encased in cartilage.

The ectopterygoid is a curved and folded sheet of bone, with the two lamina being mostly in contact. The postero-dorsal region of the medial lamina projects posteriorly as an angular process separating the quadrate from the endopterygoid. The styllet-shaped anterior end of the ectopterygoid overlaps (laterally) the posterior end of the palatine, and the ventral edge of the ectopterygoid is notched to receive the posterior tip of the palatine. In large adults (greater than 25 cm SL) there is an elongate patch of villiform teeth on the medial side of the middle part of the ectopterygoids. This tooth patch is not present in fish less than 15 cm SL.

The anterior end of the maxillary process of the palatines is capped with a cartilaginous condyle that articulates in the groove of the dorsal edge of the maxilla just postero-lateral to the attachment of the ethmo-maxillary ligament. The strong palato-premaxillary ligament runs from the dor-somedial region of the base of the maxillary process and crosses over the ethmo-maxillary ligament to attach along the ascending process of the premaxilla. The articulation with the rounded (anterior) facet of the lateral ethmoid is located immediately posterior to the attachment of the palato-premaxillary ligament. The anterior end of the body of the palatine is tightly bound to the side of the vomer by a short, thick ligament. The ventral surface bears a band of small, sharp, conical teeth. A shallow groove runs along the lateral surface and is roofed over anteriorly to form a short blind canal.

OPERCULAR BONES (Figs. 6 & 7): The posterior edge of the preopercle is distinctly serrate, with the serrae at the angle being noticeably enlarged, and diminishing in size anteriorly along the ventral edge of the bone. The preopercular sensory canal runs along the lateral face of the bone; it has three or four broad openings along its ventral limb, in
addition to the terminal openings at the dorsal and ventral ends of the bone. The preopercle receives its branch of the laterosensory canal from the ventral branch of the pterotic.

The opercle ends posteriorly in two distinct points (flattened "spines"); the third (ventralmost) point characteristic of serranid fishes is lacking in *Dinoperca*. The dorsoanterior edge bears a deep notch just dorsal to the socket for articulation with the hyomandibula. The hyomandibular socket is supported by a horizontal ridge on the medial face of the bone extending about halfway to the tip of the lower spine. This ridge also serves as the ventral part of the insertion for the adductor operculi muscle.

The subopercle overlaps the medial side of the posteroventral edge of the opercle, and a pointed process extends dorsally from its lower anterior margin, just anterior to the ventral end of the opercle.

The posterior end of the interopercle overlaps laterally the anterior margin of the subopercle below the pointed process. The interopercle is also joined via skin and connective tissue to the preopercle, branchiostegal rays and the epihyal bone, and there is a ligamentous connection between the ventral end of the interhyal and the dorsal edge of the interopercle and between the anterior end of the interopercle and the angular bone.

![Figure 7. *D. petersi*, 113 mm SL, lateral view of left opercular bones: IOP - interopercle, O - opercle, SOP - subopercle.](image)

JAW BONES (Fig. 8): The upper jaw of *Dinoperca petersi* is slightly protrusile, consequently the ascending process of the premaxilla is rather long. The flattened, hastate, ascending process is flanked laterally by the thick, rounded articular process. The ascending and articular processes are mostly separate. The broad lateral process arises halfway between the articular process and the distal tip of the premaxilla. The large outer teeth are fixed, but the much smaller inner teeth are slightly depressible.

The maxilla is broadly expanded distally. Both maxillae of the 113 mm specimen have a low step-like process on the ventral edge of the distal end, but in the 268 mm specimen, the maxillae lack this process and have the ventral edge smoothly curved. The supramaxilla is a long slender bone lying along the dorsal edge of the distal part of the maxilla.

![Figure 8. *D. petersi*, lateral view of left jaw bones: AN - angular, AR - articular, ARP - articular process, ASP - ascending process, D - dentary, LP - lateral process, M - maxilla from 113 mm SL fish, m - maxilla from 268 mm SL fish, PM - premaxilla, SM - supramaxilla. Arrow indicates foramen for lateral branch of the ramus mandibularis of the trigeminal (V) nerve.](image)

The large pores on the lateral face of the dentary are completely covered by skin and scales in the intact fish and are thus not visible externally. The articulation between the dentary and articular (= ? angulo-articular of Nelson, 1973) is a synchondrosis and easily disarticulated, that between the articular and angular (= ? retroarticular of Nelson, 1973) is a synarthrosis.

HYOID BONES (Fig. 9): The interhyal is a short rod capped with cartilage on each end. The dorsal end of the bone articulates with the cartilage between the ventral arm of the hyomandibula and the symplectic; the ventral end articulates with the concave facet at the posterior end of the epihyal. The triangular epihyal is connected to the posteri-
or edge of the ceratohyal by intervening cartilage and by bridging sutures on the medial face of these bones. The seven branchiostegal rays articulate in the usual percoid pattern: the four posterior rays joining the lateral side, with two rays on the anterior corner of the epiphay and two on the posterior corner of the ceratohyal; the anterior (anterior) ray is suspended from the ventral edge of the ceratohyal, and the second and third rays somewhat on the medial side of the ceratohyal. The anterior process of the ceratohyal fits into a socket on the ventral hypohyal. The dorsal hypohyal bears a round facet for articulation (via cartilage) with the anterior face of the ceratohyal.

A finger-like process projects anteriorly from the dorsoanterior region of the urohyal (Fig. 10) and attaches via connective tissue to the medial ends of the first hypobranchials and the posterodorsal edge of the first basibranchial. The ventral part of the urohyal widens into a shallow trough that is roofed over anteriorly to form a blind channel. The anterior end of the urohyal is connected by two strong ligaments to the medial face of the ventral hypohyals.

BRANCHIAL ARCHES (Fig. 11): The deltoid basihyal is greatly expanded laterally at its anterior end. The first basibranchial is vertically expanded, its depth subequal to its length, and articulates on each side with the dorsal hypohyals. The fourth basibranchial is cartilaginous. The first pharyngobranchial articulates with the prootic. The well developed interarcual cartilage articulates with the short uncinate process of the first epibranchial and the anterodorsal corner of the second pharyngobranchial. The second and third pharyngobranchials are fused with their respective tooth plates. The unossified fourth pharyngobranchial is attached to the dorsal side of the anterior part of its tooth plate. There is a small tooth plate at the dorsal end of the second and third epibranchials; the second epibranchial is not fused with its tooth plate, but the third epibranchial and its tooth plate are fused.

VERTEBRAL COLUMN (Fig. 12): There are 26 vertebrae: 10 precaudal and 16 caudal vertebrae (including the terminal vertebral element). The autogenous neural arch of the first vertebra attaches to the skull by a stout ligament from the exoccipital on each side of the foramen magnum; these two ligaments join the neural arch just above the articulation of the first epipleural ribs. Epipleural ribs occur on vertebrae one through 11 (first caudal vertebra). On the first two vertebrae, the epipleurals articulate in sockets at the base of the neural arches. The 3rd through 7th epipleurals articulate to the pleural ribs distal to their medial end; the 8th epipleurals attach to the medial end of the pleurals; the 9th and 10th epipleurals are joined to their respective paraphyses; and the 11th epipleural ribs are attached to the sides of the haemal arch of the 11th vertebrae.

The first pair of pleural ribs articulate in sockets at the base of the third neural arch; subsequent pleural ribs articulate in sockets (vertebrae 4-7) or at facets (vertebrae 8-10) at the tips of the paraphyses. The first paraphyses occur as raised sockets on the 4th centrum. The last pair of pleural ribs are about half the length of the penultimate ribs and somewhat broader.

Figure 10. *D. petersi*, 113 mm SL, urohyal bone, anterior to the right, lateral view (above) and ventral view (below).

Figure 11. *D. petersi*, 113 mm SL, dorsal view of branchial skeleton: BB - basibranchials, BH - basihyal, CB - ceratobranchial, EB - epibranchials, ET - epibranchial tooth plates, HB - hypobranchials, IC - interarcual cartilage, PB - pharyngobranchials, TPCB - tooth plate on 5th ceratobranchial, UP - upper pharyngeal tooth plate. Articular cartilages and gill-rakers are not shown; left epibranchials folded back to show their ventral surfaces.

Figure 12. *D. petersi*, 113 mm SL, anterior 13 vertebrae. Ribs not shown except for 1st epipleural rib; both paraphyses (left and right) are shown on 9th and 10th vertebrae.
The 9th vertebra is the first with a closed haemal arch formed by a slender bony strut that joins the parapophyses to enclose the blood vessels that run along the ventral surface of the vertebral column. The parapophyses of the 9th and 10th vertebrae extend ventrally well beyond the level of the haemal canal; and on the 11th (1st caudal) vertebra, the parapophyses are replaced by a median haemal spine. The first haemal postzygapophyses occur on the 12th centrum, and the first haemal prezygapophyses are on the 16th centrum. There are no ventrolateral foramina on any of the vertebrae.

CAUDAL FIN SKELETON (Fig. 13): The caudal fin skeleton exhibits the primitive (plesiomorphic) perciform pattern (Gosline, 1961; Patterson, 1968): no neural spine on the 2nd preural centrum, 3 epurals, 2 pairs of uroneurals (the anterior pair fused with the neural arch material of the first preural and ural centra to form the autogenous stegural), no free ural centra, 5 autogenous hypurals, parhypural and haemal arches of 2nd and 3rd preural centra autogenous. There is a well-developed procurent spur (Johnson, 1975) on the posteriormost, ventral, procurent caudal ray. The 2nd uroneurals form a slender trough-like bone overlying the anterodorsal edge of the 5th hypural and extending proximally into the gap between the stegural and the tips of the pseudurostyles. The proximal end of the 5th hypural lies between the tips of the pseudurostyles.

There are no 3rd preural radial cartilages (Johnson, 1983: 780). There is a curved radial cartilage between the ends of the 2nd and 3rd preural haemal spines and medial of the left and right halves of the 2 or 3 procurent rays that lie in this space. This cartilage runs between the left and right halves of the first (posteriormost) procurent ray just proximal to the procurent spur and meets a separate round cartilage between the bases of the ventralmost principal caudal ray.

Figure 13. *D. petersi*, 113 mm SL, caudal fin skeleton: EP - epurals, H - hypurals, HA - haemal arches, HS - haemal spines, NA - neural arch, NS - neural spines, PH - parhypural, PSU - pseudurostyle, PU - preural vertebrae, RC - radial cartilages, S - stegural (= uroneural 1 + neural arches of preural 1 + ural centra), TVE - terminal vertebral element (= preural 1 + ural 1 + pseudurostyle). Second uroneural in black; cartilage in heavy stipple. Middle caudal fin rays have been displaced posteriorly.

PREDORSAL BONES AND DORSAL FIN SUPPORTS (Fig. 14): The predorsal bones formula (Ahlstrom et al., 1976) is 0/0/0+2+1/1/1/. All three predorsals are expanded in the median plane at their distal end. The distal radial of the first and all succeeding dorsal fin pterygiophores are autogenous. The first pterygiophore bears two supernumerary (non-serially associated) spines, which are attached to the pterygiophore by interlocking bony loops between the spines and the pterygiophore. The bony loop at the base of the first spine is not quite complete, there being a narrow gap in the middle of the bony strut forming the loop. In three of the five skeletal preparations that we examined, the gap at the base of the first dorsal spine was sufficiently narrow that the spine could not be slipped off the bony ring of the pterygiophore. The distal radials of the pterygiophores supporting the spines are moveably articulated (synarthrosis) with their serially associated fused proximal + middle radials. The distal radial of the last spine, however, is well separated by cartilage from its serially associated proximal + middle radials and is shaped like the distal radials of the soft-rays (i.e., it lacks the narrow lateral processes of the anterior radials).

All of the dorsal fin pterygiophores are bisegmental (i.e., with fused proximal + middle radials) except for the posterior 4 pterygiophores (Fig. 15), which are trisegmental (with separate proximal, middle and distal radials). The distal radials associated with the soft-rays are thin, paired, laterally expanded bones that resemble a broad-brimmed hat sitting on the dorsal surface of the lens-shaped cartilage visible at the proximal end of each soft-ray. The distal radials are mostly hidden (in lateral view) by the left and right halves of each ray base. The last ray is double, with the base of the anterior element overlapping laterally the anterior part of the posterior ray; the bases of this double ray enclose a single distal radial. The last proximal radial is expanded posteriorly, and there is a saddle-shaped bony stay adjoining the rear edge of the last middle radial. This bony stay is included in a larger block of hyaline cartilage that also includes the last middle radial and joins the dorso-posterior edge of the last proximal radial.
The last pterygiophore of the dorsal fin of the 113 mm specimen is abnormally developed (Fig. 15) with the middle and proximal radials fused into a short, reniform plate articulating with the penultimate and last (double) fin rays.

**Figure 15.** *D. petersi*, diagrammatic lateral view of posterior dorsal fin rays and their supports: 113 mm specimen on left (note abnormally developed last pterygiophore with fused and misshapen proximal and middle radials); 126 mm specimen on right. Cartilage: heavy stipple; bone: light stipple. Ossified distal radials are mostly hidden between left and right halves of each fin base and are not visible in lateral view.

ANAL FIN SUPPORTS (Figs. 16 & 17): The first pterygiophore supports all three fin spines and extends dorsally to between the last pair of pleural ribs and the first haemal spine. The first two anal spines articulate in the usual percoïd "chain-link" manner of interlocking bony loops. The third spine articulates with a separate distal radial at the ventroposterior end of the pterygiophore (Fig. 16). Dorsally this distal radial bears a rounded condyle that fits into a socket in the rear end of the pterygiophore, and the anterior end of the distal radial has a concave facet for its synarthrosis with the rear end of the bony loop with which the second anal spine articulates. The rear end of the distal radial passes through the arch in the base of the third anal spine and then widens laterally to lock the spine and bone together. Although the third spine is locked onto the distal radial, which is tightly bound to the first pterygiophore, it is free to move in the vertical plane through an arc of about 90°. The third anal spine also articulates with the anteroventral edge of the second pterygiophore, and the anteroventral corner of the second pterygiophore articulates directly with the rear end of the first pterygiophore just dorsal to its distal radial. The dorsal end of the second pterygiophore is bound to the rear edge of the first haemal spine.

All of the anal fin pterygiophores are bisegmental, except for the last 3 or 4, which are trisegmental (Fig. 17). The 113 mm specimen has 4 trisegmental pterygiophores, while the 126 mm specimen has 3 trisegmental pterygiophores. The posteriormost support elements are similar to those of the dorsal fin, with the proximal radial expanded posteriorly, and the middle radial also expanded and included in a block of hyaline cartilage with its posteriorly adjoining bony stay.

PECTORAL GIRDLE (Figs. 4 & 18): The *posttemporals* have the usual two processes for articulation with the cranium: the dorsal limb joining the facet at the lateral end of the epioccipital and the ventral limb attaching to the intercalar facet. The flattened body of the posttemporal overlaps laterally the dorsal end of the supracleithrum. Two irregular flanges arise from the mid-lateral part of the anterior edge to form a bridge over the laterosensory canal leading from the ventroposterior part of the ventral extrascapular bone. This canal passes through the posttemporal to exit on the medial side of the ventral margin of the bone, where it joins the lateral foramen of the canal that passes through the dorsal end of the supracleithrum to join the canal of the first lateral-line scale.
The elongate supracleithrum overlaps laterally the dorsal end of the cleithrum. The dorsal postcleithrum overlaps the medial face of the cleithrum, with the dorsal end of the postcleithrum being opposite the ventral end of the supracleithrum. The knife-like ventral postcleithrum has its "handle" articulating with the anteromedial margin of the ventral end of the dorsal postcleithrum.

The first (dorsalmost) pectoral fin ray articulates directly with the scapula. The first and second proximal radials articulate with the scapula; the third proximal radial attaches at the junction of the scapula and coracoid, and the fourth proximal radial articulates mainly with the coracoid. The tiny bead-like distal radials are entirely cartilaginous; and, except for the ventralmost (which is completely exposed), each distal radial lies between the bases of the medial and lateral half of each pectoral ray. There is a large foramen in the middle of the supracleithrum. The dorsal postcleithrum overlaps laterally the dorsal end of the ventral postcleithrum. Baudelot's ligament curves round the posterior edge of the dorsal end of the cleithrum to attach on the medial face of the supracleithrum.

PELVIC BONES (Fig. 19): The pelvic bones (basipterygium) are of the usual percoid configuration: elongate, pointed, trough-like bones, narrowing anteriorly and sutured to each other posteriorly along their medial edges. The flattened, finger-like postpelvic processes project posteriorly and slightly dorsally from the posteroventral margin of each bone. The posterolateral corner of each bone bears a concave facet for articulation with the pelvic fin spine. The long, slender, flexible subpelvic processes are visible on the ventral surface of the pelvic bone; they project anteriorly from the median edge of the thickened, articular base of the bone. These subpelvic processes are easily lost in skeletal preparations.

OTOLITHS (Fig. 20)

Otolith terminology follows Hecht (1978). Margin entire to crenate; rostrum prominent and rounded anteriorly; antero-rostro minute; the sulcus acusticus is open anteriorly and closed posteriorly and clearly divided into ostium and cauda; ostium ca. 48% of total sulcus length; the ostium has a unique dorsal retroflexion above the antirostrum; the posterior section of the cauda has a posteroventral angle of ca. 90°; anterior and posterior colliculi are present, the anterior colliculum is sometimes divided by a collicular groove; the cristae superior and inferior are absent; the otolith is medially strongly convex.

In order to describe a generalized serranid otolith we examined a size range of sagittae from 15 species: Acanthistius sebastoides (Castelnau, 1861), Aethaloperca rogaa (Forsskål, 1775), Anthias squamipinnis (Peters, 1855), Epinephelus albo-marginatus Boulenger, 1903; E. areolatus (Forsskål, 1775), E. rivulatus (Valenciennes, 1830), E. guaza (Linnaeus, 1758), E. fasciatus (Forsskål, 1775), Cephalopholis hemisstiklos (Rüppell, 1830), C. miniata (Forsskål, 1775), C. sonnerati (Valenciennes, 1828), Holanthias natans (Fowler, 1925), Nemanthias carberry Smith, 1954; Plectropoma maculatus (Bloch, 1790) and Variola louti (Forsskål, 1775). Despite distinct interspecific differences, and to a limited extent intraspecific variation, there are 4 distinctive recurring characters that delimit a serranid sagitta from those of other percoid families (Fig. 21): (1) a sharp and narrow crista superior, (2) a wide and robust crista inferior, (3) a wide angle of the posteroventral section of the cauda and (4) the presence of a posteroventral groove that opens onto the ventral margin below the postero-ventral section of the cauda. Also, the sagittae of serranid species, with a few exceptions, are generally pointed anteriorly as well as posteriorly (Fig. 21).

The sagitta of D. petersi on the other hand is unlike that of any of the serranid otoliths examined. This conclusion was reached after examining the otoliths of 26 specimens, ranging from 165 to 622 mm total length. None of the 4 characteristic serranid features is evident on the sagitta of D. petersi. Furthermore, the dorsal retroflexion of the ostium is unique among the otoliths of percoid fishes.

Considering the above evidence and that otoliths are often species specific and also that certain features can be used unequivocally to delimit families within orders (Schmidt, 1968; Hecht & Hecht, 1978), the otolith configuration supports removal of D. petersi from the Serranidae. Furthermore the sagitta of this species shows no particular affinity to that of any other percoid families.
Figure 20. Sagittae from right side of D. petersi: A, 165 mm TL; B, 235 mm TL; C, 280 mm TL; D, 361 mm TL; E, 362 mm TL; F, 427 mm TL; G, 444 mm TL. Arrow indicates the retroreflection of the ostium above the antirostrum.

Figure 21. Sagittae from right side of six serranid species illustrating the four recurring features characteristic of the family: A, Cephalopholis miniata 370 mm TL; B, C. miniata 372 mm TL; C, Aethaloperca rogaa 370 mm TL; D, A. rogaa 400 mm TL; E, Variola louti 224 mm TL; F, Acanthistius sebastoides 215 mm TL; G, Anthias squamipinnis 102 mm TL; H, A. squamipinnis 145 mm TL; I, Epinephelus albomarginatus 240 mm TL; J, E. albomarginatus 325 mm TL. Arrow indicates the posteroventral groove.

SWIM-BLADDER

The anterior end of the large swim-bladder (Fig. 22) is directly connected to the ventral surface of the fourth through seventh centra and, via connective tissue, to the ventral postcleithrum and pleural ribs. The posterior half of the swim-bladder is almost completely covered by three pairs of overlapping muscles. The swim-bladder wall is of thick, tough connective tissue. The gas gland covers the anterior half of the ventral region of the inner surface. There are no internal partitions of the swim-bladder. The “oval” for gas resorption is located on the ventral surface near the posterior end of the swim-bladder. Examination of swim-bladders from adult males and females revealed no apparent sexual dimorphism.

Figure 22. D. petersi, 236 mm SL, swim-bladder in dorsal (top), lateral (middle), and ventral (bottom) views: M - muscles, DA - dorsal attachment area.

MYOLOGY

CHEEK MUSCLES and LIGAMENTS (Figs. 23 & 24): Section A1 of the adductor mandibulae originates on the lateral side of the dorsal part of the preopercle; anteriorly it joins the aponeurosis inserting on the medial and lateral sides of the maxilla just distal to the articulation of the palatine. This broad sheet of connective tissue also attaches along the dorsolateral edge of the middle part of the maxilla, and ventrally it narrows into a strap-like tendon attaching to the articular just anterior to the quadrature articulation. There is a partly separate, dorsal division of A1, anteriorly. The origin of this separate division is on the dorsal fibres of the main A1 division.

There is no separate A2 section of the adductor mandibulae. The A2 section lies ventral to, and is overlapped laterally by, the ventral part of A1. It originates from the lateral surfaces of the ventral parts of the preopercle, hyomandibula and metapterygoid; anteriorly it has an aponeurotic connection with the A4 section and also sends some fibres onto the maxillo-mandibular aponeurosis. The mandibular branch of the trigeminal (V) nerve passes medial to A1 and laterally across the anterior end of A1, where it bifurcates, one branch passing into the foramen
on the lateral side of the articular just anterior to the quadrato condyle, and the other branch running into the Aw section on the medial face of the articular. In Johnson's (1980) work on the classification of the Haemuloidea, Lutjanioidea and Sparioidea; all of his figures of the cheek muscles of fishes of these three superfamilies show the trigeminal nerve as unbranched at the rear end of the lower jaw, the nerve simply passing into the Aw section on the medial side of the lower jaw. It seems that the bifurcate condition of the mandibular branch of the trigeminal nerve is common in percoid fishes. We have found it in a few serranids, lutjanids, haemulids and sparids that have been dissected.

The Aw section originates via a broad aponeurosis covering the ventral part of the quadrate and symplectic and the anterior portion of the preopercle. Aw also attaches posteriorly to the aponeurosis of A1 and A2. Aw inserts broadly over the medial surface of the lower jaw, attaching directly to the dentary and articular.

The well developed palato-premaxillary ligament attaches to the dorsomedial edge of the base of the palatine maxillary process and joins its fellow on the dorsal surface of the rostral cartilage. The ethmo-maxillary ligament runs from the end of the transverse supraethmoid ridge under the palato-premaxillary ligament to the anterolateral surface of the maxilla.

RETRACTOR DORSALIS: The retractor dorsalis muscle originates on the 2nd centrum only and inserts on the 3rd pharyngobranchial and 4th upper pharyngeal tooth plate.

Centrarchops chapini Fowler, 1923

Centrarchops chapini Fowler, 1923: 2 (mouth of the Congo River); 1936: 746, Fig. 331; Poll, 1954: 42, Fig. 10. Pl. 2, Fig. 2.

DESCRIPTION: (Based on Fowler, 1936; Poll, 1954; and 4 specimens 213-238 mm SL.) Dorsal-fin rays X, 18-19; dorsal fin margin notched before the soft-rayed portion; the spines stout, heteracanthous; interspinous membranes deeply incised, their rear edge attached to the lateral surface of each spine. Anal fin rays III,13; anal spines stout, the second longer than the third. Soft dorsal and anal fins high anteriorly. Caudal fin truncate, with 9+8 principal rays, 8+7 branched rays, and 11 or 12 procurent rays. Pelvic fins with 1 spine and 5 branched rays. Pectoral fin with 17-19 rays, the dorsalmost 2 rays unbranched and the rest branched.

Body oblong-oval, compressed; greatest depth 1.9-2.0 in SL; greatest body width 2.2-2.5 in body depth. Head length 2.6-2.9 in SL. Eye diameter 4.1-4.4 in head length.

Head, body, and proximal part of fins covered with ctenoid scales; scales on body and head with tiny auxiliary scales at their base. Cheeks scaly; preorbitals and posterolateral part of lower jaw with embedded scales, maxilla naked. Lips, front part of lower jaw, maxilla, snout, and gular area covered with fleshy villi and rugose skin, which give the lips and chin a furry appearance. Chin with 4, large, tubular pores. Branchiostegal rays and membranes naked. Spinous dorsal fin naked distally, but with scales at the base running up the leading edge of each spine. Lateral line curving slightly dorsally from head to caudal peduncle, then running straight along midlateral part of peduncle and along middle caudal rays halfway to rear margin of fin; 50-53 tubed scales to base of caudal fin. No enlarged scale or scaly axillary process at base of pelvic fins. No scaly flap of skin at upper end of pectoral-fin base.

Rear edge of opercle with 2 distinct, flat points. Preopercle serrate, the serrae at the “angle” enlarged; subopercle and interopercle smooth. Maxilla mostly exposed when mouth is closed; posterior edge of maxilla slightly concave; supramaxilla large. Nostrils large, elongate, the anterior one larger, with a skinny rim produced into a large flap posteriorly; posterior nostril with a narrow, fringed, skinny rim. Olfactory organ elongate, with about 18 lamellae on medial side of rachis and about 20 on the lateral side of a fish 21 cm SL.

Premaxillae slightly protrusile; a band of small, slightly curved, conical teeth in both jaws, the outer teeth slightly enlarged; a narrow V-shaped band of small, conical teeth on vomer and a band of similar teeth on palatines. Teeth on jaws, vomer and palatines mostly hidden by fleshy villi. No teeth on ectopterygoids, endopterygoids or tongue. Cheek muscles as described for Dinoperca petersi.
Figure 25. Centrarchops chapini, 283 mm TL, after Poll, 1954.

Branchiostegal rays 7. Gills 4, with a slit behind the last gill. Pseudobranch large, with about 46 filaments. Gillrakers (12-13)+(21-24); longest raker on first arch shorter than longest gill-filaments.

Vertebræ 10+16; epipleural ribs are present on first 10 vertebrae. Distal radial of first dorsal fin pterygiophore autogenous. Predorsal bones formula 0/0/0+2/1/1/. There is a 1:1 relationship between the 2nd through the 8th spinous dorsal fin pterygiophores and their neural spines. In specimens larger than about 20 cm SL, the neural spines of vertebrae 3-17 are expanded in the saggital plane; and the haemal spines of vertebrae 11-15 are expanded distally.

Swim-bladder large, with thick, tough walls and 3 pairs of large, intrinsic muscles that cover the posterior two-thirds of the swim-bladder. Anterior end of swim-bladder firmly attached to vertebral column.

**DISTRIBUTION:** C. chapini is known only from the northern coast of Angola.

**DISCUSSION**

The following discussion is based mainly on the excellent work of G. David Johnson (1980, 1983 & 1984). He has laid the foundation for a modern analytical approach to percoid systematics, and provided a framework of anatomical characters that can be tested as indicators of phylogenetic relationship. In the Suborder Percoidei, Johnson (1984) recognizes 80 families, with 12 genera, including Dinoperca, relegated to the incertae sedis category. With 26 of the 80 percoid families being monotypic, one might ask "Does it serve a useful purpose to create one more small family for Dinoperca and Centrarchops?" We believe the answer to this question is "yes" for at least three good reasons: 1) The taxonomic limbo of "incertae sedis" is unsatisfactory from the utilitarian aspect of classifications. Filing fishes on shelves in a fish collection, or filing literature references usually requires that genera be assigned to families. 2) In science generally, and especially in systematic research, analysis must precede synthesis. Therefore, as part of the process of working out the relationships of Dinoperca, one must start with a detailed comparative description of those anatomical features thought to be relevant to understanding the interrelationships of percoid fishes. Recognizing the Dinoperidae as a separate family will thus call attention to what we believe is the unique status of this family, and it will also serve to define the anatomical features that we believe support this taxonomic decision. 3) Many percoid families are poorly defined, i.e., they lack distinctive apomorphic (derived) features. The Dinoperidae, as here defined, seems better characterized than many other putative percoid families, and thus deserving of separate family status.

Johnson (1984) has discussed the inadequacies of the current definition of the Percoidei, as the group of perciform fishes that lack the "special peculiarities that characterize the other suborders ...". Dinoperca certainly fits this definition. Although Johnson (1983, 1984) has examined a specimen of Dinoperca and relegated the genus to the "incertae sedis" category of his percoid classification, he has not discussed the anatomy or relationships of Dinoperca except to list it in his table of "Selected Morphological Features of Adult Percoidei" (1984: 476). A comparison of Dinoperca and Centrarchops with various "likely" relatives will now be given (Table 2).

Dinoperca and Centrarchops are (superficially) most similar to Glaucosoma, a genus of four or five species of the western Pacific and eastern Indian Ocean. Katayama (1954) has briefly treated the osteology and relationships of G. fauvelii Sauvage, 1881. His illustration of the cranium shows a high, median crest on the frontals that is continuous with the supraoccipital crest; but the anterior bifurcation of the median frontal crest is constricted anteriorly. The prominent, crescentic ridge on the dorsal end of the ethmoid of Dinoperca is not shown on the skull of Glaucosoma. The ceratohyal is shown with a closed "beryciform foramen" (absent in...
<table>
<thead>
<tr>
<th></th>
<th>Dinoperca</th>
<th>Centrarchops</th>
<th>Glaucosoma</th>
<th>SERRANIDAE</th>
<th>HAEMULOIDEA</th>
<th>LUTJANOIDEA</th>
<th>SPAROIDEA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Second pair of uroneurals</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Vertebrae</td>
<td>10 + 16</td>
<td>10 + 16</td>
<td>10 + 15</td>
<td>24 to 30</td>
<td>26 or 27</td>
<td>10 + 14</td>
<td>10 + 14</td>
</tr>
<tr>
<td>Predorsal bones configuration</td>
<td>0/0/0+2+1/1/</td>
<td>0/0/0+2+1/1/</td>
<td>0/0/0+2+1/1/</td>
<td>Not as in Dinoperca</td>
<td>0/0+0/2+1+1/1/</td>
<td>0/0+0/2+1+1/1/</td>
<td>0/0+0/2+1+1/</td>
</tr>
<tr>
<td>Subocular shelf</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+ or -</td>
<td>+ or -</td>
</tr>
<tr>
<td>Branchiostegal rays</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>Openings in lateral wall of pars jugularis</td>
<td>2</td>
<td>?</td>
<td>2</td>
<td>2</td>
<td>2 or 2½</td>
<td>2 or 4</td>
<td>2 or 3</td>
</tr>
<tr>
<td>Second infraorbital as deep as rear end of preorbital</td>
<td>Yes</td>
<td>Yes</td>
<td>?</td>
<td>Yes in some, no in others</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Rear end of maxilla covered by preorbital when mouth is closed</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>Mostly</td>
<td>Partly</td>
<td>Mostly</td>
</tr>
<tr>
<td>Third epibranchial tooth plate</td>
<td>+</td>
<td>?</td>
<td>?</td>
<td>+ or -</td>
<td>+ or -</td>
<td>+ or -</td>
<td>-</td>
</tr>
<tr>
<td>Metapterygoid with haemuloid flange</td>
<td>-</td>
<td>?</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Procurent spur</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Radial cartilages anterior to neural &amp; haemal spines of PU3</td>
<td>-</td>
<td>?</td>
<td>-</td>
<td>-</td>
<td>?</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Trisegmental pterygiophores of dorsal/anal fins</td>
<td>4/3 – 4</td>
<td>1 or 2</td>
<td>10/7</td>
<td>0 – 24/0 – 19</td>
<td>0/0</td>
<td>1 – 7/1 – 7</td>
<td>1 – 4/1 – 4</td>
</tr>
<tr>
<td>Opercular “spines”</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Lateral line extends to end of caudal fin</td>
<td>Yes</td>
<td>Halfway</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>Supramaxilla</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+ or -</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Scaly axillary process at base of pelvic fins</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>
The myodome is said to be closed posteriorly (open in Dinoperca). The basihyal is not expanded anteriorly (greatly expanded in dinopercids). The swim-bladder is "ovoid and rather small. The large muscle bands from the opthotic [sic] are attached to the antero-dorsal side of the air-bladder". In dinopercids, the swim-bladder is large, elongate, and there are no muscles connecting the skull and the swim-bladder; instead the posterior part of the swim-bladder is almost completely covered by three pairs of intrinsic muscles. Other differences and similarities are listed in Table 2. The shared character states of Glaucosoma and dinopercids are either plesiomorphic (primitive) features (e.g., supramaxilla, procurent spur, subocular shelf, two uroneurals) or apparently homoplastic derived features that are also common in other percoid groups (e.g., absence of radial cartilages anterior to neural and haemal spines of the third preural vertebra).

Although the bifurcate, median frontals crest of Glaucosoma might represent an earlier stage in the evolutionary development of the crest occurring in dinopercids, there are no other apomorphic features shared by these two taxa which would indicate their sister-group relationship. Furthermore, the distinctive autapomorphies of these two taxa (swim-bladder anatomy and configuration of the predorsal bones plus anterior dorsal fin pterygiophores) are evidence for their placement in separate families. Glaucosoma has been placed in its own family by Jordan (1923), Berg (1940), Katayama (1954) and Nelson (1984). Until someone puts forth a convincing argument that Glaucosoma should be assigned to one of the other percoid families, it seems reasonable to accept the Glaucosomatidae as a distinct family.

The next most likely candidate for the status of sister-group to the Dinopercidae seems to be the Serranidae. The shared similarities of dinopercids and the Serranidae are, however, plesiomorphic features of no value in indicating phyletic relationships. The "loss" of the second free uroneurals and the loss of the procurent spur are two derived character states (Johnson, 1983) that characterize the Serranidae and distinguish this family from dinopercids (which have free second uroneurals and a procurent spur).

Johnson (1983) has questioned Greenwood's (1977) interpretation of the caudal skeleton of Niphon spinosus Cuvier (a primitive serranid). It appears to us that Greenwood is correct in interpreting the absence of second free uroneurals in Niphon as the result of its [phylogenetic] fusion with the first uroneurals (stegurals). Greenwood's illustration of the caudal skeleton of a specimen 156 mm SL (here included in Fig. 26) shows "2 uroneurals very closely applied to one another and apparently fused basally." Johnson (1983: 785) argues "There is no reason to believe that the distal processes on the uroneurals [stegurals] actually represent remnants of two uroneurals. One specimen I examined ... showed two of these processes on one side and three on the other. They are most likely secondary in origin." It seems to us that an extra process on one side of the distal end of the stegurals does not, ipso facto, refute the hypothesis of fusion with the second uroneurals. The extra process (or processes) could well be secondary or examples of a developmental lability in this part of the skeleton. But the fusion hypothesis is supported by (1) the fact that the largest process on the stegurals of Niphon is in the correct position (posterior and distal to the stegurals) to represent fused second uroneurals; (2) stegurals of serranids and the centropomid Psammoperca are generally longer than the stegurals of perciform fishes with free second uroneurals (e.g., pteropids, Leptobranchia, Centropomus, Lates), implying fusion with the more distally located second uroneurals; (3) the skeleton of a 375 mm SL specimen of Epinephelus faveatus (Valenciennes, 1828) (Fig. 26, b & c) clearly shows a free second uroneural on the left side and a fused second uroneural on the right side; and (4) ontogenetic fusion of the second pair of uroneurals with the first uroneurals is known in percoid fishes (described and illustrated for Coryphaena equiselis Linnaeus by Potthoff, 1980). Nevertheless, reduction and actual loss of the second uroneurals, and even the stegurals (= first uroneurals fused with the neural arches of the first preural and ural

Figure 26. Caudal fin skeletons of (a) Niphon spinosus, 156 mm SL, X: point at which the two uroneurals fuse (after Greenwood, 1977: Fig. 1); (b) Epinephelus faveatus, 375 mm SL, right side, lateral view, H = hypurals, RU + S = right second uroneural fused with stegural, TVE = terminal vertebral element; and (c) E. faveatus, 375 mm SL, left side, dorsolateral view, lettering as for right side except S = left stegural, U = separate second uroneural of left side.
percoid fishes except for the Sciaenidae. In fact, this feature also occurs in Dinoperca, Moronidae, Sillaginidae, Pempheridae, Neoscorpis, and in some species of Latijanus. In Centrarchops, the lateral line extends halfway to the rear margin of the caudal fin.

The discovery of teeth on the eopterygoids of large specimens of Dinoperca was unexpected. Very few percoids have teeth on the eopterygoids; they have been described in kuhliids and centrarchids (Boulenger, 1895), Leptobrana (Tomininga, 1965), Oscaryus and Rhomboplites (Lutjanidae, 1980), percids (Osse, 1969), centropomids (Greenwood, 1976), and in some apogonids (Fraser, 1972). We would not be surprised to learn that large adults of Centrarchops have teeth on their eopterygoids.

Centrarchops and Dinoperca have the lips and lower jaw covered with villi, but in Centrarchops the villi extend onto the snout, maxilla and gular area and are much larger and conspicuous. The chin pores of Centrarchops are also very conspicuous despite the villi. There are no visible chin pores in Dinoperca.

In addition to their synapomorphies (discussed above), Centrarchops and Dinoperca are similar in many other features. The general shape of the body and fins is virtually identical. The protruding lower jaw, scaly cheeks, exposed maxilla, large supramaxilla, free 2nd uroneurals, 7 branchiostegal rays, 10+16 vertebrae, scaly fins, broadly rounded tongue, 2 opercular spines, absence of pelvic axillary scale, villous lips and lower jaw, subocular shelf, and procurent spur are all features that do not, individually, indicate a close relationship between these genera. But taken together, these features distinguish the dinopercids from other percoid families, and thereby establish a circumscribed case for a sister-group relationship for these two genera.

Centrarchops was regarded as a synonym of Dinoperca by Johnson (1983: 781), but he did not examine specimens of Centrarchops. The similarity in external features of C. chapini and D. petersi is striking, however there are substantial differences in the well-developed tubular chin pores of Centrarchops (no chin pores in Dinoperca), the configuration of predorsal bones, dorsal fin pterygiophores and neural spines, and the enlarged median fin spines. We judge that these differences warrant separate generic status for these two taxa.

**DINOPERCIDAE fam. n.**

**TYPE GENUS:** Dinoperca Boulenger, 1895.

**DIAGNOSIS:** (Features with an asterisk have not been verified in Centrarchops). Percoid fishes with a single dorsal fin, the margin notched before the soft-rayed portion, with 9-11 spines and 18-20 soft-rays. Anal fin with 3 spines and 12-14 soft-rays. Caudal fin truncate, with 9+8 principal rays and 8+7 branched rays. Pelvic fins with 1 spine and 5 branched rays.

Body oblong-oval, moderately compressed, the greatest depth 1.9-2.5 in SL. Head length less than body depth; eye large, its horizontal diameter 2.9-4.4 in head length.

Head, body and fins covered with small, ctenoid scales. Lateral line curving slightly dorsally from head to caudal peduncle, then running straight along midlateral part of peduncle and along middle caudal rays at least halfway to the rear edge of the fin.

Rear edge of opercle with 2 flat points. Preopercle serrate; subopercle and interopercle smooth. Maxilla mostly exposed when mouth is closed; posterior (distal) edge of maxilla slightly concave; supramaxilla well-developed.

Premaxilla slightly protrusile, with a well-developed lateral process. Jaws, vomer, and palatines with a band of short, curved, conical teeth; endopercygyoids without teeth. Tongue wide, broadly rounded and edentate.

Branchiostegal rays 7, the membranes separate, free from the isthmus. Gill 4, with a slit behind the last. Pseudobranch large.

Cranium with a high, median frontal crest continuous with that of the supraoccipital and deeply excavated dorsally to form a narrow, median sulcus, which continues posteriorly almost to the supraoccipital and ventrally to the base of the crest and roof of the brain cavity. Parietal crests continuous with posterolateral frontal crests*. Myodome open posteriorly*. Dorsal end of supraethmoid with a prominent, crescentic, transverse ridge which abuts the rostral cartilage*. Exoccipitals with two, contiguous, large condyles for articulation with the first centrum*.

Second infraorbital bone as deep as rear part of first (preorbital). Third infraorbital bears the large subocular shelf. Dermosphenochis fused with sphenotics in large specimens*.

Vertebræ 10+16 including terminal vertebral element. Predorsal bones pattern 0/0/0+2+1/1 or 0/0/0+2/1.

Caudal fin skeleton with a free 2nd pair of uroneurals, 3 epurals, 5 autogenous hypurals, parhypural and haemal spines of 2nd and 3rd preural vertebrae autogenous, no neural spine on 2nd preural centrum, no free ura centra; no radial cartilages anterior to neural and haemal spines of 3rd preural vertebra. Procurent spur present.

Last 1-4 pterygiophores of dorsal and anal fin trisegmental.

Otolith (sagitta) with a distinctive dorsal retroflexion of the ostium above the antirostrum*.

Swim-bladder large, attached to the 4th through the 7th centra; the posterior half almost completely covered by 3 pairs of large, overlapping, intrinsic muscles.

Adductor mandibulae with distinct A₁ and A₂ sections, no separate A₃ section, A₃ section with a separate dorsal division.

**POSTSCRIPT** (by P.C. Heemstra): In the Serranidae account of the FAO Species Identification Sheets for Fishery Purposes, Western Indian Ocean (Heemstra & Randall, 1984), the family name Dinopercidae was used unintentionally for the first time. The name was included in a list of families similar to the Serranidae that occur in the western Indian Ocean and was accompanied by a statement of characters by which the family could be readily distinguished from the Serranidae: "Dinopercidae (previously considered as part of Serranidae): anterior dorsal and anal fin rays much longer than posterior ones; anal fin soft-rays 13 (7 to 10 in Serranidae)."

When the Heemstra and Randall manuscript was completed in 1983, it was intended that the present paper would be published before the FAO publication appeared. Unfortunately, that intended sequence has not happened. Although the family name Dinopercidae Heemstra and Randall, 1984 appears to be technically valid, it was certainly unintentional. To rectify my nomenclatural faux pas, I suggest that the 1984 use of the name be considered a nomen praematurum and that it be disregarded for purposes of nomenclatural priority. Furthermore, the name as used by Heemstra and Randall (1984) was proposed conditionally; and, according to Article 15 of the third (1985) edition of the International Code of Zoological Nomenclature, it is therefore not available.
ACKNOWLEDGEMENTS

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