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THE PHYLOGENETIC IMPLICATIONS OF CENTRARCHID KIDNEYS

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Hin-Kiu Mok (1981) The phylogenetic implications of centrarchid kidneys. *Bull. Inst. Zool., Academla Sinica* **20**(2): 59-67. A survey of the gross kidney morphology of 23 centrarchid species was conducted, and its implications for the phylogeny of the Centrarchidae are discussed. No synapomorphies were found for the family as a whole. The monophyly of the group including *Lepomis, Enneacanthus, Ambloplites, Acantharchus, Archoplites, Centrarchus* and *Pomoxis* is supported by the possession of extreme posterior kidney. *Centrarchus* and *Pomoxis* form a monophyletic group by sharing two synapomorphic character states: the fused extreme anterior kidneys and fusion of the posterior kidneys behind the first haemal spine. The monophyly of *Lepomis* is indicated by the thick tissue layer over the extreme posterior kidney. *Pomoxis* is a monophyletic group as shown by the V-shaped extreme posterior kidney. Conflicts among some characters of centrarchid kidneys found in this study indicate possible convergences or parallelisms. Based on kidney characters, a centrarchid phylogeny is hypothesized and comparisons to previous hypothesized phylogenies are made.

There are presently few published studies on the gross morphology of perciform kidneys, and none of the results of any of these studies(5,8) have ever been subjected to cladistic analysis in order to determine the phylogenetic relationships of these fishes. Ogawa(8) has classified teleost kidneys into five configurational classes on the basis of the type of fusion between the two kidneys and has shown associations of kidney types and their related groups. Still further subdivision of his classification is possible if additional morphological characters, such as the degree development of the extreme anterior and posterior portions of the kidneys, are taken into consideration.

The present study was initiated when different kidney types of the north American freshwater centrarchids were discovered. These variations offered some promises for a further understanding of the interrelationships among centrarchids, a group for which hypotheses of generic interrelationships have already been proposed by other authors such as Bailey(2), Smith and Bailey(10), Branson and Moore(3), and Avise, Straney and Smith(1).

MATERIALS AND METHODS

Specimens examined in the present study were from the collections of the American Museum of Natural History (AMNH) and California Academy of Science (CAS). Some specimens were donated by Dr. Edward Brothers of Cornell University (CU) and are now deposited in the American Museum of Natural History.

Material examined (Measurements are standard length in millimeters):

Acantharchus: *A. pomotis*, AMNH 5376, 74 mm

Ambloplites: *A. cavifrons*, AMNH 30262, 87 mm; *A. rupestris*, AMNH 20982, 87 mm.
Archoplites: *A. interruptus*, CAS 39681, 72 mm, 82 mm, 85 mm.
Centrarchus: *C. macropterus*, AMNH 3220, 85 mm.
Elassoma: *E. zonatum*, CU uncat., 22 mm, 22 mm.
Enneacanthus: *E. chaetodon*, AMNH 33543, 38 mm, 45 mm; *E. gloriosus*, AMNH 26270, 45 mm; *E. obesus*, AMNH 23742, 60 mm.
Lepomis: *L. cyanellus*, AMNH uncat., 65 mm, 80 mm; *L. gibbosus*, AMNH uncat., 24–70 mm, 36 specimens; *L. gulosus*, AMNH uncat., 88 mm; *L. humilis*, AMNH uncat., 48 mm, 60 mm; *L. macrochirus*, AMNH uncat., 96 mm; *L. marginatus*, CU 15261, 78 mm; *L. megalotis*, AMNH uncat., 72 mm; 95 mm; *L. microlophus*, AMNH uncat., 80 mm, 97 mm, 97 mm; *L. punctatus*, CU 26230, 72 mm; *L. symmetricus*, CU 21286, 32 mm.
Micropterus: *M. coosae*, AMNH uncat., 110 mm; *M. sarmoides*, AMNH 30003, 104 mm.
Pomoxis: *P. annularis*, AMNH 20979, 93 mm, 102 mm; *P. nigromaculatus*, AMNH 30128, 150 mm, 170 mm.

All dissections were made through the right side of the abdominal wall. The gastrointestinal tract and swimbladder were removed to expose the kidney and permit observation of its morphology. Characters studied include the distribution of the archinephric ducts in relation to the first haemal spine and the basal anal pterygiophore, the degree of development of the posteriormost portion of the kidney, the relation of the two kidneys (whether they are separate or fused, and if fused, and if fused, the point and extent of fusion).

RESULTS

For comparative purposes certain terms are applied to specific parts of kidney (Fig. 1). The extreme anterior kidney is that part lying lateral to the pharyngeal retractor muscle (M, retractor arcuum branchialium dorsales). This part has frequently been called the head or cranial kidney. The terms anterior and posterior kidneys refer tothe anterior and posterior parts from the rear of the extreme anterior kidney to the point directly in front of the base of the of the first haemal spine. These parts often been referred to as the trunk kidney. The extreme posterior kidney is that portion adjacent to the base of the basal anal pterygiophore.

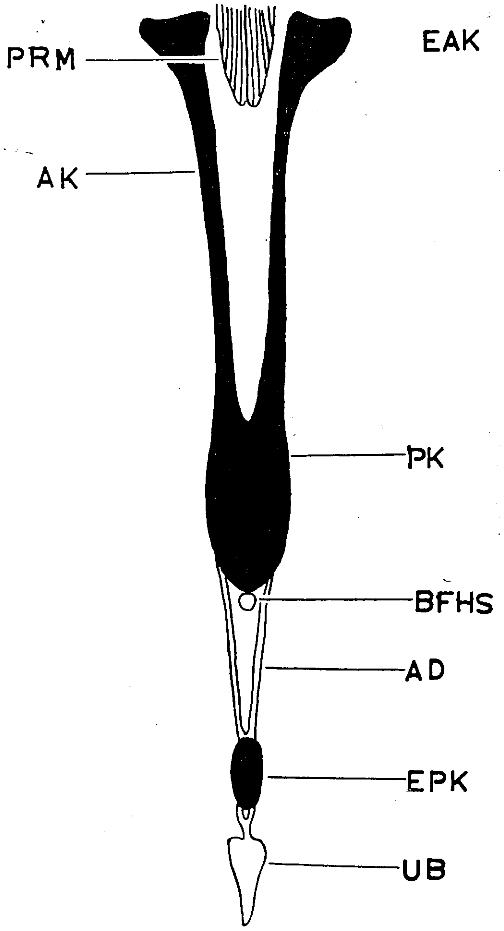

Fig. 1. Diagrammatic ventral view of a centrarchid kidney. AD—archinephric duct, AK—anterior kidney, BFHS—base of the first haemal spine, EAK—extreme anterior kidney, EPK—extreme posterior kidney, PK—posterior kidney, PRM—pharyngeal retractor muscle, UB—urinary bladder.

The kidney morphology of 36 specimens of *Lepomis gibbosus* (24–70 mm SL) proved to be identical, and it is therefore would appear permissible to assume that kidney morphology varies little within the species of Centrarchidae.

The various configurations of centrarchid kidneys are depicted in Figure 2. *Elassoma zonatum* and *Micropterus* spp. have a kidney form (Fig. 2F and 2U) which is characterized by (1) the anterior kidneys are represented by two slender branches, (2) the extreme anterior kidneys are separate, (3) the posterior kidneys are fused before and limited entirely to the front of the first haemal spine base, (4) the archinephric ducts emerge from the posterior kidney and run on both sides of the first haemal spine on their way to the urogenital pore near which they converge into the urinary bladder, (5) no extreme posterior kidney exists. Outgroup comparison shows that this kidney form is common in the Perciformes. Accordingly, I postulate that this is the kidney type of the hypothetical ancestor of centrarchids.

In other centrarchids, kidney morphology varies from this primitive type. The extreme anterior kidneys fused in *Archoplites*, *Centrarchus*, *Pomoxis annularis*, *P. nigromaculatus*, and *Lepomis* species (including *L. gulosus* which had been placed in the abandoned genus *Chaenobryttus*), but not in *Lepomis marginatus* and *L. punctatus* (Fig. 2; arrow points to the area of fusion). This character state of the extreme anterior kidney rarely occurs in perciforms and has only been found in some percids(7). It is hypothesized as an apomorphic character state within the Centrarchidae.

It is possible to set up a transformation series of the forms of the extreme anterior kidneys within the genus *Lepomis*. *L. marginatus* and *L. punctatus* have separate extreme anterior kidneys, whereas they are fused in other *Lepomis* species. We may hypothesize either that the separate extreme anterior kidneys or fused extreme anterior kidneys is a primitive character state of the genus. Under the former hypothesis, a situation of 'covergence' must be postulated, while the latter requires a secondary loss of connection of the extreme anterior kidneys. At the present time, no other evidence (both ontogenetic and out-group comparison) from kidney morphology leads me to prefer either one of the alternative hypotheses of the primitive character state of *Lepomis*.

As I have mentioned, the posterior kidneys of most centrarchids are fused in front of the base of the first haemal spine (Fig. 2; a small circle represents the base of the first haemal spine); in *Centrarchus* and *Pomoxis*, however, the posterior kidneys fuse only behind the base of the first haemal spine (Figs. 2E, 2V, 2W)—a hypothesized derived character state.

In *Enneacanthus chaetodon*, the posterior kidneys are separate and extend to the third haemal spine before descending towards the urogenital pore near which they fuse to form the extreme posterior kidney (Fig. 2G). In *Enneacanthus obesus*, the left and right kidneys extend to the base of the basal anal pterygiophore as separate units (Fig. 2I). These are postulated as autapomorphic character states.

The posterior kidneys of *Acantharchus*, *Ambloplites cavifrons* (but not *A. rupestris*) and *Archoplites* fuse anterior to the first haemal spine, extend posteriorly on both sides of this spine towards the base of the basal anal pterygiophore and then fuse to give rise to the extreme posterior kidney (Figs. 2A, 2B, 2D). In *Acantharchus pomotis*, the kidney tissue adjacent to the first haemal spine has a highly derived and apomorphic condition: it is fused medially and covers the first haemal spine ventrally (Fig. 2A). In contrast to *Acantharchus homotis.*, *Ambloplites cavifrons*, *Archoplites interruptus*, and *Enneacanthus chaetodon*, the extreme posterior kidneys of *Ambloplites rupestris*, *Centrarchus macropterus*, *Enneacanthus gloriosus*, *Pomoxis annularis*, *P. higromaculatus*, and all species of *Lepomis* except *L. humilis* 'connect' to their posterior kidneys only through the archinephric ducts (Fig. 2). These are the apomorphic character states in relation to that of *Micropterus* spp. and *Elassoma zonatum*. The ancestral kidney form of *Ambloplites* is obscure due to the difference between *Ambloplites cavifron* and *A. rupestris*, the only two species comprising this genus. A comparison was made between *Ambloplites* and *Acantharchus*

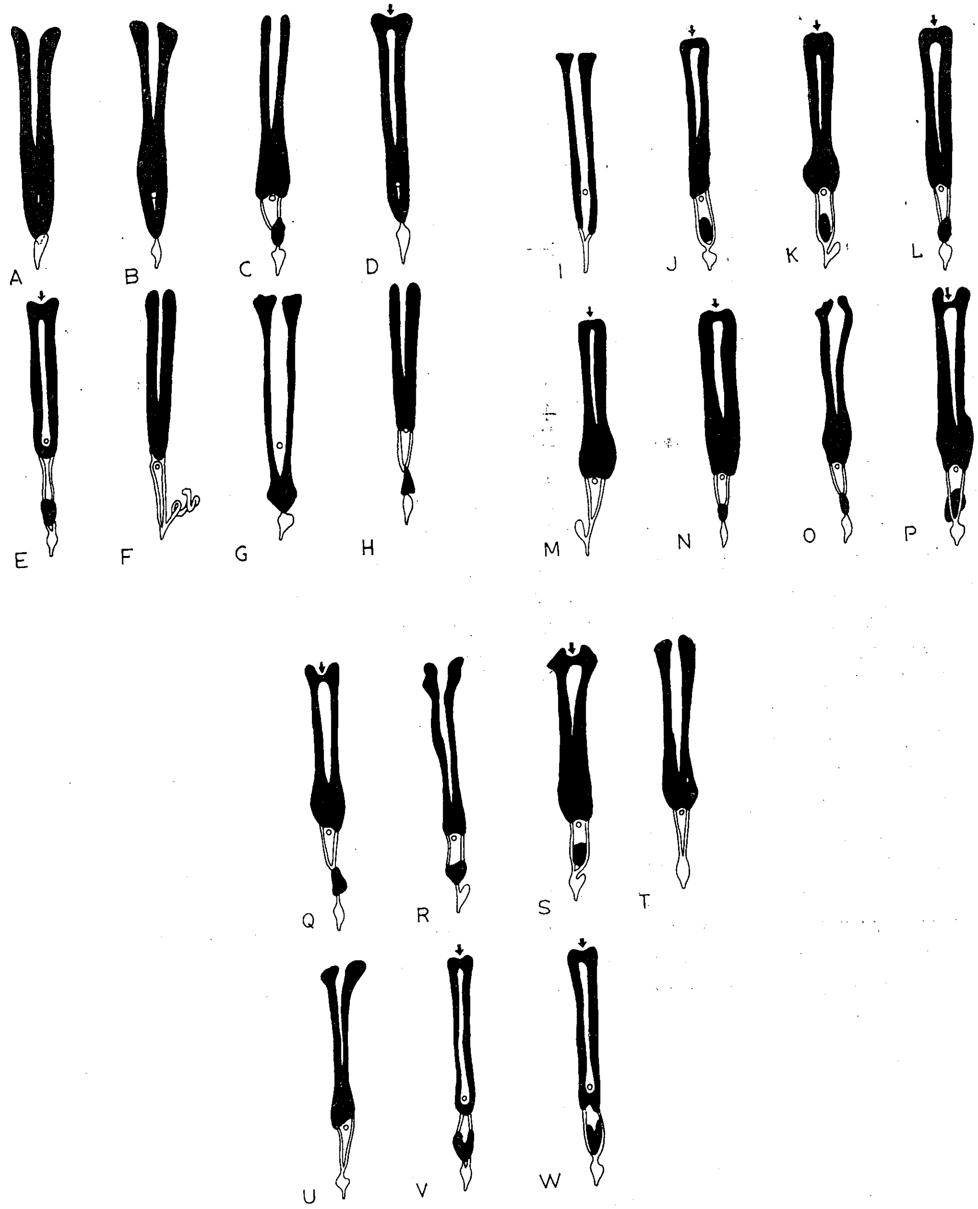

Fig. 2. Configurations of centrarchid kidney. A, *Acantharchus pomotis*. B, *Ambloplites cavifrons*. C, *Ambloplites rupestris*. D, *Archoplites interruptus*. E, *Centrarchus macropterus*. F, *Elassoma zonatum*. G, *Enneacanthus chaetodon*. H, *Enneacanthus gloriosus*. I, *Enneacanthus obesus*. J, *Lepomis cyanellus*. K, *L. gibbosus*. L, *L. gulosus*. M, *L. humilis*. N, *L. macrochirus*. O, *L. marginatus*. P, *L. megalotis*. Q, *L. microlophus*. R, *L. punctatus*. S, *L. symmetricus*. T, *Micropterus coosae*. U, *Micropterus salmoides*. V, *Pomoxis annularis*. W, *Pomoxis nigromaculatus*. Arrow points to the area of fusion of the extreme anterior kidneys. Circle represents the base of the first haemal spine.

to which the former genus may be related (see below). This comparison was grounded on the assumption that the kidney of the remote ancestor which gave rise to the ancestor of *Ambloplites* and *Acantharchus* should resemble the *Ambloplites rupestris* kidney. This assumption leads to two alternative hypotheses regarding the ancestral kidney form from which the *Ambloplites* and *Archoplites* kidneys were derived. The first hypothesis suggests that the ancestral form is characterized by the complete separation of the posterior and extreme posterior kidneys (i. e., the *Ambloplites rupestris* kidney form). The second hypothesis suggests that it is characterized by the direct connection between the posterior and extreme posterior kidneys (i. e., the *Ambloplites cavifrons* and *Acantharchus pomotis* kidney form). Both hypothetical evolutionary processes call for two morphological changes throughout the evolution of *Ambloplites rupestris*, *A. cavifrons*, and *Acantharchus pomotis*. As such, interpretation of this comparison on the basis of parsimony turns out to be unconclusive. In the lack of ontogenetic information, the *Ambloplites* ancestral kidney form is unresolved at this point.

Without ontogenetic evidence or knowledge of the sister group of *Enneacanthus*, it becomes difficult, if not impossible, to determine the character state of the hypothetical ancestor of *Enneacanthus*. Because the character states of *E. chaetodon* and *E. obesus* are unusual not only in the centrarchids but also in perciforms, and because the kidney form of *E. gloriosus* has a wider distribution within centrarchids, I assume that the form of the latter species characterizes the genus *Enneacanthus*.

The extreme posterior kidney of most centrarchids that possess this structure is overlain by a thin layer of membraneous tissue. In *Lepomis* species (including *L. humilis*), however, this tissue layer increases in thickness (Fig. 3). This is treated as a derived character state uniting *Lepomis* species as a monophyletic group.

The shape of the extreme posterior kidney varies. The deep V-shaped configuration of *Pomoxis* (Figs. 2V, 2W) differs from the oval-shape, which generally appears in other centrarchids. This can be treated as a derived character state supporting the monophyly of *Pomoxis* species.

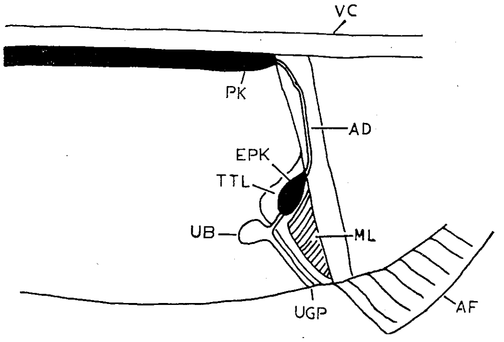

Fig. 3. left side view of a longitudinal section of the posterior part of the peritoneal cavity of *Lepomis* sp. showing the tissue layer that overlays the extreme posterior kidney. AD—archinephric duct, AF—anal fin, CAD—common archinephric duct, EPK—extreme posterior kidney, FHS—first haemal spine, ML—musclelayer, PC—peritoneal cavity, PK—posterior kidney, TTL—thick tissue layer, UB—urinary bladder, UGP—Urogenital pore, VC—vertebral column.

The distributions of the character states of the kidney characters are summarized in Figure 4. Fusion of the extreme anterior kidneys suggests the close relationships among *Archoplites*, *Centrarchus*, and *Pomoxis*. However, the resemblance in the relation of the extreme anterior kidneys among *Archoplites*, *Amploplites cavifrons*, and *Acantharchus* makes their close relationships a possibility. Such a conflict in distribution of apomorphic character states leaves the phylogenetic position of *Archoplites* unresolved.

On the basis of kidney morphology, the following hypotheses concerning the phylogeny of centrachid genera may be reached (Fig. 5). The monophyly of the group including *Lepomis*, *Enneacanthus*, *Ambloplites*, *Acantharchus*, *Archoplites*, *Centrarchus*, and *Pomoxis* is supported by the possession of extreme posterior kidney. *Centrarchus* and *Pomoxis* form a monophyletic group (*Archoplites* and *Lepomis* may be also

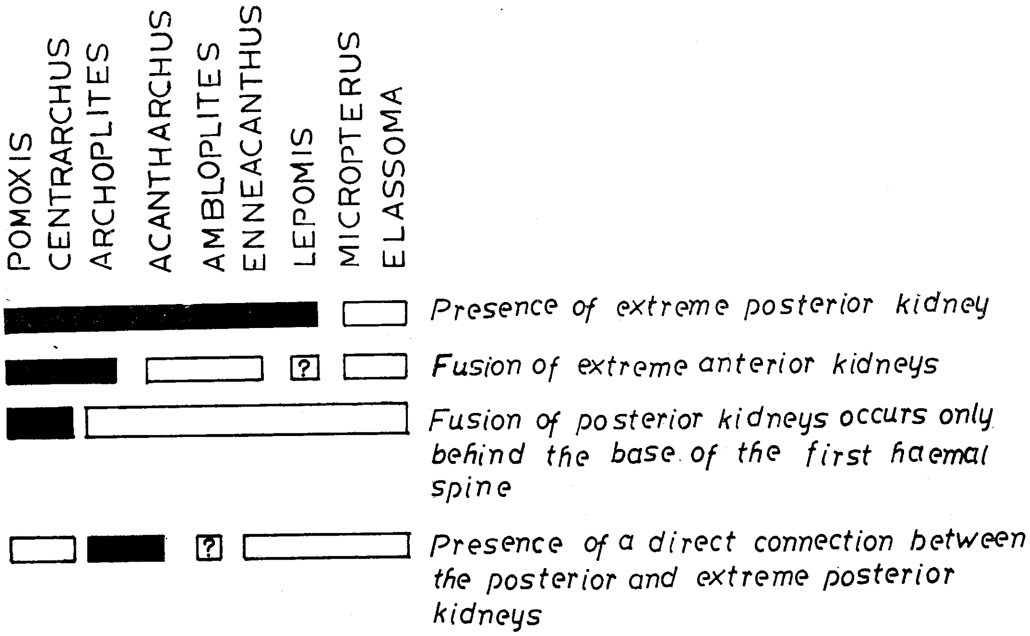

Fig. 4. Distribution of kidney character states in centrarchid genera. Shaded blocks—synapomorphic character states. Blank blocks—symplesimorphic character states. ?—character state of the genus is undetermined due to the lack of evidence.

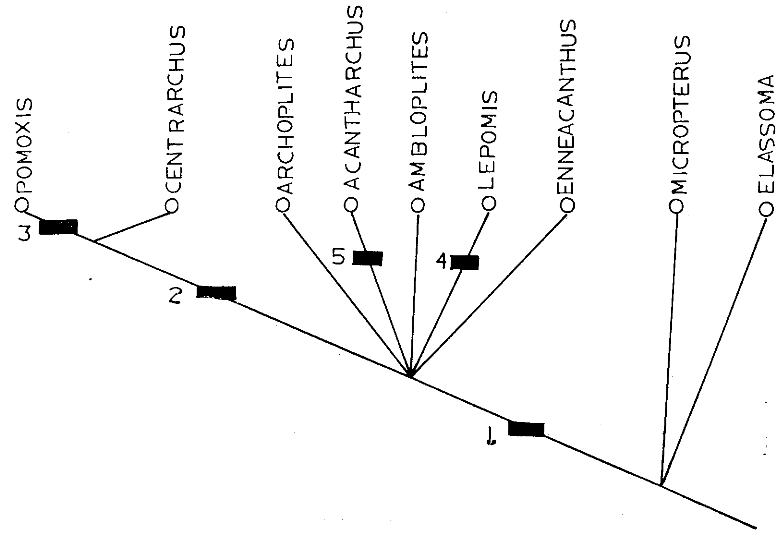

Fig. 5. A hypothesis of centrarchid phylogeny which is based solely on synapomorphic character states of the kidney characters. (1) Possession of extreme posterior kidney. (2) Posterior kidneys only fuse behind the base of the first haemal spine. (3) V-shaped extreme posterior kidney. (4) Posterior kidney is overlaid by a thick tissue layer. (5) Fused posterior kidney extends posteriorly and overlays the first haemal spine.

included) by sharing the synapomorphic character state of the fused extreme anterior kidneys. *Centrarchus* and *Pomoxis* are sister group, as suggested by the fusion of the posterior kidneys behind the base of the first haemal spine. The monophyly of *Lepomis* is indicated by the thick tissue layer over the extreme posterior kidney. *Pomoxis* is a monophyletic group as shown by the V-shaped extreme posterior kidney. No further knowledge of the phylogenetic positions of *Acantharchus*, *Ambloplites*, *Archoplites*, *Enneacanthus*, and *Lepomis* arc offered by the present study.

DISCUSSION

The study of Smith and Bailey(10) on the dorsal-fin supports of percoid fishes shows some evidence for considering *Acantharchus*, *Ambloplites*, *Archoplites*, *Centrarchus*, and *Pomoxis* as a monophyletic group since they share the synapomorphic character state of a high number of anal spines (5–9 versus 3). Branson and Moore(3), however, argued that a low number of anal spines is an apomorphic character state in the Centrarchidae. *Acantharchus* and *Ambloplites* may be sister group as indicated by the possession of one additional dorsal spine and pterygiohore(10).

Eaton's(4) study on the olfactory organs of centrachids throws light on the monophyly of *Archoplites*, *Pomoxis*, and *Centrarchus*. Two possible synapomorphies of the olfactory organs were discovered by Eaton(4). In *Archoplites*, *Centrarchus*, and *Pomoxis*, the olfactory epithelium in the floor of the olfactory sac has paired folds; alternate folds are swollen. In other centrarchids (e. g., *Elassoma*, *Lepomis*, and *Micropterus*), this pairing has not been found, and either the more posterior, or all of the folds may be swollen. *Enneacanthus* and *Elassoma* show a reduction in the number of folds.

The monophyletic status of *Pomoxis* is indicated by a lower number of dorsal spines and predorsal bones(10). However, the dorsal-fin support offers no evidence for the systematic position of the genus,

Bailey(2) and Branson and Moore(3) agreed with that *Chaenobryttus* (=part of *Lepomis*), *Lepomis*, and *Micropterus* share a common ancestor although they disagreed in how the three genera are related. Avise, Straney and Smith(1), by evidence of genetic similarity among centrarchid genera, have reached a similar conclusion. On the basis of the fin structures, *Lepomis*, *Micropterus*, and *Enneacanthus* share only primitive character states for the dorsal-fin supports (the formula of predorsal bones and pterygiophores is 0–0–0–1) and in the number of dorsal and anal spines (10 and 3, respectively; Smith and Bailey(10)). The hypothesis of Branson and Moore(3) with respect to the monophyly of *Lepomis* and *Micropterus* was founded on the interpretation that a low number of anal spines in these genera is a derived character state in Centrarchidae. Since a low anal spine count is so widely distributed among perciforms, its apomorphic nature within the centrarchids seems vague to the present author. My judgment on the character states of the acoustico-lateralis system (lachrymal with two anterior directed branches, two openings on post-temporal canal, infra-orbital canal not greatly interrupted, and five mandibular openings) common in *Lepomis* and *Micropterus* is that they are not synapomorphic states because they also occur in other centrarchid genera. According to the evidence from the gross kidney morpho logy, *Lepomis* and *Micropterus* are not sister group.

The autapomorphic character states of *Enneacanthus* (lachrymal with a single anteriorly directed branch, loss of dorsal spines and predorsal) and its plesiomorphic character state of the anal spine count (i. e., 3 anal spines) do not lead to a satisfactory conclusion with respect to its systematic position.

Lepomis humilis and *Elassoma* are controversial taxa. The former possesses many autapomorphic character states such as the absence of the extreme posterior kidney and the presence of a very large and slit-like lateral line pore (except in the lachrymal component); other species of *Lepomis* have rounded pores(3). Hubbs, in Ortenburger and Hubbs(9), erected a separate genus (*Allotis*) for this species. *L. humilis* seems more closely related to other

Lepomis species than to other centrarchids since it shares a derived character state with the members of *Lepomis* (extreme posterior kidney covered by a thick layer of tissue).

Jordan and Evermann(6) ranked the genus *Elassoma* as a separate family Elassomidae). Branson and Moore(3) echoed this classification. Avise, Straney and Smith(1) state, "Most workers feel that elassomids either diverged very early from primitive centrarchid stock or else have completely different affinities." As far as its kidney morphology is concerned, *Elassoma zonatum* possesses plesiomorphic kidney character states except the autapomorphic (elongate) urinary bladder. Although the systematic position of *Elassoma* cannot be resolved at the present time, its kidney character states lead me to agree with the general opinion of most ichthyologists(1) regarding this genus.

The hypotheses reached on the basis of my interpretations of the data of Eaton(4)(monophyly of *Archoplites*, *Pomoxis*, and *Centrarchus*) and those of Smith and Bailey(10) (monophyly of *Acantharchus*, *Ambloplites*, *Archoplites*, *Centrarchus*, and *Pomoxis*) as summarized in Figure 6 show some agreements with the phylogeny derived from kidney morphology (Fig. 5). If these hypotheses are valid, then (1) the fusion of the extreme anterior kidneys had appeared at the level of the hypothetical ancestor that would give rise to *Pomoxis*, *Centrarchus*, and *Archoplites*; (2) the occurrence of a similar character state in most *Lepomis* would be a result of 'convergence'; (3) the similarity of *Archoplites*, *Acantharchus*, and *Ambloplites* in the direct connection of the posterior and extreme posterior kidneys is a matter of 'parallelism.'

It seems clear that the disagreements in the hypotheses made by various workers are the outcomes of philosophical differences about the concept of phylogenetic relationships, namely, phenetic versus cladistic concepts. Agreement may never be reached as long as this separation of basic concepts exists.

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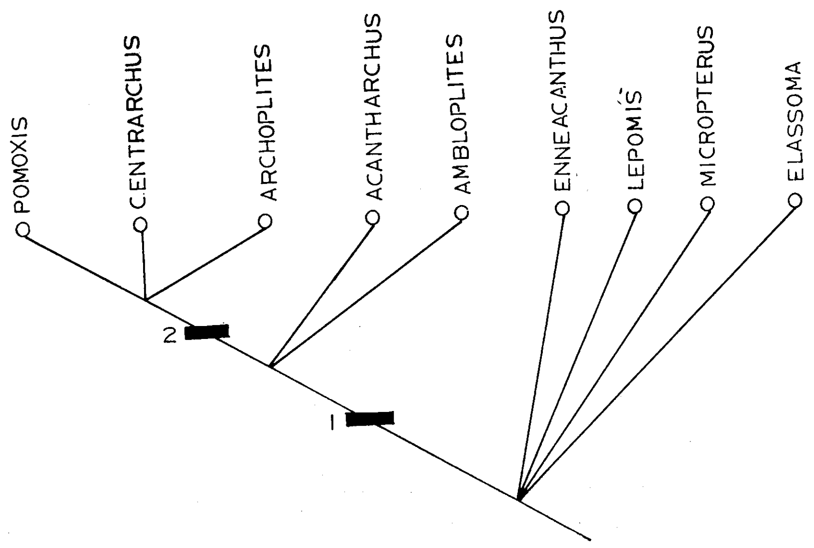

Fig. 6. A hypothesis of centrarchid phylogeny which is proposed on the basis of evidence from dorsal-fin supports, number of anal spines and olfactory organ morphology. (1) Possession of more than 3 anal spines. (2) Olfactory sac has paired folds, alternate ones are swollen.

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北美洲太陽魚類 (Centrarchidae) 腎型與親緣關係之探討

莫顯蕎

本研究比較23種北美洲淡水太陽魚類腎臟，以其形態變異來探討親緣關係上之可用性。太陽魚類並沒有獨特的腎臟形態。*Lepomis*, *Enneacanthus*, *Ambloplites*, *Acantharchus*, *Archoplites*, *Centrarchus*及*Pomoxis*之單源體系(Monophyly)關係是由於共同具有子孫形質之端腎(Extreme posterior kidney)而得之結論。*Centrarchus*和*Pomoxis*單源體系之理論是基於具有以下兩種子孫形質之共同(Synapomorphic character states)：(1)後腎(Posterior kidney)和端腎之結合，(2)左右後腎只在第一脈弧基部後方結合。*Lepomis*單源體系之證據是由於端腎上覆蓋一層很厚的組織。*Pomoxis*單源體系之證據是其端腎呈V狀形態。由於腎臟之各部份形態變異而引起證據間之衝突，可能是趨同(Convergence)和平行(Parallelism)進化之結果因本研究無法看出其祖先形質之共有(Symplesiomorphies)。根據腎臟形態之比較，作者提出一個有關太陽魚類各屬間親緣關係的假設，並和其他學者所提出的，作詳細的比較和討論。