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OSTEOLOGY OF THE SOUTHWESTERN DARTERS, *ETHEOSTOMA*
(*OLIGOCEPHALUS*) (TELEOSTEI, PERCIDAE)—WITH
COMPARISON TO OTHER NORTH AMERICAN PERCID FISHES

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ABSTRACT.—*Osteology of the southwestern darters, Etheostoma (Oligocephalus) (Teleostei, Percidae)—with comparison to other North American percid fishes.* *Occ. Pap. Mus. Zool. Univ. Michigan*, 733: 1-44, 18 figs. Darters are small, benthic fishes comprising an exclusively North American assemblage of the family Percidae. Although they form a large and important component of the North American fish fauna, there is but scant reference to their osteology in published literature. The osteology of a discrete group of species within the genus *Etheostoma*, subgenus *Oligocephalus*, from the southwestern United States and northern Mexico is provided here, with reference to other darter and percid taxa. Understanding of darter osteology can offer important insight into the systematics and phylogenetics of this group.

Key words: darters, osteology, *Etheostoma*, *Percina*, *Ammocrypta*, *Crystallaria*, Percidae.

INTRODUCTION

Darters form an exclusively North American assemblage of the teleostean family Percidae, corresponding to the subfamily Etheostomatinae of Song *et al.* (1998) and the tribe Etheostomatini (subfamily Percinae) of Collette (1963, and many others). More than 150 darter species are currently recognized, with new ones being identified and described at a steady rate (*e.g.*, Bailey and Etnier, 1988; Wood and Mayden, 1993; Norris and Minckley, 1997). Naturalists and ichthyologists have long been fascinated by these small, often colorful fishes, and a vast and growing literature exists on many aspects of their biology. Such information—taxonomy, systematics, ecology, natural history, behavior, conservation, biogeography, phylogenetics—has been gathered and

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summarized in works such as Collette (1967), Page (1983), Kuehne and Barbour (1983), Etnier and Starnes (1993), Wood and Mayden (1997), Song *et al.* (1998).

Darters exhibit extensive morphological variation and phylogenetic complexity across these 150+ species. Classification of this diversity into superspecific taxa has varied considerably over the years, tracking both increasing understanding of the North American ichthyofauna and the dictates of successive systematic or evolutionary schools of thought. Jordan and Evermann (1896), for example, recognized 15 darter genera, with Jordan *et al.*, 1930 recognizing 31. In recent decades, following Bailey *et al.* (1954), this diversity has been compressed into three genera: *Ammocrypta* Jordan, *Etheostoma* Rafinesque, and *Percina* Haldeman. *Etheostoma* and *Percina* are each subdivided into numerous subgenera, many of which are the full genera of earlier workers (*e.g.*, Jordan and Evermann, 1896; Bailey, 1941, 1948), and *Ammocrypta* has been defined to encompass darters which share elongate, transparent bodies (*Crystallaria asprella* Jordan and *Ammocrypta* spp.). Although this trigeneric classification has been useful in bringing order and stability to darter taxonomy, it has not been supported by recent phylogenetic evaluations. Simons (1991) presented morphological evidence indicating that *Ammocrypta* so defined is paraphyletic, unless the monotypic *Crystallaria* Jordan and Gilbert is removed. He placed *Crystallaria* basal to other darters and included *Ammocrypta* as a subgenus of *Etheostoma*. In phylogenetic reconstructions based on various molecular data sets, Wood and Mayden (1997) and Song *et al.* (1998) concurred with the basal position of *Crystallaria*, although did not find support for inclusion of *Ammocrypta* within *Etheostoma*, placing it rather as sister to *Crystallaria*, although highly divergent from it (also R. M. Bailey, pers. comm.). These latter interpretations echo earlier (non-cladistic) opinions of Moore (1968) and Miller and Robison (1973).

No matter how darters are classified, the basic species compositions of most of the superspecific taxa are relatively well-established. Notwithstanding, some of these groupings exist more as units of taxonomic convenience; in other words they may be paraphyletic assemblages of similar forms rather than as rigorously defined, monophyletic taxa (*e.g.*, *Ammocrypta*, *sensu lato*). Broad clarification (or at least agreement) on darter taxonomy or relationships in a phylogenetic context has not yet been achieved.

With regard to darter systematics and phylogenetics, investigators have moved from alpha and beta taxonomy using phenotypic characters (external morphology, meristics, pigmentation, behavior; *e.g.*, Collette, 1962) directly to phylogenetic reconstruction using molecular data (*e.g.*, Wood, 1996). Comparative osteology, once an important tool for

exploring many areas of a taxon's biology (e.g., Liem, 1980; Liem and Greenwood, 1981; Motta, 1984), has rarely been employed. Jordan and Eigenmann (1885) appear to have provided the earliest discussion of darter osteology with brief word-sketches of 20 darter skulls. Bailey and Gosline (1955) found systematic information in patterns of vertebral counts and structure. Wiley (1992) and Simons (1991, 1992) used limited osteological traits in percid and etheostomatine phylogenetic reconstructions, while Norris and Minckley (1997) found osteological characters useful in defining species and species groups within subgenus *Oligocephalus*. However, this study (and work yet-to-be published by others) suggests that darter osteology will be useful in teasing apart superspecific relationships, as well as providing hard characters with which the various taxa can be better identified, diagnosed, and defined. Beyond this, phylogenetic relationships hypothesized from molecular data can be tested and evaluated against those based on morphology. Finally, osteology can be integrated directly with paleontological data, providing for a more rigorous and complete evaluation of evolutionary patterns within the Percidae and beyond. As Greenwood (1992) argued, the most fruitful approach to the study of evolutionary or systematic problems in fishes is a multifaceted one, and not one confined to a restricted set of characters or driven mainly by particular methodologies and techniques.

Osteology of a group of southwestern darters is detailed herein. This assemblage, within the subgenus *Oligocephalus* and initially delineated by Norris and Minckley (1997), consists of *E. grahami* (Girard, 1859), *E. lugoii* Norris and Minckley, 1997, *E. segrex* Norris and Minckley, 1997 *E. pottsi* (Girard, 1859), *E. australe* (Jordan, 1889), and *E. lepidum* (Baird and Girard, 1853). These, in addition to some populations of undetermined taxonomic status (mostly from Mexico) form a cohesive assemblage of species (SMN, work in progress). Members of the group share distinctive characters, although none has yet been established as synapomorphic. Compared to other species presently assigned to *Oligocephalus*, interrelationships of the southwestern darters are suggested by: small body size (generally less than 50 mm SL), loss or substantial reduction of the basisphenoid, and a distinctive bony spur on the posterolateral face of the hyomandibula. Further, all have important geographic and ecological linkages in that they are confined to arid and semi-arid lands in the Rio Grande basin (Río Bravo del Norte in Mexico) and other drainages historically associated with that vast, now-disrupted watershed (e.g., ríos Nazas, Aguanaval, and uppermost Mesquital) (Smith and Miller, 1986). Beyond this region, *E. ditrema* Ramsey and Suttkus, and *E. nuchale* Howell and Caldwell appear to be their closest relatives (K. Shaw, pers. comm.).

MATERIALS AND METHODS

Osteological observations were made on cleared-and-stained specimens, prepared following the techniques of Taylor and Van Dyke (1985) with steps for alcian-blue staining of cartilage sometimes omitted. Dissections and osteological drawings were made through camera lucida-equipped Wild/Leica M-3Z and M-8 dissecting microscopes. Whenever possible multiple specimens of each taxon were evaluated (usually representing both genders, including juveniles and adults), although usually only a single specimen was fully dissected and its elements drawn. Original pencil sketches were inked, then digitized, processed and labeled with Adobe Photoshop (version 4, Adobe System, Inc.) and Corel Presentations (version 8, Corel Corporation) software. With regard to osteological nomenclature, I have attempted to utilize the terms and names commonly employed in the literature of fish systematics and phylogenetics (*e.g.*, Gregory, 1933; Harrington, 1955; Liem, 1963; Jollie, 1986); such usage does not always conform to that of works of a more developmental nature (*e.g.*, Shultze, 1993). Most elements of the cranial and appendicular skeletons are bilaterally paired; however, for clarity accounts below describe one side. Institutional abbreviations follow Leviton *et al.* (1985). In figures all scale bars are approximately 1 mm, and in figure legends “m” = male and “f” = female (in some instances gender of specimens was not known).

In osteological sections below, the main description applies directly to southwestern darters. Except where noted, these descriptions are also largely congruent with other species of *Etheostoma* examined. Of the southwestern darters, specimens of *E. lugoi*, *E. segrex*, *E. grahami*, *E. lepidum*, and *E. australe* were examined in detail. Available skeletal preparations for *E. pottsi* were unfortunately substandard, not allowing full evaluation. Osteological features in darters manifest complex patterns of interspecific variation, as well as sometimes substantial intraspecific variation (SMN, unpubl.; K. Shaw, pers. comm). In order to become familiar with basic percid morphology, the osteologies of several non-southwestern darters, as well as *Perca* Linnaeus, *Stizostedion* Rafinesque and *Gymnocephalus* Bloch were evaluated (see Materials Examined). As appropriate, significant departures from the basic pattern observed in southwestern darters are noted for these other percid taxa.

Below, darter osteology is sketched in broad strokes, at this level of detail, North American percids can be grouped into four fundamental types based on skeletal features: *Etheostoma* + *Ammocrypta*; *Percina*; *Crystallaria*; and *Perca* + *Stizostedion* (see Comparisons and Conclusions). The descriptions below are divided accordingly. Among the taxa

examined, the cranial osteology of *Ammocrypta* proved to be very similar to that of *Etheostoma*. However, given the disagreement regarding the placement of *Ammocrypta* (see above), substantial differences between it and *Etheostoma* are noted as appropriate. I do not presume to have evaluated in detail a phylogenetically meaningful cross-section of percid taxa, especially in regard to defining relationships and groupings within *Etheostoma* and *Percina*. Thus, phylogenetic inferences are avoided, but it is hoped, however, that this work will provide a foundation and stimulus for further discussion and contributions in this area.

Finally, most of this report involves the osteocranium, an intricate, three-dimensional construction, the complexity of which is difficult to convey adequately with words and two-dimensional drawings (Harrington, 1955 provided an admirable model).

DESCRIPTIVE OSTEOLOGY

Osteocranium

Olfactory Region. This region (Figs. 1-6), at the anterior end of the cranium, is dominated by the ethmoid complex. It supports the jaws and olfactory organs, frames the anterior margin of the orbit and forms the anterior myodome. Together, the paired lateral ethmoids (Figs. 1-6) delineate much of the anterior border of the orbit. Each lateral ethmoid is flat, roughly square and vertically-oriented; it is loosely articulated with and suspended from near the rostral tip of the frontal. A single foramen for the olfactory nerve (I) pierces the lateral ethmoid near its dorsomedial edge (this feature is not visible in the figures provided). Its ventromedial border is flared, projecting as an extension anteriorly towards a similar (posterior) flaring from the vomer (*e.g.*, Figs. 4a, 5d). The preorbital process of the lateral ethmoid (a lateral protrusion along the ventral border) (*e.g.*, Figs 3b, 6 c-d) forms the point of attachment for the lachrymal (infraorbital 1). In some larger darters (*e.g.*, *Percina caprodes*, fig. 6c and more prominently *Crystallaria*, fig. 6d) an additional articulation surface along the ventral border of the lateral ethmoid was observed (labeled "a" on Figs. 4 and 6). In intact specimens, this more medial articulation surface is loosely articulated to the dorsal surface of the autopalatine-palatine. In *Percina*, *Crystallaria*, *Perca*, and *Stizostedion* the lateral ethmoid is more substantial in construction and generally more firmly articulated with adjacent elements (frontal, mesethmoid, vomer) than in southwestern darters and other *Etheostoma*.

The mesethmoid (Figs. 1-4), a thin, saddle-shaped sheet of bone, concavity facing ventrad, that covers the anterodorsal surface of the

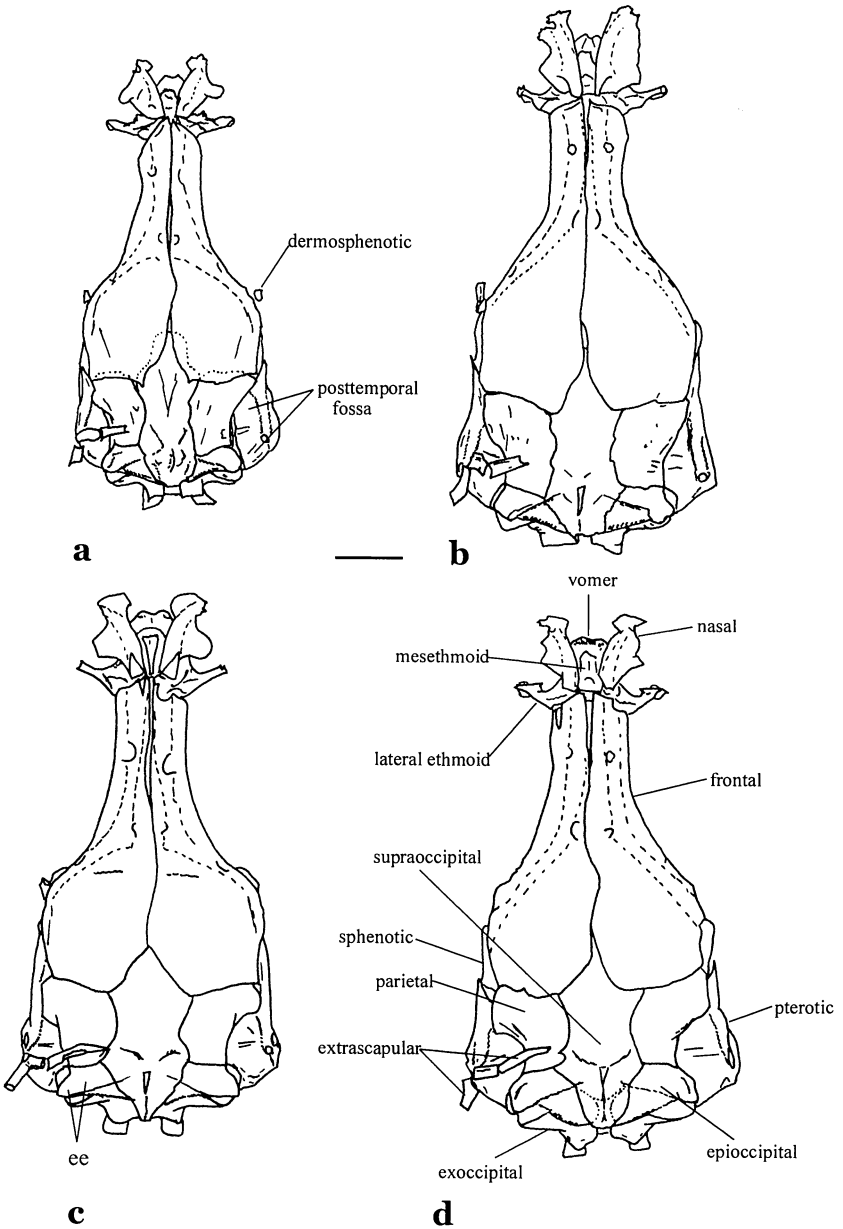


Fig. 1. Dorsal view of cranium of: **a**, *Etheostoma lugoi* (ASU 5995, 28.9 mm SL, m); **b**, *E. segrex* (ASU 5985, 37.2 mm SL, m); **c**, *E. grahami* (ASU 1021, 36.5 mm SL, f); **d**, *E. lepidum* (ASU 1756, 38 mm SL, f).

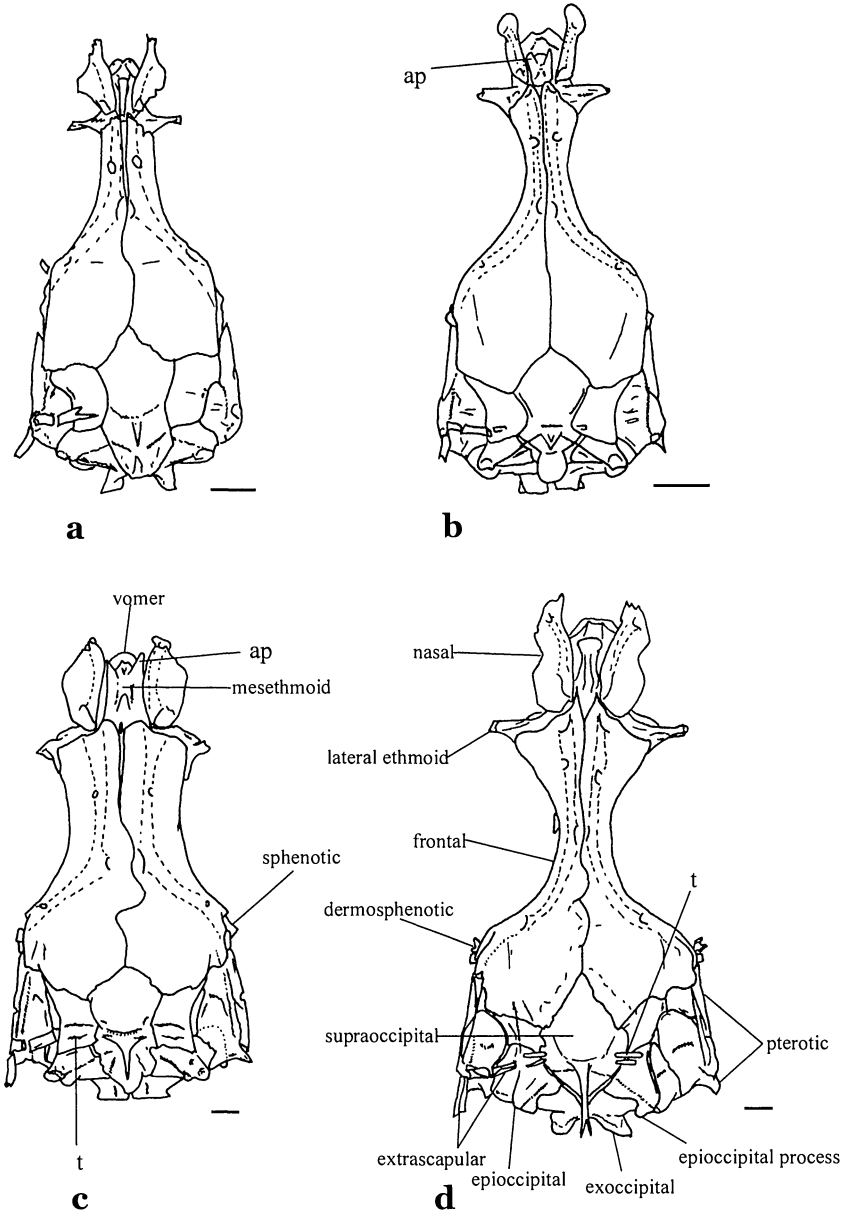


Fig. 2. Dorsal view of cranium of: **a**, *Etheostoma caeruleum* (ASU 222, 49 mm SL, f); **b**, *Ammocrypta meridiana* (UAIC 6794.20, 50 mm SL); **c**, *Percina caprodes* (ASU 2665, 85 mm SL, m?); **d**, *Crystallaria asprella* (UAIC 2705.01, ca. 120 mm SL).

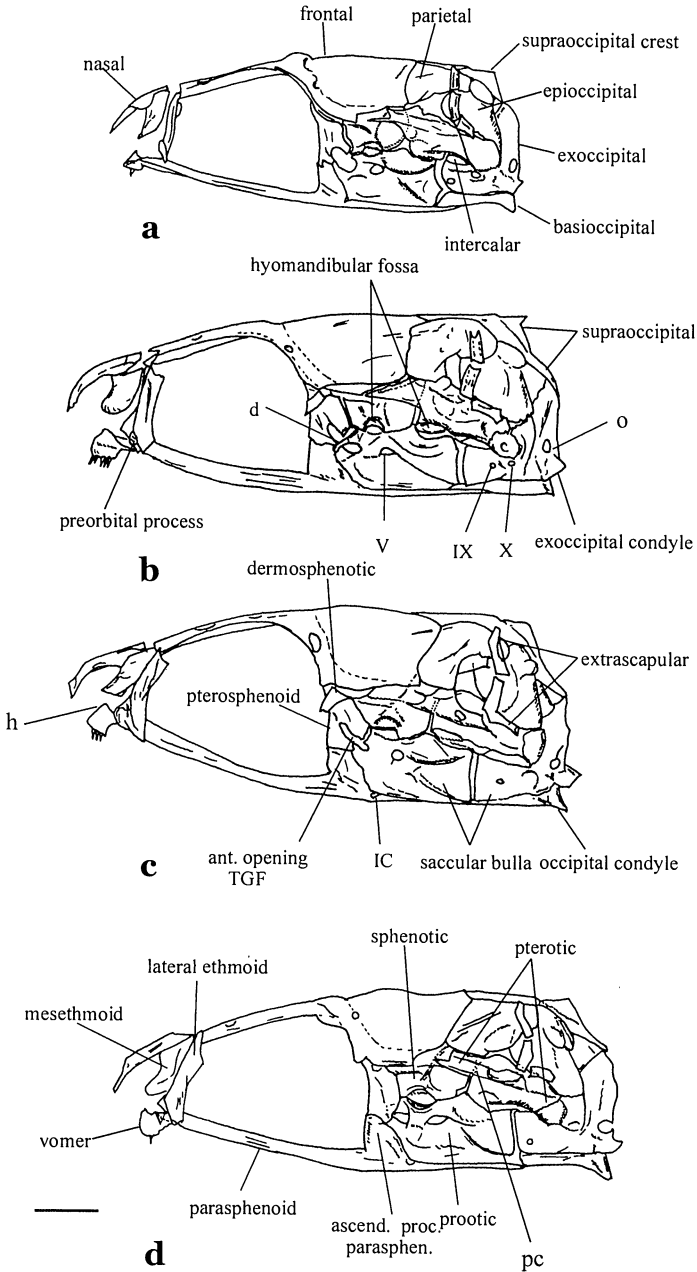


Fig. 3. Lateral view of cranium of: **a**, *Etheostoma tugoi*; **b**, *E. segregis*; **c**, *E. grahami*; **d**, *E. lepidum*. Same specimens as portrayed in Fig. 1.

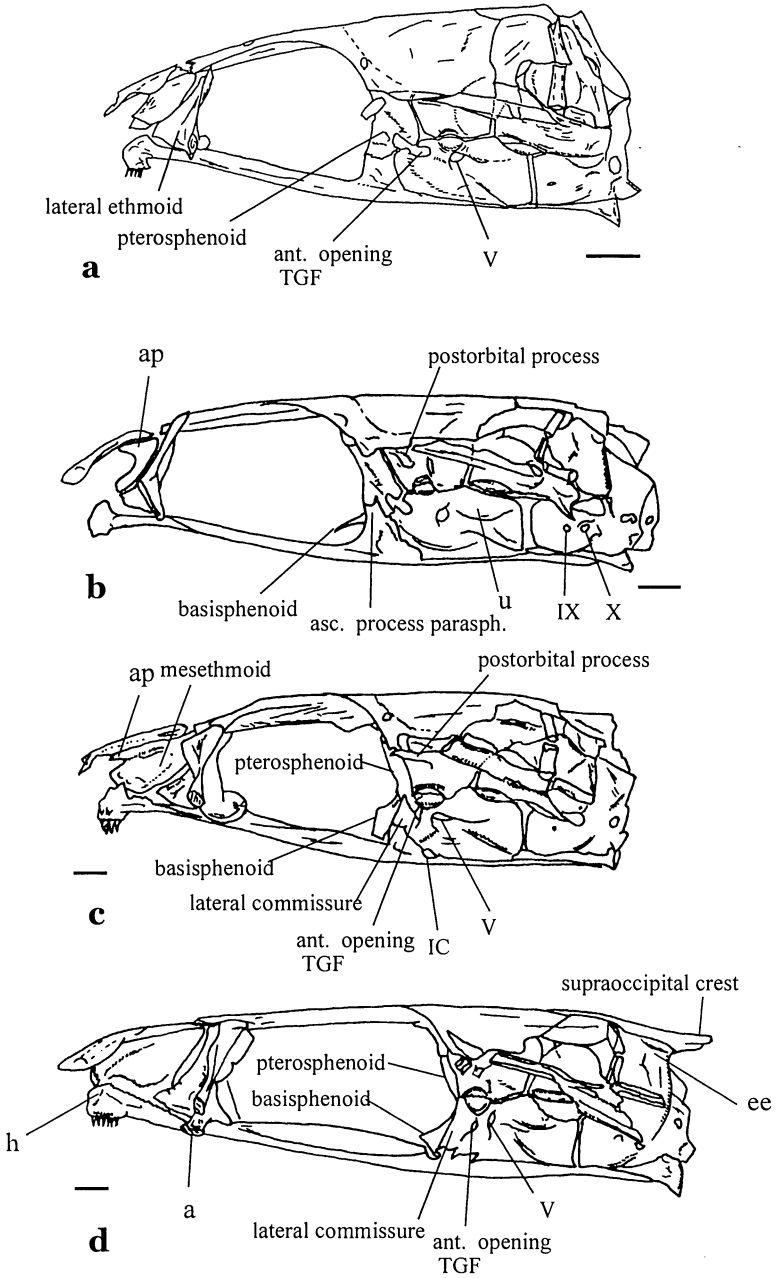


Fig. 4. Lateral view of cranium of: **a**, *Etheostoma caeruleum*; **b**, *Ammocrypta meridiana*; **c**, *Percina caprodes*; **d**, *Crystallaria asprella*. Same specimens as portrayed in Fig. 2.

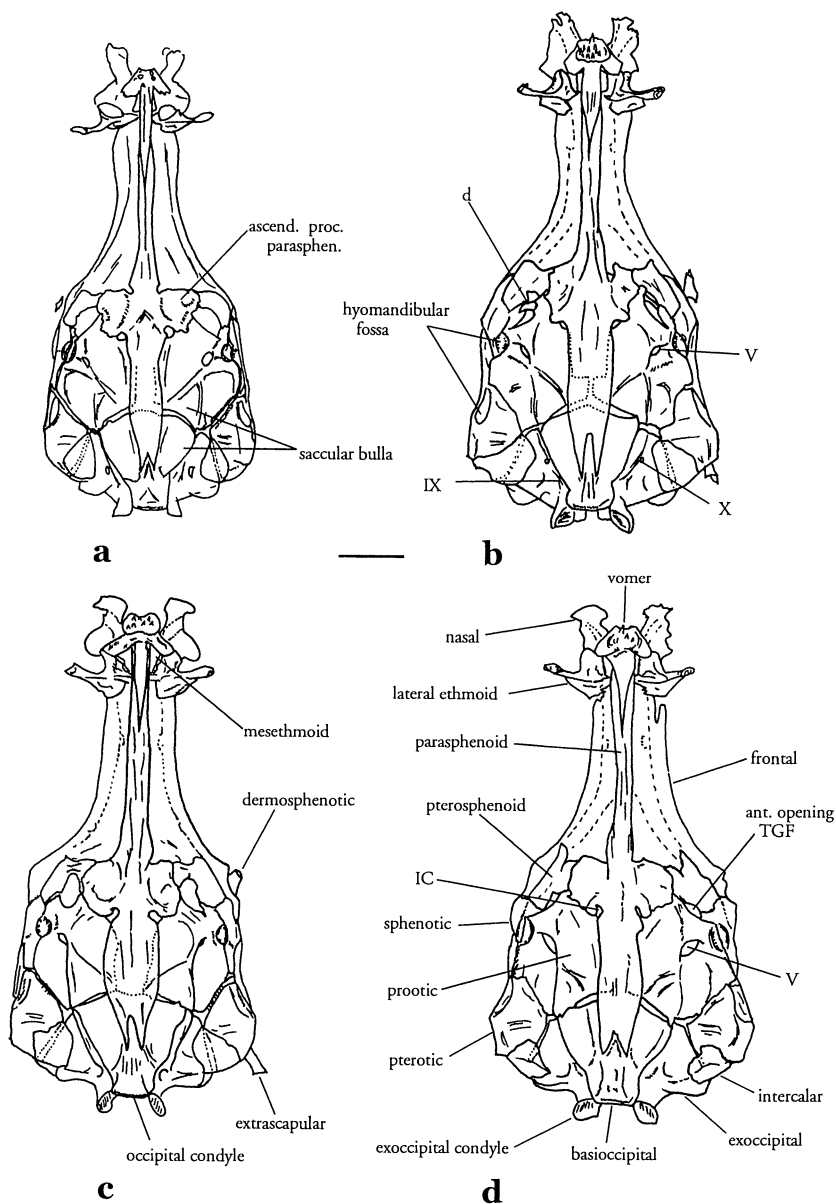


Fig. 5. Ventral view of cranium of: **a**, *Etheostoma lugoi*; **b**, *E. segrex*; **c**, *E. grahami*; **d**, *E. lepidum*. Same specimens as portrayed in Fig. 1.

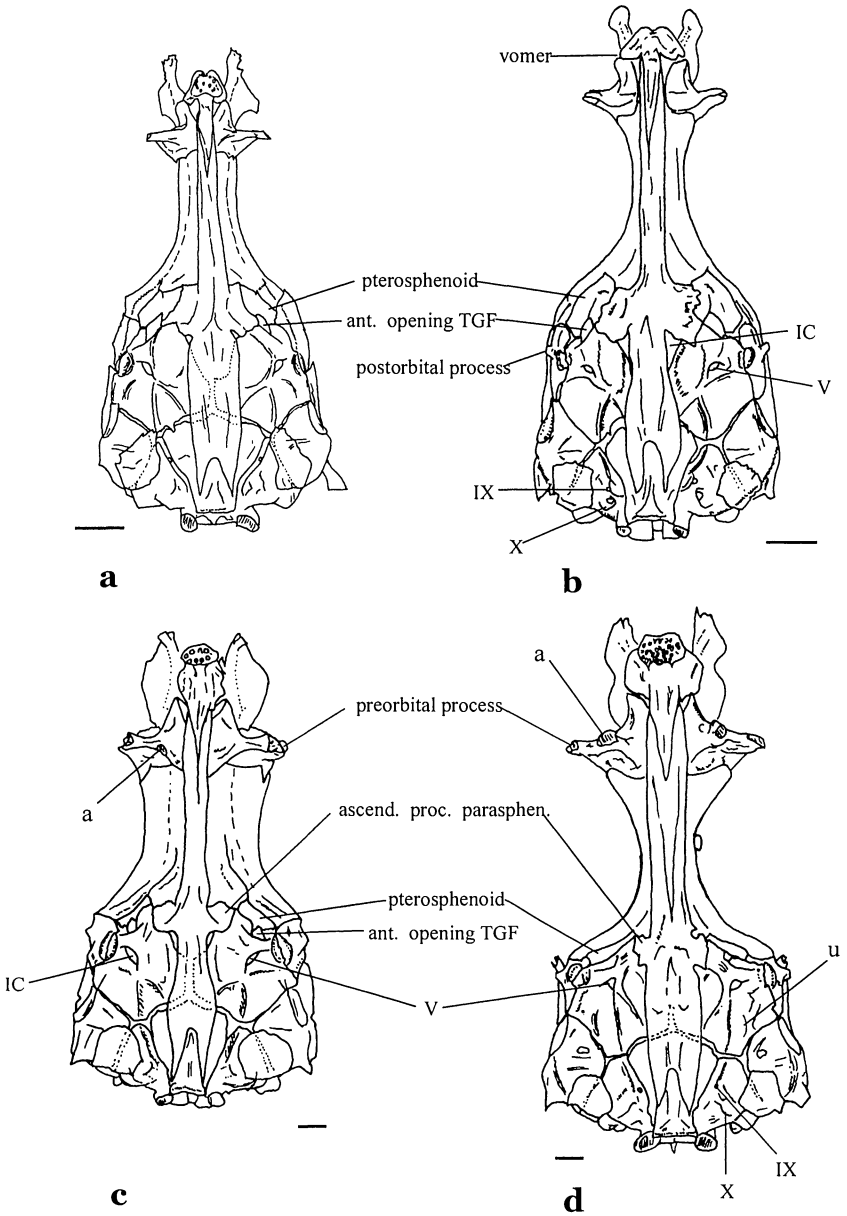


Fig. 6. Ventral view of cranium of: **a**, *Etheostoma caeruleum*; **b**, *Ammocrypta meridiana*; **c**, *Percina caprodes*; **d**, *Crystallaria asprella*. Same specimens as portrayed in Fig. 2.

ethmoid cartilage; the latter filling the central space between the mesethmoid, vomer, and lateral ethmoids. The mesethmoid has a slight angular dorsal expansion, and does not articulate directly with other bones. In some non-southwestern darters and other percids examined, the mesethmoid is more substantial with a larger dorsal expansion (with two dorsoanterior projections in *Percina* and *Ammocrypta*, labeled “ap” in Figs. 2c-d, 4c-d). In *Percina*, *Crystallaria*, *Perca*, and *Stizostedion*, this bone is directly articulated with the vomer, and lateral ethmoids. The mesethmoid, of significant functional importance, exhibits complex variation within some other percomorph groups (*e.g.*, Anabantoidae, Nandidae, Badidae; Norris, 1995, unpubl. data); its further study in darters is warranted.

The vomer (Figs. 3-6), a median, unpaired dermal ossification, forms the anterior roof of the buccal cavity. It is firmly attached via its long, spiked parasphenoid process into a slot on the ventral surface of the anterior end of the parasphenoid. Fine teeth cover the oral surface of the vomer’s ovoid or roughly triangular head (it is toothless in the *Ammocrypta* examined; Fig. 6b). A thin hood-like extension of bone projects dorsad from the anterior end of the vomer into the ethmoid cartilage and towards the mesethmoid (fusing to the mesethmoid in *Perca*, *Stizostedion*, *Percina*, and *Crystallaria*; *e.g.*, Figs. 3c, 4d, labeled “h”). Lateral projections from either side of the head of the vomer, originating just posterior to the toothed area, extend posteriad towards anterior projections of the lateral ethmoids, articulating with them in larger species.

Orbital Region. This region (Figs. 1-9), dominated by the eyes and their supporting elements, spans the distance between the olfactory region and brain case. Along the posterior border of the orbit, the pterosphenoid (Figs. 3-9) is suspended vertically from the frontal, its lateral face roughly parallel to the lateral border of the frontal. In *Etheostoma* (Figs. 3, 4a-b, 5, 6a-b, 7a), the pterosphenoid is a simple, flat or curved bone extending anteriad from the margin formed by the anterior borders of the prootic and sphenotic; it is roughly in the same plane as the latter two, framing the hypophyseal foramen but not greatly constricting it (*i.e.*, the pterosphenoid does not project sharply medially behind the orbit). Along the junction of the pterosphenoid and prootic is the large anterior opening of the trigemino-facialis (TGF) chamber (*e.g.*, Figs. 3c, 5d, 7-8), which incises deeply into both bones. Ventrad to this opening, the pterosphenoid has broad articulation with the ascending process of the parasphenoid (*e.g.*, Figs. 7c, 8c, 9c).

This arrangement is substantially different from that of other percid (and percoid) taxa. In *Percina caprodes* (Figs. 4c, 6c, 9b), the ventromedial corner of the prootic carries a narrow medial extension (a limited orbital

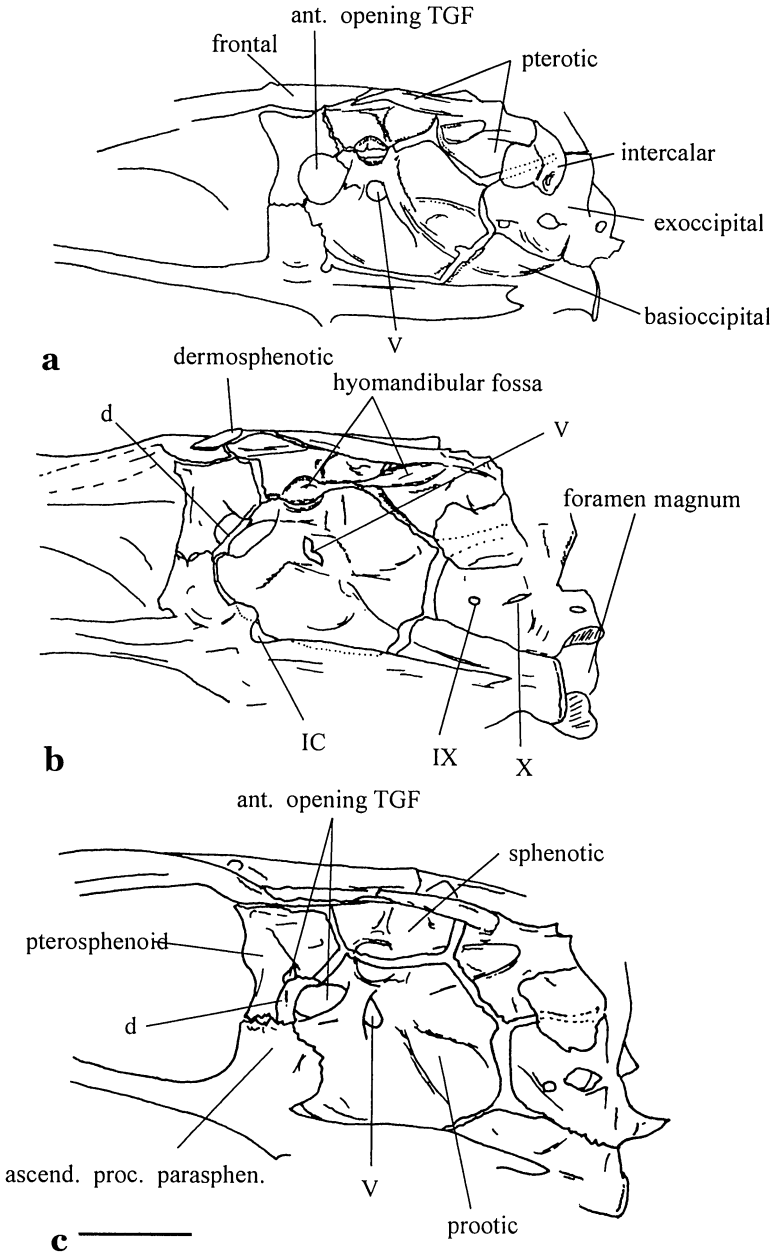


Fig. 7. Oblique ventral view of cranium of: **a**, *Etheostoma lugoi* (ASU 5995, 28.9 mm SL, m); **b**, *E. segrex* (ASU 5985, 37.2 mm SL, m); **c**, *E. australe* (UMMZ 182378 c&s, 44.7 mm SL).

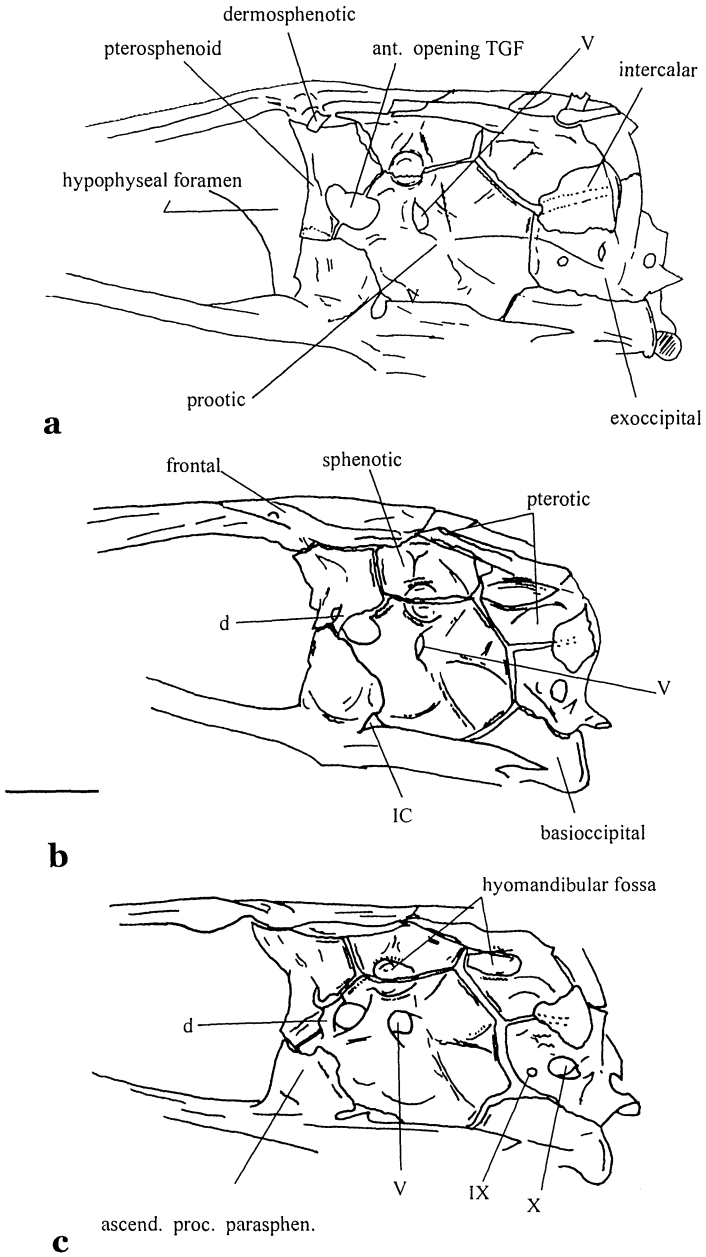


Fig. 8. Oblique ventral view of cranium of: **a**, *Etheostoma grahami* (ASU 1021, 36.5 mm SL, f); **b**, *E. grahami* (ASU 10899, 35 mm SL, m); **c**, *E. lepidum* (ASU 1756, 38 mm SL, f).

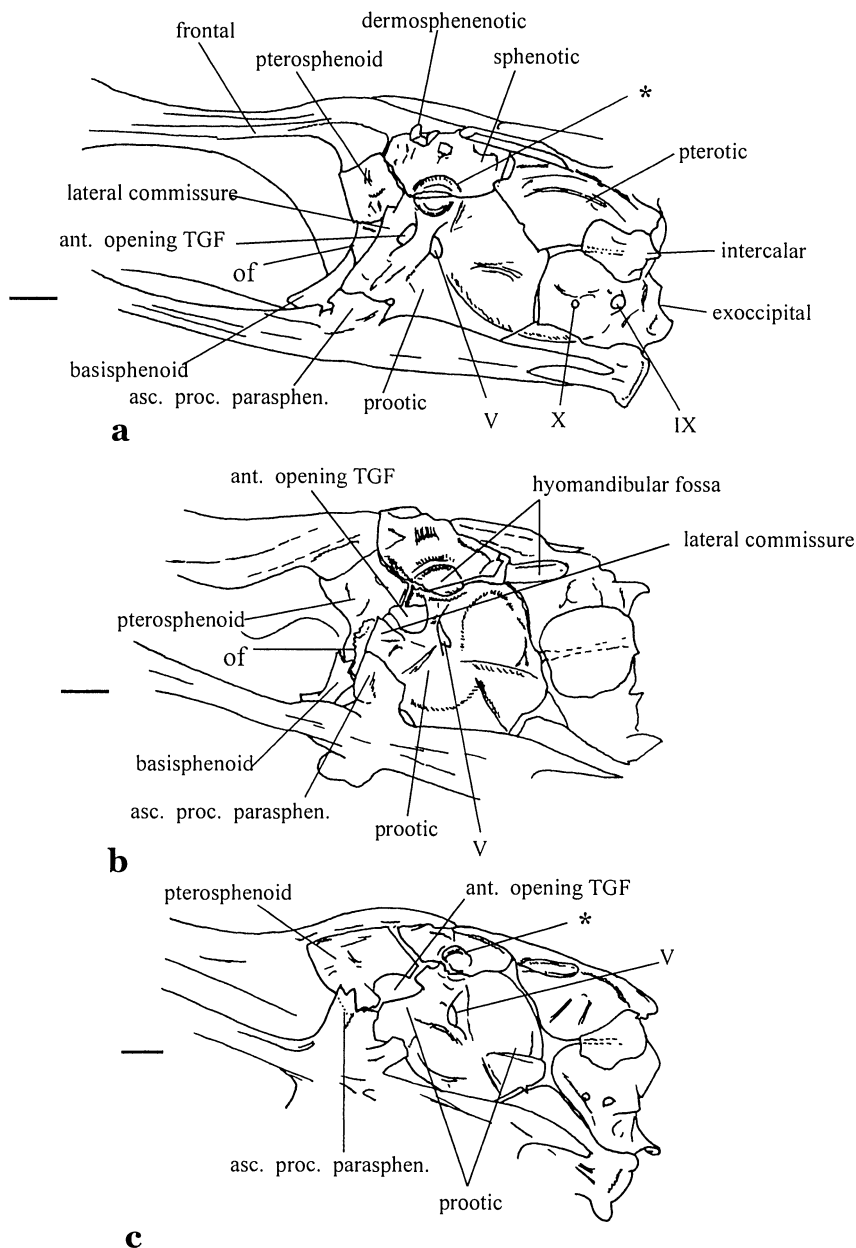


Fig. 9. Oblique ventral view of cranium of: **a**, *Crystallaria asprella* (UAIC 2705.01, ca. 120 mm SL); **b**, *Percina caprodes* (ASU 2665, 85 mm SL, m?); **c**, *Ammocrypta meridiana* (UAIC 6794.20, 50 mm SL).

face, or base of lateral commissure described below, labeled “of” on Fig. 9 a-b) which articulates with the pterosphenoid, and the pterosphenoid takes a more internal and dorsal position than in *Etheostoma*. However, in *P. maculata* (not illustrated), the pterosphenoid does articulate with the parasphenoid. In other percids (e.g., *Crystallaria*, Fig. 9a, and many other percomorphs), the pterosphenoid has an even more dorsal and internal position, extending medially from the internal base of a well-developed lateral commissure, along the anterior margin of the prootic (see below). Thus, in taxa other than *Etheostoma* and *Ammocrypta*, the pterosphenoid projects obliquely with regard to the lateral wall of the braincase behind the orbit, constricting the hypophyseal foramen. In percid taxa other than *Etheostoma* and *Ammocrypta* examined the anterior opening of the TGF chamber is partially (*Percina*, Figs. 4c, 6c, 9b) or entirely (others) excluded from the pterosphenoid (see also description of prootic below). Further, in *Crystallaria* (Fig. 4d, 6d, 9a), *Perca*, and *Stizostedion* the pterosphenoid is so far removed from the ventral aspect of the cranium that it has no articulation with parasphenoid. In *Percina* there is ventral extension of the pterosphenoid, but it articulates with the basisphenoid (*P. caprodes*, Fig. 9b) or the basisphenoid and parasphenoid (*P. maculata*, not illustrated).

The unpaired basisphenoid is absent or at best very poorly developed in southwestern darters. It was not observed in *E. grahami*, *E. lepidum*, *E. lugoi* or *E. australe*, and could not be resolved in available specimens of *E. pottsi*. In *E. segrex*, paired, fine, rod-like ossifications (presumably representing dorsal limbs of the basisphenoid) were on medial surfaces of the prootics. In other percids (and many perciforms) the basisphenoid is generally a sturdy, Y-shaped bone, with a single ventral pedicel and two dorsolateral limbs. It forms the ventral border of the hypophyseal foramen, its two dorsal limbs straddling the opening. Surrounding the pedicel is the opening of the posterior myodome. In all darters in which a complete basisphenoid was observed it was comprised of three ossifications, one each for the dorsal limbs, with a Y-shaped element ventrad. In adults the three are fused but the separate components are often still discernable.

Occurrence of the basisphenoid is spotty in other *Etheostoma* examined (and throughout the darters, K. Shaw, pers. comm.): absent from *E. fonticola*, *E. radiosum*, and *E. rufilineatum*; present in *E. nigrum*, *E. spectabile*, *E. exile*, *E. caeruleum*, *Ammocrypta meridiana* (Fig. 4b), and *A. beani*. When present in *Etheostoma* (not illustrated), its dorsal arms are braced against the inner faces of the anteroventral corners of the prootics. It is well-formed in *Percina* (Figs. 4c, 9b), in which each dorsal arm is braced against a flange on the inner face of the prootic and against a thin ventral

extension of the pterosphenoid. It is also well-formed in *Crystallaria* (Figs. 4d, 9a), *Perca*, and *Stizostedion*, in which each dorsal arm articulates with the internal flange of the prootic, but not with the pterosphenoid. This latter arrangement is the more typical percoid condition.

The infraorbital canal (Fig. 10) in southwestern darters is incomplete and ossified only at its anterior (lachrymal) and posterior (dermosphenotic, third and fourth infraorbital) ends. The triangular or elongate lachrymal, bearing four pore openings of the cephalic lateralis, is well ossified and anchored to the preorbital process of the lateral ethmoid. At the posterodorsal border of the orbit the canal passes through two or three fine and incompletely ossified third and fourth infraorbital bones (U-shaped in cross-section), and the dermosphenotic (the dorsal-most infraorbital). The latter is loosely attached to the osteocranium (frontal); the former ossified only in adults. A similar arrangement is also found in the diminutive *E. fonticola*, and other species of *Oligocephalus* examined (e.g., Fig. 10b). In *E. rufilineatum* and *Ammocrypta* (Fig. 10c) the series is complete (lachrymal, 3 or 4 infraorbitals, dermosphenotic), but sometimes (excepting the lachrymal) lightly ossified, with the infraorbitals and dermosphenotic not completely enclosing the infraorbital canal. The canal is complete and well ossified in *Percina* (Fig. 10d), *Crystallaria* (Fig. 10e), *Perca*, and *Stizostedion*.

Otic Region. This region comprises the major part of the cranium (Figs. 1-9, 11). It houses the brain, hearing, and equilibrium organs, and supports other functional units such as the suspensoria, pectoral girdles, and branchial skeleton.

The sphenotic (Figs. 1-9, e.g., Figs. 1d, 3d, 5d) is positioned laterally at the anterior end of the otic region. It is bounded by the pterosphenoid (anteriad), frontal (dorsad), pterotic (posteriad), and prootic (mediad), and overlain dorsolaterally by an anterior projection from the pterotic. The anterior half of the hyomandibular fossa (e.g., Figs. 3b, 7b) (a feature of the sphenotic, prootic, and pterotic from which the hyomandibula is suspended) is a round socket, the lateral half of which is carried by the sphenotic at its anteromedial corner (the medial half is carried by the prootic). The postorbital process (a lateral projection from the lateral face of the sphenotic) was not observed in *Etheostoma* or *Crystallaria*; a thin blade-like postorbital process is present in *Percina* and *Ammocrypta* (Figs. 4b-c; 6b-c), and a more prominent one in *Perca* and *Stizostedion* (not illustrated).

The prootic forms a major portion of the ventromedial osteocranium (Figs. 3-9, e.g., Figs. 3d, 5d, 7c). Anteriad it articulates with the pterosphenoid and parasphenoid, laterad with the sphenotic and pterotic, posteriad with the pterotic, basioccipital, and intercalar. The medial

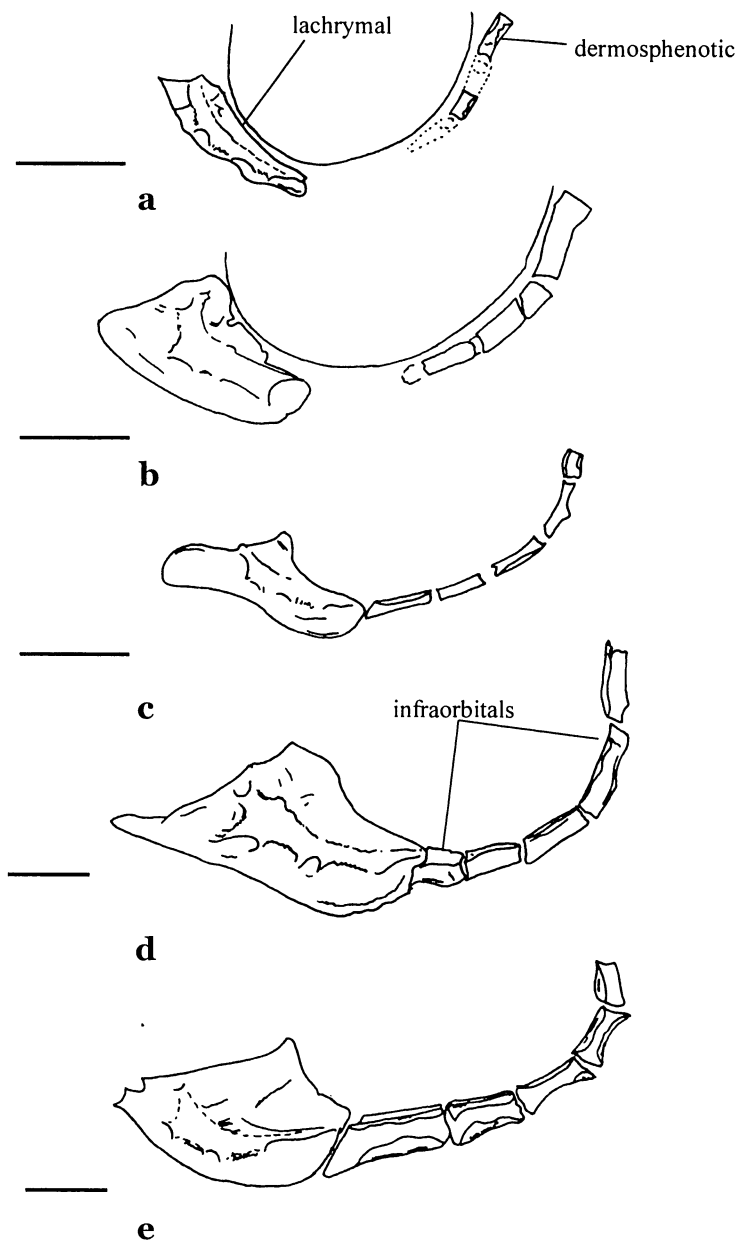


Fig. 10. Infraorbital series of: **a**, *Etheostoma lepidum* (ASU 1756, 38 mm SL, f); **b**, *E. spectabile* (ASU 2138, 45 mm SL, m); **c**, *Ammocrypta meridiana* (UAIC 6794.20, 50 mm SL); **d**, *Percina caprodes* (ASU 2665, 85 mm SL, m?); **e**, *Crystallaria asprella* (UAIC 3096, ca. 70 mm SL).

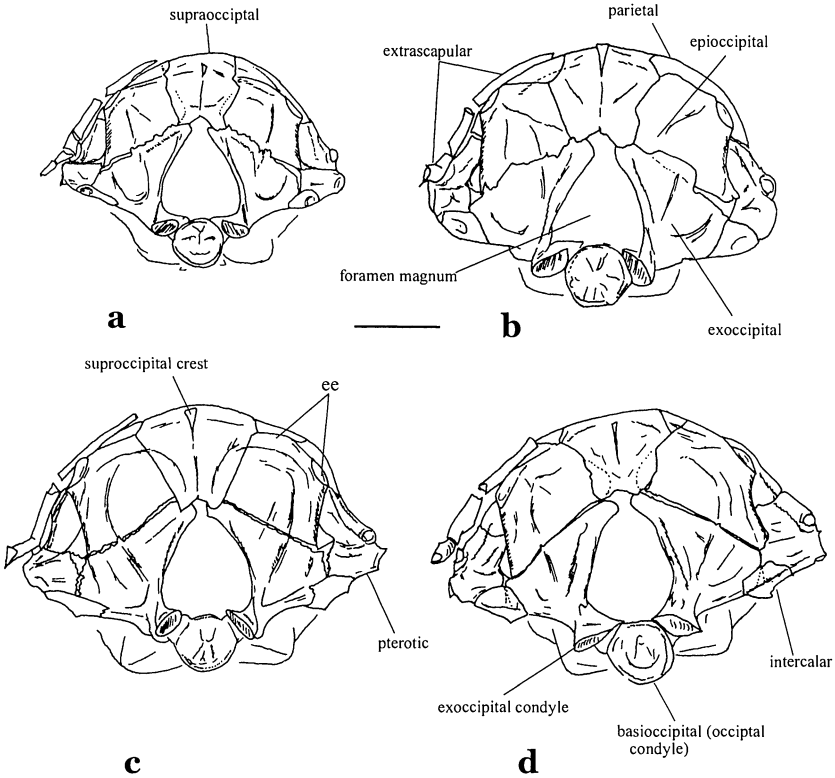


Fig. 11. Posterior face of cranium of: **a**, *Etheostoma lugoi*; **b**, *E. segrex*; **c**, *E. grahami*; **d**, *E. lepidum*. Same specimens as portrayed in Fig. 1.

margin of each prootic approaches that of the other along the ventromesial axis of the neurocranium, which is completely covered by the parasphenoid (Figs. 5-6). The anterior half of the saccular bulla (*e.g.*, Fig. 3c) occurs posteromedially on the prootic; the smaller utricular swelling is dorsolaterad (*e.g.*, Figs. 4b, 6d). Along its lateral articulation with the sphenotic, the prootic bears the anterior half of hyomandibular articulation socket (of the hyomandibular fossa) (*e.g.*, Figs. 3b, 7b). The prootic makes only a slight contribution of the anterior socket of the hyomandibular fossa in *Ammocrypta* compared to other percids examined (compare Fig. 9a and 9c, socket indicated with an asterisk).

The functional division between orbital and branchial regions of the cranium can be defined as running along the anterior border of the otic region. In many percomorphs, this division is marked by a distinct feature known as the lateral commissure, a bony ridge from the sphenotic across

the prootic to the latter's articulation with the ascending process of the parasphenoid (similar to the pattern seen in *Crystallaria* [Fig. 9a], and found in *Perca* and *Stizostedion* [not illustrated]); the pterosphenoid articulates with the inner (medial) base of the lateral commissure (its orbital face), projecting obliquely, constricting the hypophyseal foramen. In *Etheostoma* the orbital face of the prootic is absent (compare Figs. 8a and 9a), and (as noted above) the pterosphenoid projects directly anteriorly off its anterior margin, thus taking a more lateral position than in the more typical percoid pattern (Fig. 7, 8, 9c). In *Percina caprodes*, at least ventrally the prootic does bear a small orbital face (Fig. 9b, labeled "of"). In *P. maculata* (not illustrated) the orbital face is not developed, and the pterosphenoid takes a somewhat lateral orientation, making the arrangement similar to that in *Etheostoma*. In *Perca*, *Stizostedion*, and *Crystallaria* (Fig. 6d, 9a) the prootic bears a well-formed orbital face. In these genera, the pterosphenoid takes a more interior position, based on this orbital face and extending medially constricting the hypophyseal foramen.

The trigemino-facialis chamber underlies the lateral commissure forming a passage from the branchial chamber to the orbit. A number of neural and circulatory elements traverse the lateral commissure via the TGF chamber, or exit/enter the cranial interior via its medial wall. In *Etheostoma* the anterior opening to the TGF chamber is a large ovoid foramen at the prootic-pterosphenoid junction, as noted above, incising deeply into both bones (e.g., Figs. 3, 5, 7, 9c). The posterior opening (labeled "V," e.g., Figs. 3b, 5d, 7c) (through which passes the hyomandibular branch of the facial nerve [V]) is smaller and recessed, placed ventrad to the hyomandibular articulation socket. In *E. segrex*, *E. lepidum*, *E. australe*, and *E. grahami*, the anterior opening is, at least sometimes, bisected by a fine splint of bone (labeled "d" on Figs. 3, 5, 7, 8). This splint is variable in appearance and form, sometimes differing bilaterally on the same specimen. In *E. australe* it is less developed in smaller specimens, and in *E. grahami* and *E. segrex* it is present in only rudimentary form in some specimens (e.g., compare Fig. 8a and 8b). It was not observed, even in rudimentary form in *E. lugoi*; condition in *E. pottsi* is unknown. The developmental origin of the splint is not entirely clear; it appears in many specimens to extend ventrally into the opening from the pterosphenoid (e.g., Figs. 7c and 8b), while in others it appears more closely associated with or fused to the prootic (e.g., Fig. 8c). One specimen of *E. lepidum* (Fig. 8c) might be interpreted as having a partial splint based on the pterosphenoid, with a full one on the prootic. Among southwestern darters, this feature was initially thought to be unique to *E. segrex* (Norris and Minckley, 1997: Fig. 10), however, further evaluation of

additional specimens reveals it to be a common feature of this group. It shows scattered occurrence among other *Etheostoma* (e.g., *E. exile*) (this study; K. Shaw, pers. comm.). Its functional significance is unknown.

In *Perca*, *Stizostedion*, and *Crystallaria* (Figs. 4d, 6d, 9a) the pterosphenoïd is completely excluded from the anterior opening of the TGF chamber, which is borne by the small and recessed orbital face of the prootic. In *Percina* the anterior opening of the TGF chamber is at the prootic-pterosphenoïd juncture (Figs. 4c, 6c, 9b), though occurring largely on the prootic and slightly recessed, a condition intermediate to those found in *Etheostoma* vs. *Perca* + *Stizostedion* + *Crystallaria*. These features of the cranium (the *pars jugularis*) show interesting and important variation across the bony fishes (see discussions in Greenwood, 1986; Patterson, 1964, 1975; Goodrich, 1930), and their form and variation are other potentially fruitful avenues of investigation in terms of percid phylogenetics.

The posterior myodome is a conical chamber along the ventral surface of the percid neurocranium in which extrinsic muscles of the eye originate; its anterior opening is bounded laterally by the ascending processes of the parasphenoïd, and bisected by the pedicel of the basisphenoïd (when present). It is not as fully enclosed by bony elements (especially dorsally, by internal extensions of the paired prootics) in darters examined as it is in *Perca* or *Stizostedion* (and some other percoids, e.g., *Morone*, *Micropterus*).

The posteroventral aspect of the cranium (exoccipitals and basioccipital) is relatively consistent across the percid taxa examined, generally conforming to the basic percid pattern. The exoccipital is situated posteromedially, contributing to the ventral, lateral, and posterior surfaces of the cranium (Figs. 3-9, 11). The triangular ventral surface is bounded anteriorly by the prootic and laterally by the pterotic, with the intercalary overlying the latter articulation in darters (Figs. 5-6). The unpaired basioccipital lies across the ventromedial edges of the right and left exoccipitals. The exoccipital, along with the basioccipital, bears the posterior half of the saccular bulla (e.g., Fig. 5a). The foramen for the glossopharyngeal (IX) nerve pierces the exoccipital towards the posterodorsal border of the saccular bulla; the larger foramen for the vagus (X) nerve is somewhat posterodorsal to this (e.g., Figs. 6b, 7b). The lagenae (not visible in figures) underlies the exoccipital posterodorsal to the posterior end of the saccular bulla.

On the posterior face of the neurocranium (Fig. 11), the exoccipitals frame the foramen magnum, each projecting a hood posteriad around the opening (e.g., Fig. 3a). This hood is pieced ventrad by a single large foramen (apparently for the occipital nerve, e.g., 3b, labeled "o"). The

exoccipital at its ventromedial corner carries an exoccipital condyle which articulates with the first vertebra.

The unpaired basioccipital lies mesially at the posteroventral border of the cranium (Figs. 3-8, 11). Anteriad it articulates with the prootics and along with the exoccipitals bears the posterior halves of the paired saccular bullae (e.g., Fig. 5a). Its anteromedial section (between the saccular bullae) is overlain by the posterior end of the parasphenoid. Laterally, the basioccipital is bounded by the exoccipital. Posteriad it carries the prominent occipital condyle (e.g., Figs. 3c, 5c, 11d) which articulates with the centrum of the first vertebra. The paired Baudelot's ligaments (not illustrated) attach to the lateral rims of the occipital condyle.

The epioccipital comprises much of the posterior and posterodorsal faces of the neurocranium (Figs. 1-4, 11). It bears a posterior epioccipital extension (e.g., Figs. 1c, 4d, 11c labeled "ee") from which the pectoral girdle is suspended (via the epioccipital process of the supratemporal). Ventrally, the epioccipital articulates with the exoccipital and is bounded ventrolaterad by the floor of the posttemporal fossa (a medial expansion of the pterotic). It does not contribute to the border of the foramen magnum. Medially, the right and left epioccipitals are separated by the supraoccipital; anteriad, each is bounded by a parietal. A small epioccipital process (a point of tendon or muscle attachment) is present in some darters examined (e.g., Fig. 2d) (e.g., *E. grahami*, *E. segrex*, *P. caprodes*, *P. maculata*, *Crystallaria*) and *Perca*; this feature is prominent in *Stizostedion*.

The supraoccipital occupies the median position on the posterior and dorsal surfaces of the osteocranium (Figs. 1-4, 11). Its elongate dorsal surface (with acute anterior border) articulates anteriad with the frontals, and it is bounded laterad with the right and left parietals and epioccipitals. The posterior face is roughly triangular (Fig. 11), its lateral borders articulating with the epioccipitals, and the ventrally directed apex contributing the dorsal border of the foramen magnum. In southwestern darters (and other *Etheostoma* examined) the supraoccipital crest is limited to a small, thin vane along the median axis of the posterodorsal face of the supraoccipital (e.g., Fig. 11c). The supraoccipital crest is strongly developed in *Perca* and *Stizostedion* but weakly developed in *Crystallaria* and *Percina* (e.g., Fig. 4d).

The pterotic (supratemporal-intertemporal, Harrington, 1955; supratemporal, Liem, 1963; intertemporo-supratemporotabular, Jollie, 1986) is a compound element that wraps around the lateral edges of the cranium posterior to the orbit (Figs. 1-9, 11). Anterodorsally it articulates with the frontal and sphenotic; it is bounded dorsomedial by the parietal and partially covered posterodorsad by the extrascapular. Its posterolateral

corner is depressed forming a broad posttemporal fossa on the dorsolateral face of the neurocranium (*e.g.*, Fig. 1a), a shallow cavity forming a site for muscle attachment (note that the right extrascapular is removed in all figures to reveal the underlying posttemporal fossa). Ventrad (Figs. 5-6), forming the lateral portion of the branchial chamber roof, the pterotic articulates with (from anterior to posterior) sphenotic, prootic, and exoccipital. On its ventrolateral surface, the posterior half of the hyomandibular fossa (a slightly elevated and elongate articulation surface) accepts the posterior neurocranial condyle of the hyomandibula (*e.g.*, Fig. 5b). The ossified postocular commissure of the cephalic lateralis is partially embedded along the lateral surface of the pterotic (*e.g.*, Fig. 3d, labeled "pc"), extending anteriorly from the main body of the pterotic in a narrow process over the lateral face of the sphenotic (*e.g.*, Fig. 3d).

The intercalar in all darters examined (*Etheostoma*, *Percina*, and *Crystallaria*) is a small, flat plate overlying the pterotic-exoccipital junction along the posterior edge of the cranium (Figs. 5-9, 11). In adult *Perca* and *Stizostedion* it is larger and wedged **between** the pterotic and exoccipital with exposure on the floor of the posttemporal fossa (dorsal surface). In all percids examined the internal limb of the posttemporal braces against the intercalar.

The parasphenoid is a shaft-like, median element extending longitudinally along most of the ventromedial axis of the cranium (Figs. 3-6). Anteriorly, below the mesethmoid, it is capped by the vomer, from there extending posteriorly between the expanded ventral ends of the paired lateral ethmoids. The dorsal surface of the parasphenoid gives rise to paired, dorsolateral ascending processes at the level of the posterior border of the orbit (*e.g.*, Fig. 4b, 5a). Each of these flat, broad extensions articulates with the anteroventral corner of the prootic and ventral border of the pterosphenoid (below the anterior opening of the TGF chamber). Together the ascending processes frame the opening of the anterior myodome. Just posterior to the ascending process is the foramen for the internal carotid artery, a narrow slot in the border of the parasphenoid along its articulation with the prootic (labeled "IC," *e.g.*, Figs. 3c, 5b). From this point a flat posterior extension of the parasphenoid overlies the medial margins of the right and left prootics and the anterior half of the basisphenoid; its posterior tip is forked (Figs. 5, 6). In *Perca*, *Stizostedion*, and *Crystallaria* (Figs. 6d, 9a) the ascending process does not articulate with the pterosphenoid, although it does in some *Percina* (Fig. 9b).

Dermal Roofing Bones. These four, paired bones (Figs. 1-4) are dermal ossifications originally associated with elements of the cephalic acoustico-lateralis system. One pair, the supratemporals (enclosing the postocular commissure of the cephalic lateralis) contribute to the complex bone

described above as the pterotic. In darters (*Etheostoma*, *Percina*, and *Crystallaria*) the dermal roofing bones are relatively smooth and flat. In adult *Perca* and *Stizostedion* some are heavily sculptured.

The nasal is a narrow, elongate bone, projecting anteriorly from the rostral end of the frontal and enclosing the nasal canal (Figs. 1-4). A pore opens at its rostral tip, another, broader pore opens near its base. The bone bears a thin lateral expansion posteriorly, and in southwestern darters, it carries a similar medial expansion at its rostral tip.

Together, the right and left frontals form the largest single portion of the cranial roof (Fig. 1-4). They are sutured to one-another medially and bounded posteriorly by the pterotics, parietals, and supraoccipital. Rostrally, over the orbit, the frontals narrow sharply, with a pterosphenoid and a sphenotic suspended from the ventrolateral surface of each. The frontal encloses the supraorbital canal of the acoustico-lateralis. The canal enters the frontal near its posterolateral corner and passes anteriorly, giving rise to three pores before emerging along its anterior margin. In *Crystallaria* (Fig. 2d), the frontal has a marked expansion on its rostral end, anterior to the narrowing over the orbit. The frontal is not as dramatically narrowed in *Percina* (Fig. 2c), but it too shows a rostral expansion. In *Perca* and *Stizostedion* the frontal narrows gradually without a severe restriction at the orbit or an expansion at the rostral tip. The bone is heavily sculptured in adults of the latter two genera.

The parietal forms much of the posterodorsal and posterolateral surface of the cranium (Figs. 2-4, 11). It is rhomboid, with the posterolateral corner taken by the posttemporal fossa; it bends ventrally along its lateral edge to form the medial face of the posttemporal fossa. Anteriorly the parietal articulates with the frontal and medially with the supraoccipital; it is bounded laterally by the posttemporal fossa (pterotic), and posteriorly by the epioccipital. The parietal in *Crystallaria* (Fig. 2d) is relatively smaller than that of other darters. Adult *Perca* and *Stizostedion* have a heavily sculptured parietal.

The extrascapular encloses the supratemporal canal (Figs. 1-4, 11) overlying the posttemporal fossa. In percids it is divided into 3 or 4 separate ossifications, 3 in southwestern darters. The supratemporal canal extends across the posterior margin of the supraoccipital (just above the base of the supraoccipital crest). This reach of the canal is not ossified in southwestern darters, although it is partially to fully ossified in other darters and percids examined (*e.g.*, Fig. 2c-d, ossified features labeled "t").

Visceral Skeleton and Associated Dermal Ossifications

This visceral skeleton is comprised of the pharyngeal arches. The first

two pairs, the mandibular and hyoid, form and support the jaws. The remaining five are branchial arches, supporting or forming respiratory and food processing structures. Ossifications of the visceral skeleton are discussed below along with their associated dermal structures.

Suspensorium. The suspensorium is an L-shaped assemblage of bones that support the jaws linking them to the cranium (Figs. 12-13). The suspensorium hangs, via the hyomandibula, from the hyomandibular fossa (a feature of the sphenotic, prootic, and pterotic, described above).

Furthest rostrad is the autopalatine-palatine (*e.g.*, Fig. 12c) (frequently termed “palatine,” *e.g.*, Liem, 1963; Rojo, 1991). This compound unit, positioned at the anterior border of the roof of the mouth, has an elongate body with a stout, rod-like, maxillary process projecting anteriorly from the anterodorsal corner (*e.g.*, Fig. 12c, labeled “mp”) and a flat, ventral caudal process projecting posteriorly from the posteroventral corner (*e.g.*, Fig. 12c, labeled “vc”). The maxillary process overlies the anterior end of the maxilla and is loosely attached to the underside of the lateral ethmoid. The ventral caudal process serves to join the autopalatine-palatine to an arm formed by the entopterygoid and ectopterygoid. The autopalatine-palatine generally bears fine teeth along its ventral surface; teeth were absent only from *Ammocrypta* (which also lacks vomerine teeth). The autopalatine-palatine in *Crystallaria* bears fine teeth, although this is not well portrayed in the drawing (Fig. 13d), as the toothed surface is directed dorsomedially, away from the perspective of the drawing, a feature unique to this genus.

The entopterygoid and ectopterygoid are two elongate, toothless, dermal elements forming an arm based against the quadrate and metapterygoid, with the autopalatine-palatine at its rostral apex. The entopterygoid (the more dorsal and medial of the two) has a broad, medial expansion underlying the eye; the ectopterygoid is smaller with a shorter anterior reach. The ectopterygoid in *Crystallaria* is smaller than in other percids, with no direct articulation with the autopalatine-palatine.

The quadrate is a roughly triangular element. The lower jaw is suspended (via the angular) from the angular condyle at the quadrate’s anteroventral apex (*e.g.*, Fig. 13d). The preopercular process of the quadrate (*e.g.*, Fig. 12d) is an extension from the posteroventral corner that reaches posteriorly ventral to the symplectic and along the dorsal edge of the horizontal arm of the preoperculum.

The metapterygoid is situated at the angle between the two arms of the suspensorium between the hyomandibula (to its posterodorsal border), symplectic and quadrate (to its ventral face), and entopterygoid (anteroventrad). In southwestern darters (Fig. 12) it is irregularly shaped, generally with ventral and posterior indentations. In other species of

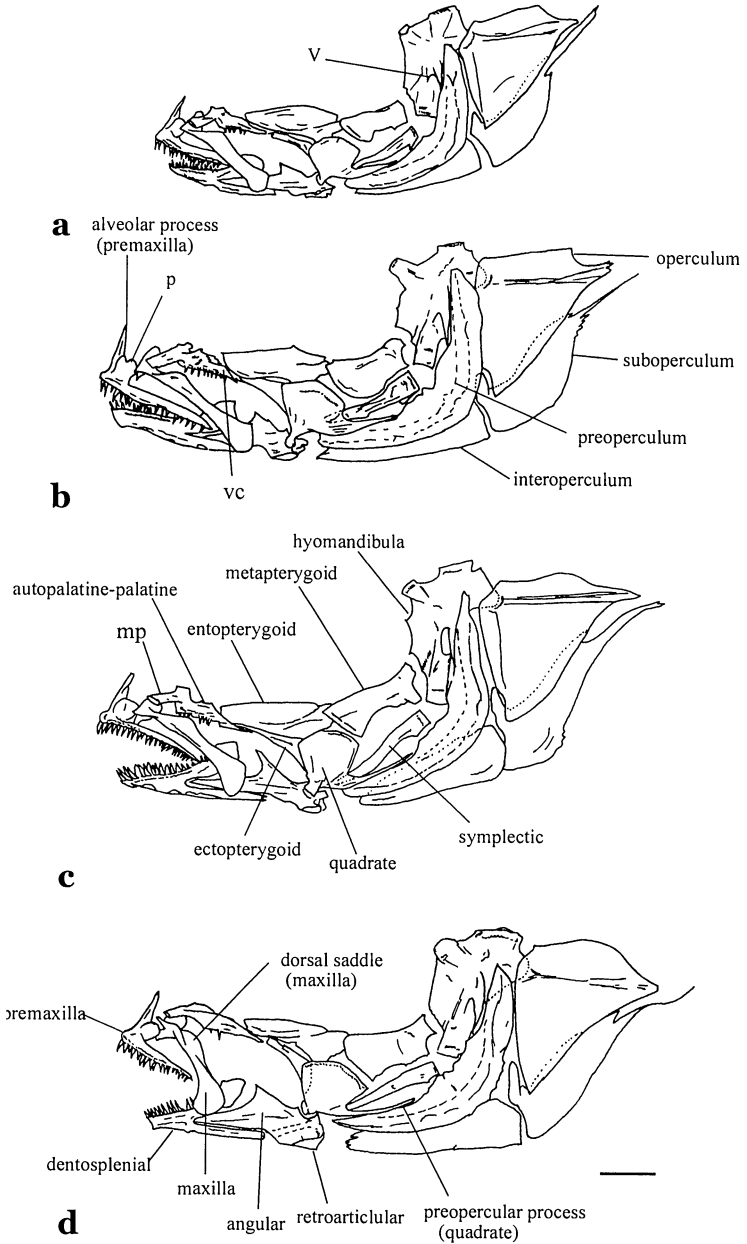


Fig. 12. Suspensorium of: **a**, *Etheostoma lugoi*; **b**, *E. segrex*; **c**, *E. grahami*; **d**, *E. lepidum*. Same specimens as portrayed in Fig. 1.

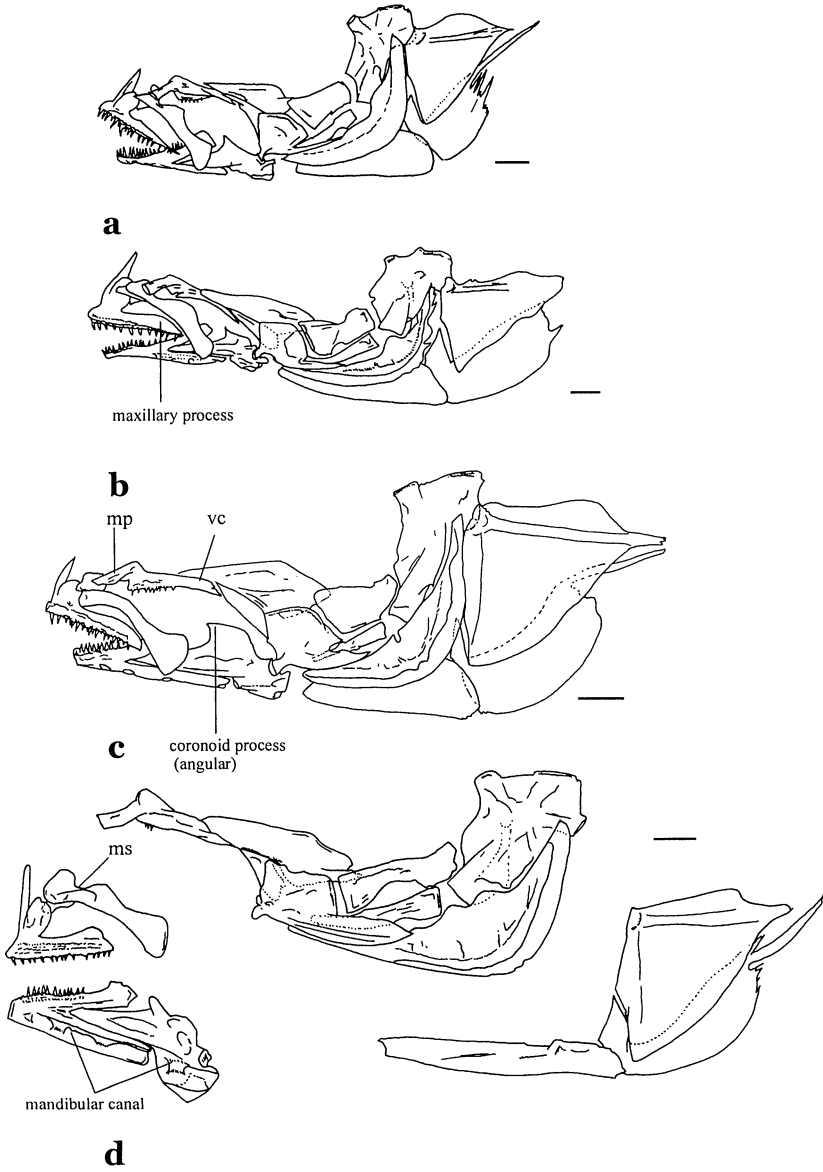


Fig. 13. Suspensorium of: **a**, *Etheostoma caeruleum*; **b**, *Ammocrypta meridiana*; **c**, *Percina caprodes*; **d**, *Crystallaria asprella*. Same specimens as portrayed in Fig. 2.

Oligocephalus examined it is more rectangular (e.g., Fig. 13a). It does not articulate directly with the hyomandibula in southwestern darters (or *Ammocrypta*), but is more closely associated with the hyomandibula in other *Etheostoma*, *Percina* and *Crystallaria* examined. In *Perca* and *Stizostedion* it is a much deeper bone, firmly articulated with both the ectopterygoid and the hyomandibula.

The hyomandibula (Figs. 12-14) is rhomboid, with a cross-shaped set of axes and two dorsal articular surfaces by which it is suspended from the hyomandibular fossa. Anteriad, the rostral neurocranial condyle articulates with a cup-shaped hyomandibular socket (sphenotic, prootic), and posteriad the caudal neurocranial condyle fits against an elongate articulation socket of the pterotic. The opercular condyle extends posteriad from the main body of the hyomandibula, providing the point of attachment for the operculum. The bone is pierced by a canal for the hyomandibular branch of the facial (V) nerve (labeled "V" on Fig. 14c). A sharp vertical ridge (labeled "r" on Fig. 14d) passes down the posterior border of the hyomandibula, this ridge the anterior face of the preoperculum. In southwestern darters this ridge forms a small point (labeled "s" on Fig 14b) projecting ventrally off the posterior face of the hyomandibula; a larger and not entirely similar process is observed in *A. meridiana* (Fig. 14e). The hyomandibula in *Crystallaria* (Fig. 14g) has a broad wing of bone extending posteriad and somewhat laterad off the central (vertical) axis; its lateral extension causes a noticeable swelling of the cheek in intact specimens. Along the posterior margin (lateral face) of this posterior hyomandibular extension is a second, thin wing of bone (labeled "w" in Fig. 14g); the anterior face of the preoperculum is sandwiched between this wing and the main hyomandibular body. The specific arrangement (lateral projection of the cheek and grasping of the preoperculum by the hyomandibular) was not observed in other percids examined.

The symplectic (Figs. 12-13) is an elongate, curved splint of bone with a slight distal expansion. It is partially contained in the symplectic incisure of the quadrate, otherwise not directly articulating with any other bony element.

The preoperculum (Figs. 12-13), an ossification formed around the preoperculomandibular canal, is a flat, crescent-shaped structure with the incompletely enclosed canal running along its lateral face. Its distal border may be serrated (*Perca*, *Stizostedion*) or entire as in all darters examined.

Jaw Apparatus. The jaws (Figs. 12-13) consist of five paired elements: dentosplenials, angulars, retroarticulars, premaxillaries, and maxillaries. Posteriad, the jaw apparatus is suspended by the angular from the

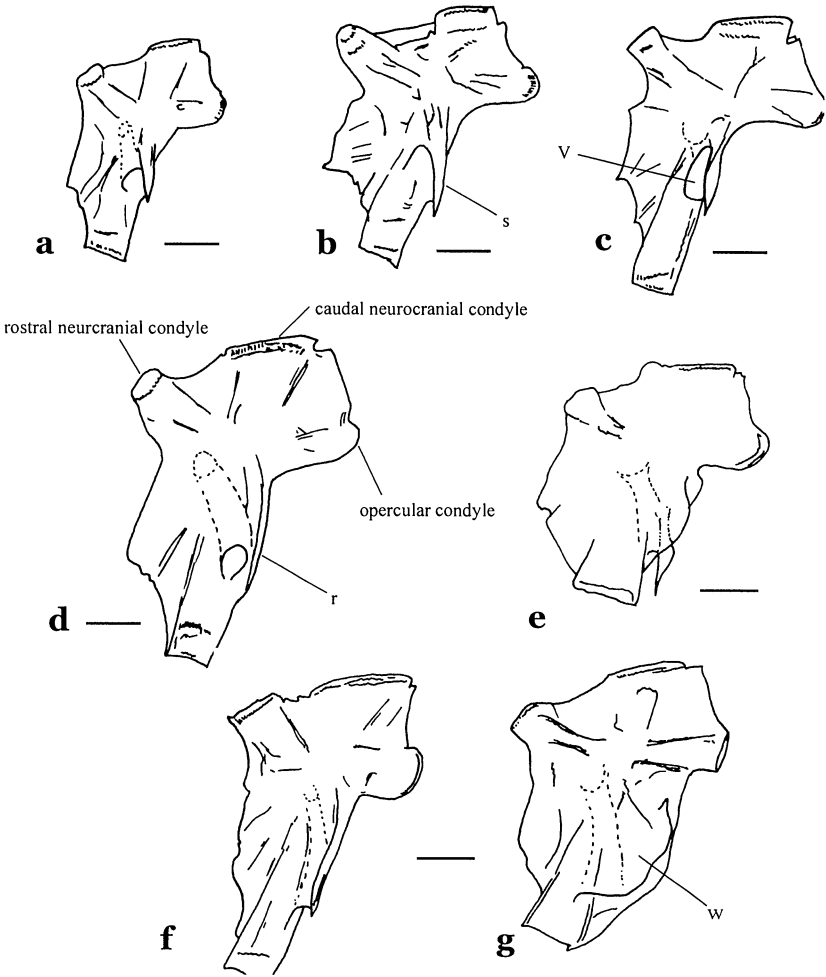


Fig. 14. Representative darter left hyomandibulae: **a**, *Etheostoma lugoi*; **b**, *E. segrex*; **c**, *E. grahami*; **d**, *E. caeruleum*; **e**, *Ammocrypta meridiana*; **f**, *Percina caprodes*; **g**, *Crystallaria asprella*. Same specimens as portrayed in Figs. 1-2 (minus *E. lepidum*).

quadrate; at the rostrum, the two alveolar (ascending or nasal) processes (e.g., Fig. 12b) of the premaxillaries slide into a space between the nasals.

The dentosplenial (dentary of many authors; e.g., Harrington, 1955; Liem, 1963) is composed of two stout limbs which form a V-shaped structure, with its apex directed anteriorly, and a deep recess in the inner angle of the V. The right and left dentosplenials conjoin at the chin. The

dorsal surface of each bears several rows of simple, conical teeth along approximately two-thirds of its length. In *Crystallaria* the teeth are fine, borne on a somewhat medially directed surface (as noted above the palatine teeth also take a medial orientation). The mandibular canal of the acoustico-lateralis (not always fully enclosed in bone) passes through the ventral limb, giving rise to three sensory pores (best seen in Fig. 13c). The dorsal limb forms a shallow coronoid processes.

The main body of the angular (+ articular) is rectangular, with a blade-like anterior process that wedges into the recess in the posterior face of the dentosplenial. Its dorsal surface bears an acute coronoid process (e.g., Fig. 13c); a stout ligament extending from the tip of the process to the dorsal wing of the maxilla was evident in many specimens (both southwestern darters and other percids), but could not be visualized in all specimens examined. Its posterodorsal corner bears the quadrate facet, which pivots against the angular condyle of the quadrate. The posterior reach of the mandibular canal is enclosed along the lateral face of the angular (carrying the canal from the preopercular to the dentosplenial) (e.g., Fig. 13d). The retroarticular is an irregular or triangular bone attached to the ventroposterior corner of the angular.

The premaxilla is a toothed element forming the anterior-dorsal border of the mouth. The alveolar process of the premaxilla (e.g., Fig. 12b) positioned at a right angle to the dentigerous arm, lies in a slot between the vomer, medial ethmoid, and nasal bones. In southwestern darters its length varies from about half to about equal the length of the dentigerous arm. Just posterior to the alveolar process is a second, rounded dorsal process (e.g., Fig. 12b, labeled "p") which articulates with the maxilla. The dentigerous arm bears several rows of simple, conical teeth across most of its ventral length. As on the dentosplenial, the toothed surface of the premaxilla in *Crystallaria* is somewhat medially directed. Southwestern darters examined lacked maxillary processes (a shallow dorsal expansion towards the posterior end of the dentigerous arm), although these were observed in some other *Etheostoma*, as well as *Ammocrypta* (e.g., Fig. 13b), *Percina*, *Crystallaria*, *Perca*, and *Stizostedion*.

The maxilla is a long, toothless, dermal bone, excluded from the gape. Its forked anterior ends grasp the posterior dorsal process of the premaxilla. The maxillary process of the autopalatine-palatines rests in the maxillary saddle (e.g., Fig. 13d, labeled "ms"), a curved surface on the anterodorsal face of the maxilla. A shallow expansion, the dorsal wing (e.g., Fig. 12d) is present on the maxilla of *Etheostoma*, *Percina*, and *Crystallaria* examined, but lacking in *Perca* and *Stizostedion*.

Hyoid Apparatus. The main structures of the hyoid apparatus are the paired ceratohyal bars which straddle the urohyal and from which are

suspended the branchiostegal rays. Two ceratohyals (Fig. 15a), anterior and posterior, are coarsely sutured together end-to-end, forming each ceratohyal bar. The posterior ceratohyal is deep and triangular; the anterior ceratohyal narrows sharply anteriorly. The interhyal, a small bony cylinder, suspends the posterior ceratohyal from the suspensorium. Its ventral end attaches into a small articulator cup on the posterodorsal surface of the posterior ceratohyal, with its dorsal end articulated with a small block of cartilage on the inner face of the suspensorium (off the posterior end of the symplectic). Two hypohyals (ventral and dorsal) articulate with the anterior end of the anterior ceratohyal, together forming a broad anterior end for the ceratohyal bar. The right and left pairs of hypohyals articulate, joining the two ceratohyal bars into a V-shaped unit. The elongate, slightly flattened basihyal (not illus.) projects anteriorly from a narrow slot on the dorsal surface at the apex of the V formed by the ceratohyal bars, forming the base of the tongue.

The urohyal (not illus.) is a median ossification situated in the inner angle of the two ceratohyal bars. It is a flat plate-like element with broad lateral surfaces for attachment of sternohyoid muscles and a narrow horizontal plate along its ventral surface.

The branchiostegal rays (Fig. 15a) originate along the ventral face of the ceratohyal bars, extending posteriorly to supporting the branchiostegal membranes. There are 7 ($n = 3$) in *E. lugoi*, and 6 in all other percids examined, with 4 (or 5 in *E. lugoi*) inserting on the anterior ceratohyal, 2 on the posterior ceratohyal. The 2 (3 in *E. lugoi*) anterior-most rays are fine and whip-like; the remaining (more posterior) ones are broader, flat structures with the most posterior one in all percids examined much broader than any of those preceding.

Branchial Skeleton. All branchial basket ossifications, save the basibranchials, are paired. For all paired branchial arch elements, the proximal end is defined as the end nearest the mesial base (the point where they meet the basibranchials).

Three toothless basibranchials (not illus.) are arranged end-to-end behind the basihyal. They form the ventral, median axis of the branchial basket, providing the base for the branchial arches. Three pairs of angular hypobranchials (not illus.) project laterad from the basibranchial chain; all are toothless.

Five pairs of ceratobranchials (not illus.) project dorsolaterad from the distal ends of the hypobranchials and third basibranchial. The first four are narrow and elongate, carrying gill filaments along their aboral faces and articulating distally with an epibranchial. The gill rakers are round and stout in southwestern darters increasing in size and length proximally to distally; they are elongate and spike-like in other percids

examined. The fifth ceratobranchial (sole element representing the fifth visceral arch) is a narrow triangular structure, bearing conical teeth on its dorsal surface. It forms the ventral biting surface for the pharyngeal jaws.

Four elongate epibranchials (Fig. 15b-c) form the roof of the branchial basket; all carry both gill tissue and gill rakers. The third and fourth epibranchials are stouter than the first two and both bear fine dorsal processes, which articulate with one another. Along the posterior face of the fourth epibranchial is a flange (quite distinct and produced into a finger-like process in *E. australe*, Fig. 15c). In at least some forms (e.g., *E. australe*) this flange is cartilage-capped.

In all darters examined there are three fully ossified infrapharyngobranchials (pharyngobranchials of Liem, 1963; Harrington, 1955). These are the most distal and dorsal elements of the branchial arches, suspending the branchial basket from the cranium. The first infrapharyngobranchial is missing from darters, but is well developed in *Perca* and *Stizostedion*, in which (in typical percoid form) it is a small bony shaft projecting anteromedial from the distal end of the first epibranchial. All three infrapharyngobranchials in darters are rounded plates with fine teeth on their oral surfaces. As a unit these bones form the dorsal biting surface of the pharyngeal jaws.

Opercular Series

The three paired opercular bones (Figs. 12-13) are relatively simple, flat structures that reinforce the opercular membranes, thus protecting the underlying branchial skeleton. The operculum is largest, most lateral, and most dorsal. It is triangular with an articulator cup on its medial surface just ventral to the anterodorsal corner. A strut, extending posteriad from the articulator cup on the bone's medial surface, is projected into a single, stout "spine" at the posterodorsal corner of the bone. The suboperculum is an elongate bone in southwestern darters, somewhat deeper in other darters examined (and *Perca* and *Stizostedion*); it bears a distinctly broadened anterior dorsal process in *Ammocrypta* and *Crystallaria* (Fig. 13b, 13d). The interoperculum is shallow and elongate in all percids examined, somewhat triangular in most darters (very long and shallow in *Crystallaria*). All opercular bones are entire in adult all southwestern darters and *Ammocrypta* and *Crystallaria* examined. In *Perca*, *Stizostedion*, *Percina* and larger species of *Etheostoma*, the suboperculum and interoperculum may be finely serrated. The development and number of serrations are possibly positively correlated with body size, as was observed in anabantid fishes (SMN, unpubl. data; using much larger

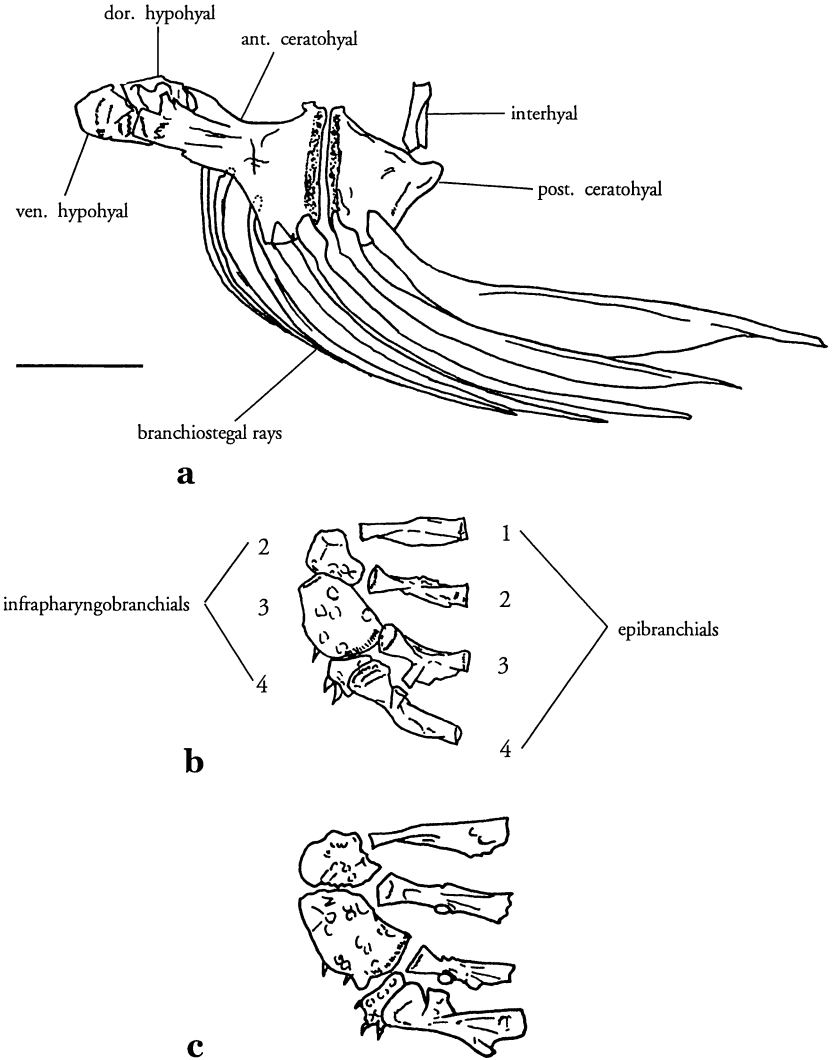


Fig. 15. Branchial basket elements: **a**, right hyoid apparatus of *E. lugoi* (ASU 5995, 28.9 mm SL, m); dorsal branchial elements (left side, dorsal view, anterior to top of page) of **b**, *E. lugoi* (ASU 5995, 28.9 mm SL, m); **c**, *E. australe* (UMMZ 182378 c&s, 44.7 mm SL).

sample sizes than employed in this study). However, despite size (and possible gender) effects, patterns of development and number of serrations did show taxon specific patterns in the Anabantidae, and may for percids as well.

Axial Skeleton

Pectoral Girdle. All pectoral girdle elements are paired (Figs. 16-17). The posttemporal, the most dorsal element, connects the pectoral girdle to the cranium. Its flat, angular body encloses the posttemporal canal (passing it posteriad into the lateral line). A spatulate dorsal limb (epioccipital process) projects anteriorly and articulates with the distal end of the epioccipital extension (epioccipital). A more cylindrical, ventral (internal) limb extends ventromedially from the anterior inner face of the posttemporal, its distal end articulating with the intercalar.

The supracleithrum is a simple ovoid or rectangular plate in most darters examined; in *Perca* and *Stizostedion* it is vertically elongate with a serrated posterior margin. The supracleithrum extends ventrad from the posttemporal and overlies the dorsal end of the cleithrum. It is not penetrated by the posttemporal canal. The cleithrum, an elongate, vertically oriented structure, forms the central frame for the pectoral girdle. Its dorsal end, underlying the supracleithrum, bears a pointed dorsal process and from its posterodorsal face a narrow, flat process extends caudad, the posterior process (Fig. 16a, labeled "pp"). The posterior face of the cleithrum has articulation sites for the coracoid and scapula. At its ventral end the cleithrum bears another posterior extension, the ventral process (*e.g.*, Figs. 16 b-c, labeled "vp"), which articulates with the anterior end of the pelvic girdle. At their ventral tips the right and left cleithra are conjoined at the cleithral symphysis, just below the heart. The cleithrum in *Crystallaria* (Fig. 17b) is more heavily constructed than in other darters, with a much deeper transverse profile. In *Perca* and *Stizostedion* the dorsal, posterior expansion of the cleithrum is absent, the dorsal reach of the bone may be serrated and the ventral posterior expansion (articulating with the pelvic girdle) is only weakly developed (present in *Gymnocephalus*). The posterior process and ventral process are present in the European *Gymnocephalus*.

The postcleithrum is represented by a pair of ossifications, both vertically oriented and medial to other pectoral-girdle elements. The dorsal postcleithrum is a flat, relatively featureless, ovoid or rectangular structure. Its dorsal end is loosely articulated with the inner face of the dorsal, posterior expansion of the cleithrum. This bone is broader in *Crystallaria* than in other darters; its posterior margin is serrated in *Perca* and *Stizostedion*. In all darters examined save *Crystallaria*, the ventral postcleithrum is a fine splint of bone, sometimes with a slight dorsal expansion; it lies free in the lateral body musculature below the ventral end of the dorsal postcleithrum. This element could not be resolved in

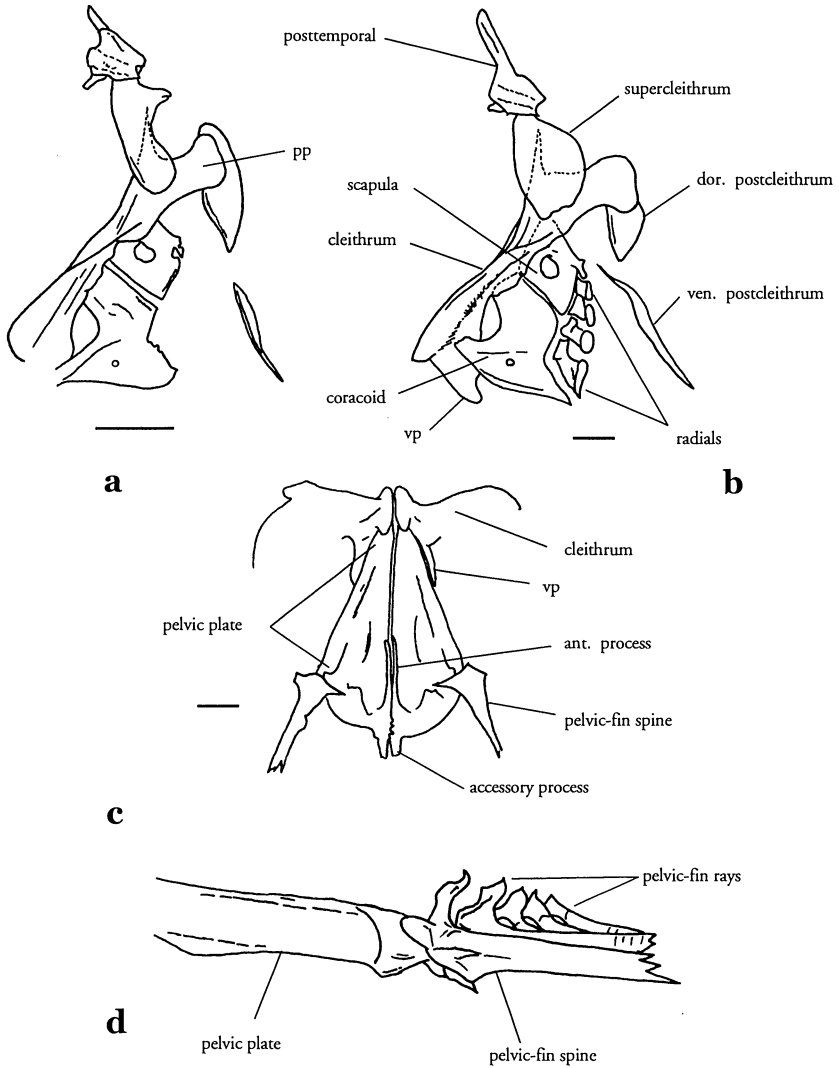


Fig. 16. Appendicular girdles: **a**, pectoral girdle of *Etheostoma lugoi* (ASU 5995, 28.9 mm SL, m); **b**, pectoral girdle of *E. spectabile* (ASU 2138, 45 mm SL, m); **c**, articulation between pelvic and pectoral girdle (ventral view) in *E. spectabile* (ASU 2138, 45 mm SL, m); **d**, detail of pelvic-fin and ray bases in *Percina caprodes* (lateral view, innermost [5th] ray not visible in this view) (no scale) (ASU 2665, 85 mm SL).

any of the available specimens of *E. australe* (the absence of this fine structure could be a fixation or clearing artifact, although other fine ossifications did persist in these specimens). In *Crystallaria* (Fig. 17b) the ventral postcleithrum is an angled element, somewhat more substantial

than in other darters examined with its dorsal end articulated directly with the ventral end of the dorsal postcleithrum. It also projects a lengthy and thin shaft of bone anteromedially from its medial face. The latter feature is highly unusual and was not observed in any other percid taxa, although in *Ammocrypta* (Fig. 17a) the ventral postcleithrum is long with its main axis projecting medially, in a fashion that is perhaps functionally similar to the medial process seen in *Crystallaria*. In *Perca* and *Stizostedion* the ventral postcleithrum is more substantial than in darters and directly articulated to the ventral end of the dorsal postcleithrum with no medial extension or process.

The scapula is roughly square, its anterior border articulated to the posterior face of the cleithrum. Its center is pierced by a round, scapular foramen, and its posterodorsal corner carries an indentation that accepts the dorsal-most ray of the pectoral fin. The flat, posterior face of the scapula supports two and a half of the four pectoral fin radials.

Greatly idealized, the coracoid is an h-shaped element with the end of each "leg" articulated to the posterior face of the cleithrum. It lies in the same vertical plane as the scapula, immediately ventral to the latter, supporting the ventral-most one and one half radials. The ventral border is projected into an acute posterior process, which in *Etheostoma* directly underlies the ventral-most radial. In all percids examined a small foramen pierces the coracoid midventrally. This bone is thick and substantial in *Crystallaria* and is also distinctly bowed ventrally along its longitudinal axis. The radials are partially fused to the coracoid and to the scapula.

Pelvic Girdle. The pelvic girdle (Fig. 16c) is composed of two bilaterally symmetrical pelvic plates (Stiassny and Moore, 1992) (basipterygia of Norden, 1961; Liem, 1963, and most others), which are in a thoracic position just below the pectoral girdle. The elongate, triangular plates are conjoined along their thickened posterior ends, with their narrower anterior reaches extending anteriorly and terminating dorsal to the cleithral symphysis. The paired ventroposterior expansions of the right and left cleithra form a bracket that firmly grips the anterior end of the pelvic girdle. On its ventral and lateral surfaces, the pelvic plate bears an external dorsal wing, an external ventral wing, and an anterior process, along with a knob-like accessory process posteromedially (Stiassny and Moore 1992).

The pelvic-fin spine articulates with the lateral corner of the posterior face of the pelvic plate, with the pelvic fin rays inserting medially to this. The spine and the rays all bear fine dorsal processes on their bases (Fig. 16d), presumably for attachment of fin-controlling ligaments and muscles. The latter feature was noted in all darters examined, but was prominent in neither *Perca* nor *Stizostedion*.

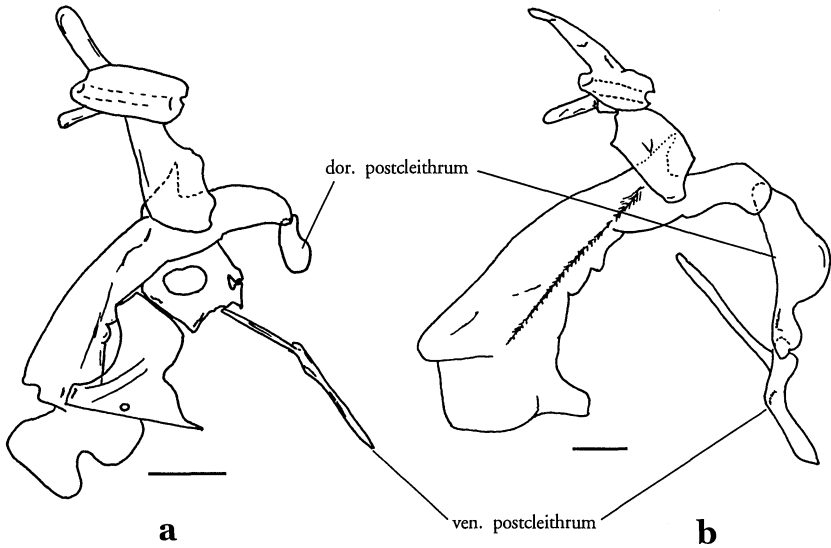


Fig. 17. Pectoral girdle: a, *Ammocrypta meridiana* (UAIC 6794.20, 50 mm SL); b, *Crystallaria asprella* (coracoid and scapula omitted for clarity) (UAIC 2705.01, ca. 120 mm SL).

Caudal Skeleton and Supraneurals. The same basic caudal skeleton structure was noted in all percids examined (Fig. 18). There are (dorsal to ventral) three epurals, one bilaterally paired uroneural, three dorsal hypural plates, two ventral hypural plates and a parhypural. The first hypural does not articulate directly with the urostyle, the others and the parhypural do, although they are not fused to it. The hemal arch of the penultimate vertebra is often not fused to the centrum. Near its base, the parhypural bears a hypurapophysis (a spiked posterodorsad-directed process) that is not as prominent in small darters as in larger ones or in *Perca* and *Stizostedion*. Various caudal skeleton units (epurals; hypurals 1-3; hypurals 4-5 + parhypural) were commonly fused (e.g., 17b).

Supraneurals were not observed in any darter taxon, a single supraneural is present in *Perca*, *Stizostedion* and *Gymnocephalus*.

COMPARISONS AND CONCLUSIONS

Within the North American Percidae, there is a transition in cranial construction from large forms (*Perca* + *Stizostedion*) through to the smallest

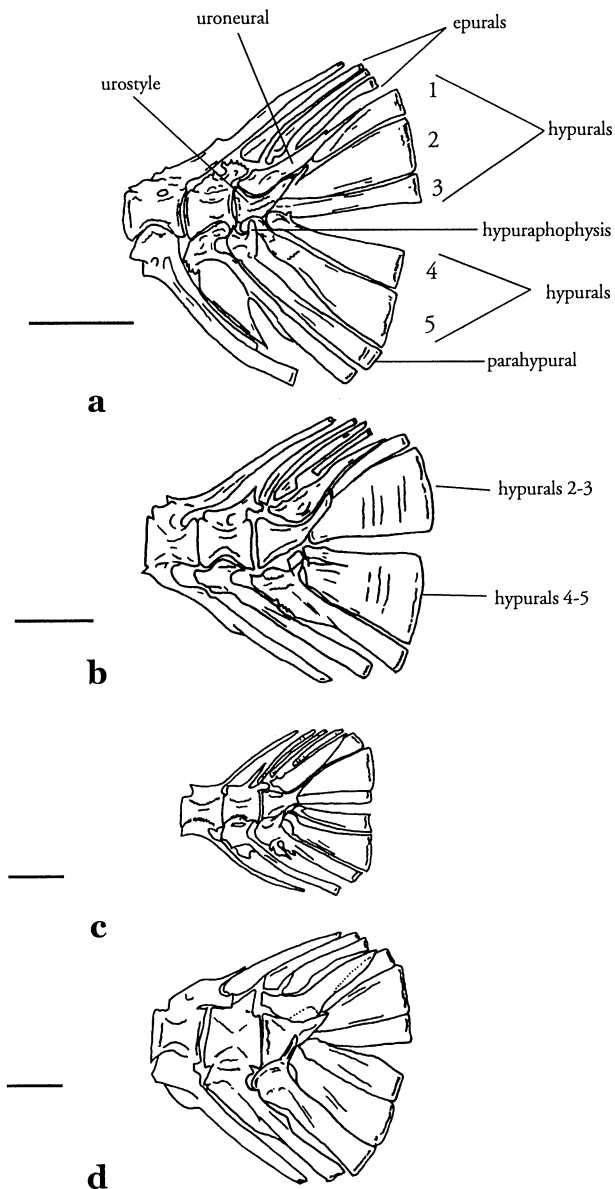


Fig. 18. Caudal skeleton: **a**, *Etheostoma lugoi* (ASU 5995, 28.9 mm SL); **b**, *E. australe* (note fusion of hypurals 2-3 and 4-5) (UMMZ 182378 c&s, 44.7); **c**, *Ammocrypta meridiana* (UAIC 6794.20, 50 mm SL); **d**, *Crystallaria asprella* (UAIC 2705.01, ca. 120 mm SL).

arters examined (*Etheostoma lugoi* and *E. fonticola*). The cranial elements in larger forms are generally more heavily constructed, and more firmly articulated to one-another, providing a somewhat more substantial skull. In addition, certain elements, especially some associated with the cephalic lateralis (e.g., extrascapular, infraorbital series) are incompletely ossified or unossified in many of the smaller forms, although fully ossified in larger species. Such allometric variation is probably not unusual with groups spanning such a large size range and has also been noted in the percomorph groups Anabantoidei, Nandidae, and Badidae (Norris, 1994; 1995; see also Weitzman and Vari, 1988).

However, beyond size variation, there is a range of fundamentally different skull types observed in the North American Percidae; this is particularly apparent with regard to arrangement of the sphenotic region, and the relationship of the pterosphenoid to its surrounding elements, and the bordering of the hypophyseal foramen. *Perca*, *Stizostedion*, and *Crystallaria* (also *Gymnocephalus*) show a typical percoid pattern with the paired pterosphenoids projecting medially from the internal base of the lateral commissures (prootics + sphenotics), constricting this opening. *Etheostoma* (and *Ammocrypta*) show a strongly modified pattern in which the pterosphenoid takes a more lateral and ventral position, projecting more rostrally off the anterior margin of the prootic, framing, but not constricting the hypophyseal foramen. Further, the pterosphenoid contributes to the anterior opening of the trigemino-facialis chamber, and articulates ventrally with the parasphenoid. Interestingly, the pattern in at least some *Percina* may be seen as intermediate between these two extremes. In *P. caprodes*, the pterosphenoid takes a more medial position than in *Etheostoma*, articulating with the internal face of the limited lateral commissure which is present ventrally on the prootic. This suite of characters does not support inclusion of *Crystallaria* within either *Etheostoma* or *Ammocrypta*. While *Ammocrypta* has a cranial osteology that is highly congruent with *Etheostoma*, its ventral postcleithrum shows unusual medial extension, similar to that of *Crystallaria*. This apparent incongruity in expression of morphological traits could be resolved with a broader examination of character distributions across the Percidae using osteology, and possibly understood in ecological, adaptational or functional contexts with comparative behavioral or life history studies.

ABBREVIATIONS

a: accessory articulation surface of lateral ethmoid.
ant.: anterior.

- ant. opening TGF: anterior opening of the TGF chamber.
 ap: anterior projections of mesethmoid.
 asc. process parasphen.: ascending process of the parasphenoid.
 d: splint of bone that divides the anterior opening of the TGF chamber.
 dor.: dorsal.
 ee: epiocitipal extension.
 f: female.
 h: dorsal hood-like extension of vomer.
 IC: foramen for passage of the internal carotid artery
 m: male.
 mp: maxillary process of the autopalatine-palatine.
 ms: maxillary saddle of maxilla.
 o: foramen in exoccipital, presumably for passage of the occipital nerve.
 of: orbital face of prootic.
 p: dorsal process of premaxilla.
 pc: ossified tract of the postocular commissure of the cephalic lateralis (partially embedded in pterotic).
 post.: posterior.
 pp: posterior process of cleithrum.
 r: vertical ridge along lateral face of hyomandibula.
 s: fine point projecting off vertical ridge of hyomandibula.
 t: ossified tract of the supratemporal canal (applied to parietal and supraoccipital).
 TGF: trigemino-facialis.
 V: foramen for hyomandibular branch of the facial nerve.
 vc: ventral caudal process of the autopalatine-palatine.
 ven.: ventral.
 vp: ventral process of the cleithrum.
 w: wing of bone projecting laterally off posterior margin of hyomandibula.

OSTEOLOGICAL MATERIAL EXAMINED

All are cleared and stained specimens, unless otherwise indicated.
Ammocrypta beani Jordan: UAIC 893.13, \pm 45 mm SL, MS: Stone Co. *A. meridiana* Williams: UAIC 6794.20, 50 mm SL, AL: Bibb Co., UAIC 7196.21, 75 mm SL, AL: Bibb Co. *Crystallaria asprella*: UAIC 2705.1, ca. 120 mm SL, AL: Pickens Co.; UAIC 3096, ca. 70 mm SL, AL: Greene Co. *Etheostoma australe*: UMMZ 182378 c&s, 31.1-44.7 mm SL, MX: Coahuila, Río Santa

Isabel. *E. (Oligocephalus) caeruleum* (Storer): ASU 222, 49 mm SL, MI: Allegan Co. UMMZ 212288, 27, 44.5, 49 mm SL, MI: Washtenaw. *E. grahami*: ASU 1021, 36.5 mm SL, TX: Val Verde Co. ASU 10899, 35 mm SL, TX: Nuevo Leon Co. *E. (Oligocephalus) exile* (Girard): ASU 2628, 39, 41 mm SL, MN: Clearwater Co. *E. (Microperca) fonticola* (Jordan and Gilbert): ASU 15776, 25, 25, 21 mm SL, Captive stock, Dexter National Fish Hatchery, Dexter, NM. *E. lepidum*: ASU 1756, 38 mm SL, NM: Eddy Co. *E. lugoï*: ASU 5995, 28.9 mm SL, MX: Coahuila. *E. (Boleosoma) nigrum* (Cope): ASU 2660, 55, 56 mm SL, MN: Clearwater Co. *E. pottsi*: ASU 9185, 35 mm SL, MX: Zacatecas, Río Aguanaval. *E. (Oligocephalus) radiosum* (Hubbs and Black): ASU 16179, 51, 47, 25 mm SL, AR: Howard Co. *E. (Nothonotus) rufilineatum* (Cope): ASU 4372, 55 mm SL, AL: Franklin Co. *E. segrex* ASU 5985, 37.2 mm SL, MX: Coahuila. *E. (Oligocephalus) spectabile* (Agassiz): ASU 13867, 40 mm SL, TX: Hayes Co. ASU 2138, 45 mm SL, KS: Wabaunsee Co. *Gymnocephalus cerva*: UMMZ 201214, 42.5, 85.7 mm SL, Norway: Oppland. *Perca flavescens* (Mitchill): ASU 2532 MN: Clearwater Co. ASU 11141, MN: Clearwater Co. UMMZ 223595, 22, 42.5 mm SL, MI: Marquette Co. *Percina (Percina) caprodes* (Rafinesque): ASU 2666, 85 mm SL, MN: Cass Co. *P. (Alwordius) maculata* (Girard): ASU 2626, 65 mm SL, MN: Clearwater Co. UMMZ 65788, 26, 52.3 mm SL, MI: Alcona Co. *Stizostedion vitreum* (Mitchill) (dry skeleton): ASU 2860, 250 mm SL, AZ: Maricopa Co. (stocked population). UMMZ 101026, ca. 120 mm SL, IW: Dickison Co. UMMZ 177335-S, 296 mm SL, MI: Delta Co. UMMZ 223930, 32 mm SL, MI: Luce Co. *Morone saxatilis* (Walbaum): uncat. dry cranium, AZ: Mohave Co. (stocked population). *Micropterus salmoides* (Lacepède): uncat. dry cranium, no data.

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