

Dismantling the Trachinoidei: evidence of a scorpaenoid relationship for the Champsodontidae

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Abstract An examination of the osteology and myology of the Champsodontidae reveals a number of apomorphic features (e.g., double-headed palatine, large pelvic radial, epaxial muscle inserting on the medial pelvic-fin ray, posterior levator internus inserting on the third epibranchial). The evidence for a Champsodontidae/Chiasmodontidae relationship is examined through a re-evaluation of the basal characters used to define the suborder Trachinoidei. The Champsodontidae are removed from the Trachinoidei and a chiasmodontid sister relationship is rejected. After investigation of several possible alternative relationships (Paracanthopterygii, Gobioidae, Callionymoidae, Kurtoidei, Apogonidae, Blennioidei, Trichodontidae), champsodontids are hypothesized to be members of the perciform suborder Scorpaenoidei. This hypothesis is based largely on the synapomorphy of a parietal spine with an opening for passage of the supratemporal sensory canal, a unique condition of champsodontids and some scorpaenoids. A shared Type 1 epaxial muscle morphology, with separate fibre insertions on the distal tips of the spine-bearing dorsal-fin pterygiophores, is unusual and probably derived among perciforms. Champsodontids also share with some scorpaenoids Type 5 spinoid scales and the origin of Baudelot's ligament from the first vertebra rather than the basi-occipital, although neither of these features is unique to these taxa. The occurrence of an enclosed sensory canal on the parietals of Trichodontidae suggest that their relationships might also lie with the Scorpaenoidei. Arguments pertaining to the removal of champsodontids from the trachinoids apply equally to the hypothesized membership of the Cheimarrichthyidae, Pinguipedidae, Percophididae, Trichonotidae, Creediidae, Chiasmodontidae, and notothenioids in the Trachinoidei. Inclusion of these taxa within the Trachinoidei is not well-supported, and their relationships require further investigation.

Key words. — Champsodontidae; phylogeny; Scorpaenoidei; Trachinoidei.

The Champsodontidae, commonly known as gapers, are a family of small, elongate fishes found at depths between 50–400 m throughout the tropical Indo-Pacific. They are currently considered to be members of the large order Perciformes. A recent taxonomic review recognized one genus, *Champsodon*, with 13 species (Nemeth, 1994). Externally, the adults

are characterized by a large head and mouth, small pectoral fins, very large pelvic fins, unusual pedicellate spinoid scales, and series of sensory papillae on the head and body (Fig. 1a). Early authors had difficulty aligning the genus among other groups due to its unusual morphology. Traditionally, it has been placed in the suborder Trachinoidei, a taxon that has had a fluid

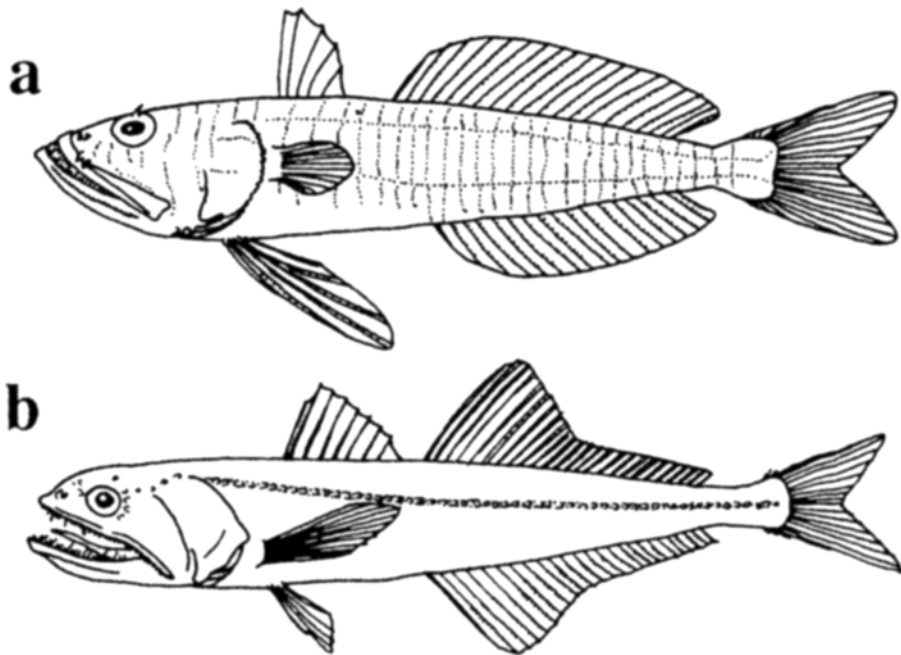


Fig. 1. General body forms of the Champsodontidae and Chiasmodontidae. a) *Champsodon capensis* (after Smith and Heemstra, 1986: fig. 229.1); b) *Pseudoscopelus scriptus* (after Norman, 1929: fig. 11).

membership. Among the trachinoids, *Champsodon* has been most frequently allied with the Chiasmodontidae (swallowers) to which it bears a superficial resemblance (Fig. 1), but opinions vary among authors and little, if any, evidence has been provided to support these opinions.

Pietsch (1989) and Pietsch and Zabetian (1990) provided a cladistic definition of a Trachinoidei that included the Champsodontidae and Chiasmodontidae as sister taxa. Reservations concerning their evidence and conclusions were voiced by Johnson (1993) and Mooi and Gill (1995), who suggested alternative relationships including placement among the Scorpaenoidei (sensu Mooi and Gill, 1995). These same reservations cast some doubt on the integrity of the Trachinoidei as a whole.

The contentious phylogenetic position of the Champsodontidae and its possible implications for higher relationships provided the impetus for the current study. After a brief taxonomic history, we present a detailed description of the osteology and myology of *Champsodon*, revealing

a number of unique features that corroborate monophyly, as well as some unusual characteristics that are found in only a few acanthomorph taxa. These apomorphies may prove to be synapomorphies of *Champsodon* and other groups upon further study. We re-examine and discount the current hypothesized affiliation with trachinoids, and comment on the composition of the Trachinoidei based on reinterpretation of evidence and removal of the Champsodontidae. We then explore alternative relationships for champsodontids with special emphasis on their ties to the scorpaenoids.

Methods

Osteological observations were made from specimens cleared and stained by various techniques (Taylor, 1967; Dingerkus and Uhler, 1977; Taylor and Van Dyke, 1985). Additional comparative information was derived from the literature, particularly Johnson and Cohen

(1974) for chiasmodontids, Nemeth (1994) regarding champsodontids, and Pietsch (1989) for trachinoids.

Vertebral counts are divided into abdominal and caudal, the first caudal defined as the anteriormost vertebra with a haemal spine. Intermuscular bones are identified as epineurals rather than epipleurals following Johnson and Patterson (1993) and Patterson and Johnson (1995). The pattern of insertion of dorsal- and anal-fin pterygiophores within interneural and interhaemal spaces are provided as "fin formulae" modified from the "anterior fin pterygiophore formulae" of Gill and Randall (1994). Neural and haemal spines are represented by slashes, pterygiophores are represented by roman numerals when bearing spines ("II" indicating a pterygiophore bearing a supernumerary and serially associated spine, "I" a pterygiophore bearing only a serially associated spine) and arabic numerals when bearing serially associated segmented rays. Spineless pterygiophores are indicated by a "P" and pterygiophores in the same interneural space are separated by "+." Terminology for caudal cartilages follows Fujita (1989).

Cheek musculature was examined in ethanol-preserved specimens by removing the eye, sub-orbitals, and skin on one side of the head. Muscle bundles were identified, drawn under a binocular dissecting microscope through a camera lucida, then removed to reveal more medial muscle groups. Branchial, pelvic, and pectoral musculature was examined both in situ and after removing the elements from the fish. Epaxial muscle examination follows the methods of Mooi and Gill (1995). Muscle delineation was enhanced by staining with a variation on Lugol's solution (Bock and Shear, 1972). Muscle terminology follows that of Winterbottom (1974) except where noted; epaxial muscle morphology types are those of Mooi and Gill (1995).

Cladistic methodology was used to explore hypotheses of relationship.

Materials

Institutional abbreviations follow Leviton et al. (1985). Features examined by dissection of alcoholic (D) and

cleared and stained (CS) specimens are indicated; specimens not so designated were examined externally only. For *Champsodon*, alphabetically by species and institution: *C. atridorsalis*, USNM 297752 (D), USNM 323056 (D,CS); *C. capensis*, USNM 270267 (CS), USNM 307516 (D); *C. fimbriatus*, USNM 51682 (D); *C. guentheri*, USNM 150759 (CS); *C. longipinnis*, MCZ 60955 (CS), USNM 149650 (D), USNM 150948 (D); *C. nudivittatus*, USNM 122582 (D,CS), USNM 297753 (D); *C. omanensis*, USNM 305988 (D); *C. sagittus*, USNM 122405 (D); *C. seychellensis*, USNM 307487 (D); *C. snyderi*, MCZ 99264 (CS), USNM 149294 (D); *C. vorax*, USNM 122400 (CS), USNM 168220 (D), USNM 245331 (D,CS), USNM 297751 (D); *C. sp.* (unidentifiable larval material), AMS I.20948-002, AMS I.22548-003, AMS I.24553-009, AMS I.24570-013 (CS), AMS I.24898-001, AMS I.24949-003, AMS I.24953-009, AMS I.24955-001, AMS I.24967-009, AMS I.26192-002 (CS), AMS UN.91113-006 (CS), AMS UN.91113-007 (CS), MCZ 68883 (CS), USNM 245330 (CS), USNM 245331 (CS), ZMC 1368V-VI, ZMC 3724I,VI (CS).

Comparative material, alphabetically by family and institution. — Ammodytidae: *Ammodytes dubius*, USNM 302247 (CS). Anoplopomatidae: *Anoplopoma fimbria*, USNM 269910 (CS). Antennariidae: *Antennarius radiosus*, USNM 266728 (CS); *Histrio histrio*, USNM 269469 (CS). Bathyracidae: *Parachaenichthys georgianus*, USNM 301814 (CS). Batrachoididae: *Batrachoides liberiensis*, USNM 219393 (CS); *Daector dowi*, MPM 31153 (CS); *Opsanus tau*, USNM 104906 (CS); *O. beta*, MPM uncat. (CS); *O. sp.*, MPM 242; *Porichthys porosissimus*, USNM 270371 (CS). Bovichtidae: *Bovichtus variegatus*, USNM 214761 (CS). Callionymidae: *Synchiropus ocellatus*, USNM 270215 (CS). Caracanthidae: *Caracanthus maculatus*, USNM 214027 (CS). Channichthyidae: *Champsoccephalus gunnari*, USNM 305271 (CS). Cheimarrichthyidae: *Cheimarrichthys fosteri*, USNM 198509 (CS), USNM 214023 (CS). Chiasmodontidae: Chiasmodontidae sp., AMS I.16492-034, AMS I.16725-015, AMS I.24508-002, AMS I.24511-002, AMS I.24514-001, AMS I.24528-002, AMS I.24866-001, AMS I.24948-002, AMS I.24957-002, AMS I.24971-001, AMS I.25199-001, AMS I.25556-006; *Chiasmodon niger*, ARC 8600869, ARC 8600887 (CS); *C. sp.*, MCZ 65529, USNM 254264 (CS), USNM 331703 (CS); *Dysalotus alcocki*, MCZ 60722, MCZ 60760, MCZ 60806, MCZ 60807, MCZ 65494, USNM 207603 (CS); *D. alcocki?*, AMS I.27172-038; *Kali indica*, USNM 207618; *K. macrodon*, USNM 207597, USNM 207601; *K. macrura*, USNM 207608; *K. normani*, USNM 207614, USNM 207614 (CS), USNM 207987 (CS); *K. sp.*, MCZ 97798, ZMC 185 vials (list available) (1 CS); *Pseudoscopelus altipinnis*, MCZ 41116, MPM uncat. (D,CS); *P. scriptus*, MPM uncat. (D, CS); *P. scutatus*, MCZ 68462, MCZ 73015; *P. sp.*, AMS I.27172-037, AMS I.27173-034, ARC 8703596, ARC 8706465. Cottidae: *Artedius fenestralis*, USNM 188370 (CS); *Clinocottus embryum*, USNM 104648 (CS); *Cottus bairdi*, USNM 193153 (CS); *Icelus spiniger*, USNM 208352 (CS); *Myoxocephalus aeneus*,

USNM 270265 (CS); *Oligocottus maculosus*, USNM 188372 (CS). Creediidae: *Chalixodytes tauensis*, USNM 284389 (CS); *Crystallodytes cookei*, USNM 307831 (CS); *Limnichthys fasciatus*, USNM 295851 (CS). Cyclopteridae: *Cyclopterus lumpus*, USNM 177572 (CS); *Liparis fabricii*, USNM 177600 (CS). Draconettidae: *Draconetta acanthopoma*, USNM 156956 (CS). Gadidae: *Boreogadus saida*, USNM 177635 (CS); *Gadus morhua*, USNM 165302 (CS). Harpagiferidae: *Ariedidraco mirus*, USNM 301743 (CS). Hexagrammidae: *Hexagrammos decagrammus*, USNM 104656 (CS). Hoplichthyidae: *Hoplichthys citrinus*, USNM 308828 (CS). Kurtidae: *Kurtus gulliveri*, USNM 217309 (CS); *K. indicus*, USNM 305690 (CS). Leptoscopidae: *Crapatulus arenanus*, USNM 269556 (CS); *Leptoscopus macropygus*, USNM 213490 (CS). Lophiidae: *Lophioides monodi*, USNM 216979 (CS); *Lophius vaillanti*, USNM 216984 (CS). Lotidae: *Lota lota*, USNM 193117 (CS). Merlucciidae: *Merluccius albidus*, USNM 208193 (CS). Nototheniidae: *Notothenia gibberifrons*, USNM 301709 (CS). Normanichthyidae: *Normanichthys crockeri*, USNM 270261 (CS). Pataecidae: *Aetapcus maculatus*, BMNH 1865.5.29:1 (D). Percophididae: *Bembrops anatirostris*, USNM 278482 (CS), USNM 308117 (CS); *Hemerocoetes monopterygius*, USNM 214077 (CS); *Pteropsaron heemstrai*, USNM 265323 (CS). Phycidae: *Urophycis regius*, USNM 201669 (CS); *U. tenuis*, USNM 200115 (CS). Pinguipedidae: *Parapercis cephalopunctatus*, USNM 140786 (CS); *P. cylindrica*, USNM 177904 (CS); *Prolatilus jugularis*, USNM 176428 (CS). Scorpaenidae: *Scorpaenidae* sp., USNM 280116 (CS); *Inimicus* sp., USNM 269798 (CS); *Sebastes marinus*, USNM 188182 (CS); *Setarches longimanus*, USNM 136444 (CS); *Synanceia verrucosa*, USNM 149901 (CS). Trachinidae: *Trachinus draco*, USNM 198840 (CS). Trichodontidae: *Trichodon trichodon*, USNM 213532 (CS). Trichonotidae: *Trichonotus nikii*, USNM 265324 (CS); *T. setiger*, USNM 265627 (CS). Uranoscopidae: *Astroscopus ygraecum*, USNM 185669 (CS); *Gnathagnus egregius*, USNM 268441 (CS); *Kathetostoma albigutta*, USNM 185666 (CS); *Uranoscopus scaber*, USNM 198087 (CS), USNM 206551 (CS). A number of additional specimens among these groups from the collections of MPM and USNM were examined for external and muscle characters, but were not officially recorded. Examples of the Blennioidei and Gobioidi from MPM and USNM collections were also examined, but are too numerous to list.

Historical Review of Champsodontid Classification

Günther (1867), the author of *Champsodon*, placed it among the Trachinidae. Alcock (1899: 51) implied a relationship with the Chiasmodontidae by stating, "I feel pretty sure that its [*Chiasmodon*'s] place in the system is close to

Champsodon." Boulenger (1901) and Weber (1913) followed by placing *Champsodon* in the Chiasmodontidae. However, illustrating the confusion of the times, Boulenger (1901) placed *Centropercis* Ogilby, a synonym of *Champsodon*, with his Nototheniidae. Regan (1913) considered champsodontids deserving of a separate division, a ranking equivalent to present-day suborders such as the Percoidei and Trachinoidei, but he placed chiasmodontids with his trichiuroids (Regan, 1914). Jordan (1923) reiterated an alignment of the Champsodontidae with the Chiasmodontidae by placing them both within his series Uranoscopiformes. A close relationship between the two families was rejected by Norman (1929), but he offered no specific evidence; in 1957, Norman followed Regan (1913) and placed the Champsodontidae in its own division. Matsubara et al. (1964) provided a revision of the Japanese species and included a limited account of osteology and soft anatomy focussing on the hemal spines and air bladder, but these observations were not used to determine relationships. Greenwood et al. (1966) created a sixteen family Trachinoidei that included the Champsodontidae and Chiasmodontidae, whereas Gosline (1971) included both of these families in his Percoidei. Nelson followed Greenwood et al. (1966) in the 1976 edition of *Fishes of the World*, but in a subsequent edition (1984) substantially altered the composition of the Trachinoidei without explanation, although the Champsodontidae and Chiasmodontidae retained membership. Watson et al. (1984) included champsodontids and chiasmodontids in the Trachinoidei, but concluded that the suborder was probably polyphyletic and did not comment specifically on champsodontid relationships.

Pietsch (1989) provided the first cladistic analysis of the Trachinoidei while attempting to establish outgroup relationships for a study of the Uranoscopidae. Ten families were included in his phylogeny, which proposed a sister group relationship of Champsodontidae and Chiasmodontidae embedded within the middle of the group. Pietsch and Zabetian (1990) proposed a modified concept of the Trachinoidei (expanded to include the Ammodytidae), but retained a sister relationship between champsodontids and

chiasmodontids. A critical re-evaluation of Pietsch and Zabetian's evidence by Johnson (1993) suggested that the Trachinoidei sensu Pietsch and Zabetian was not adequately diagnosed, and noted that several, often informative, character complexes had not been considered. Given that these complexes exhibit morphological variation among the trachinoids, their inclusion would have considerably altered the conclusions of Pietsch (1989) and Pietsch and Zabetian (1990). Johnson (1993: 14) specifically questioned the champsodontid/chiasmodontid relationship, citing a number of trenchant differences in morphology of the dorsal-fin pterygiophores and gill arches. He implicated possible alternative phylogenetic placements of the champsodontids based on three unusual morphological characters: (1) superficial neuromasts (free sensory papillae of Johnson, 1993) on the head and body, shared with the Kurtoidei, Apogonidae and Gobioidae; (2) absence of a neural spine on the first vertebra, shared with the Blennioidei; or, most promising, (3) parietal spine with an opening for the supratemporal sensory canal, apparently uniquely shared with the Scorpaenoidei.

Mooi and Gill (1995) examined epaxial insertions on to dorsal-fin pterygiophores and determined that the variety of morphologies found among trachinoids (Types 0, 1, 2) would require a number of reversals and reacquisitions of states, casting further doubt on the integrity of the suborder as defined by Pietsch and Zabetian (1990). Of particular interest here is that chiasmodontids have no epaxial/dorsal pterygiophore insertions, whereas champsodontids exhibit attachments very similar to those found in the Scorpaenoidei, Serranidae, and a few other taxa. This provided an additional reason to question a close relationship between champsodontids and chiasmodontids, while lending a modicum of support to Johnson's (1993) suggestion that *Champsodon* could be a scorpaenoid.

Description of Champsodontid Morphology

Here we summarize osteological and myological anatomy of the Champsodontidae, focussing

particularly (but not exclusively) on apomorphic features that are either unique to the family or are unusual among Perciformes (sensu Mooi and Gill, 1995). The description is based on a fully developed specimen; consequently, figures showing larval morphology may not agree fully with the text as these specimens may not have attained a condition similar to that of adults.

Skull (Figs. 2, 3). — Serrated ridge runs contiguously along dorsal edge of nasal, along orbital margin of frontal, then branches laterally on to pterotic and medially on to parietal, the latter becoming produced as a parietal spine. Nasals with anterior lateral process for ligamentous attachment to maxilla. Frontals extend well on supraoccipital, lying between anterior halves of parietals. Parietals narrow, ending in posteriorly-produced spine, with spine base pierced by canal of supratemporal sensory system. Pterotics broad with prominent posterior, pointed spine. Median ethmoid flat dorsally without ridge for rostral cartilage, but extending posteriorly as vertical lamina to form bony interorbital septum, septum continuing in cartilage to join spatulate basisphenoid. Lateral ethmoids broad and flattened horizontally. Vomer broad anteriorly with very narrow shaft connecting to parasphenoid. Parasphenoid deeply forked posteriorly. Myodome present (not shown). Back of skull flattened vertically. Exoccipitals interdigitating with first vertebra.

Suspensorium, jaws, superficial bones of the head (Figs. 3–6). — Palatine edentate and unique in having two articulating heads for maxilla, one narrow and pointed for head of maxilla, the other ventral and cartilage-tipped, articulating with anterior maxillary shaft. Endopterygoid absent. Dorsoposterior face of ectopterygoid forms forked groove into which metapterygoid inserts, forming small pocket for muscle insertion. Metapterygoid interdigitating with hyomandibula via elongate dorsal processes. Hyomandibula with large anterolateral spur. Preopercle with large posteriorly-directed spine. Opercle moderately sized, fimbriate. Subopercle larger, fimbriate. Interopercle small, crescent-shaped, fimbriate. Dentary and anguloarticular each with two serrate ridges; coronoid process blunt with large cartilaginous edge posteriorly;

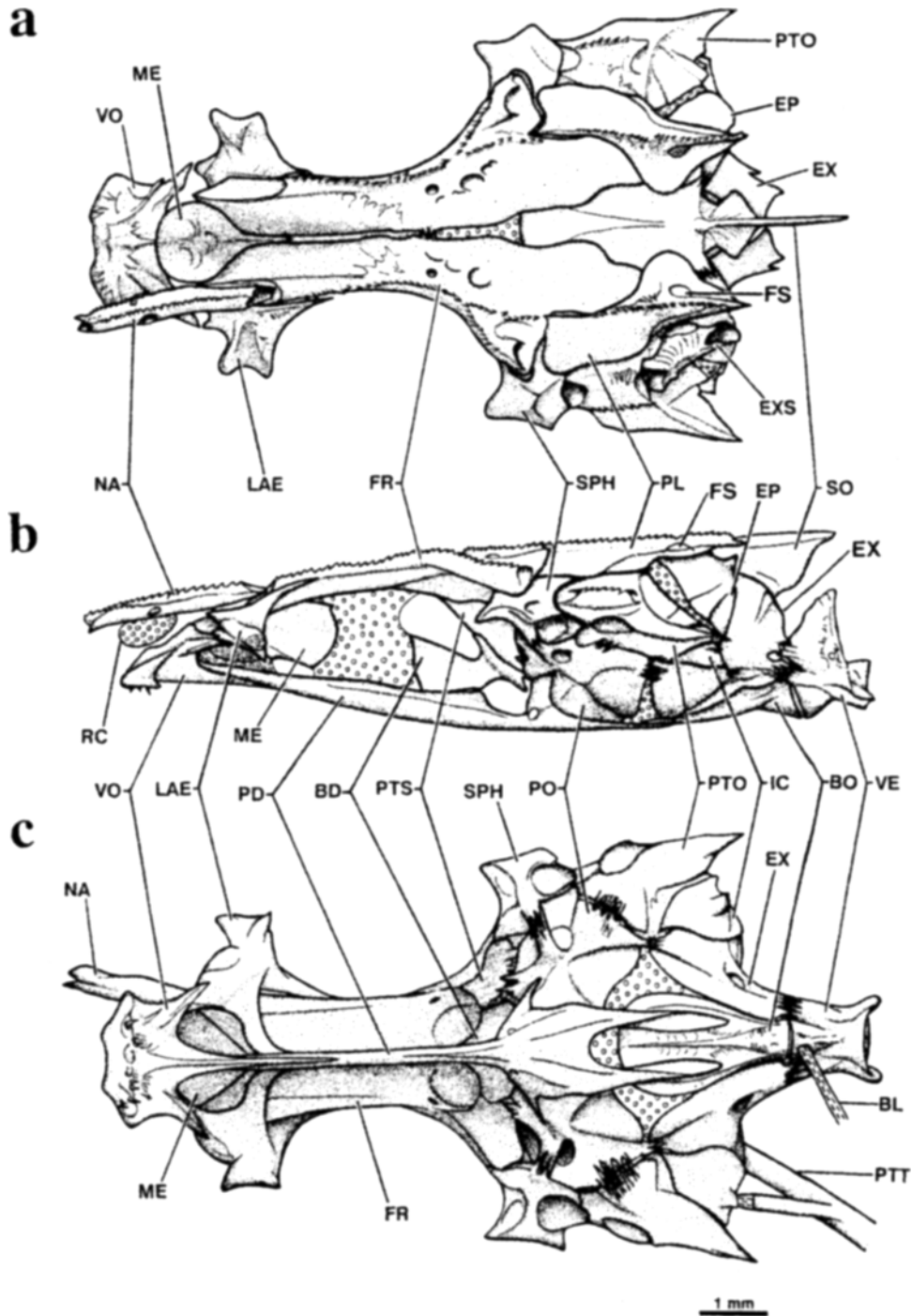


Fig. 2. Cranium of *Champsodon vorax*, USNM 245331, 50.1 mm SL. a) Dorsal view. Nasal bone and extrascapular removed from right side. b) Lateral view. First vertebra included, extrascapular removed. c) Ventral view. First vertebra and right posttemporal included. *BD*—basisphenoid; *BL*—Baudelot's ligament; *BO*—basioccipital; *EP*—epioccipital; *EX*—exoccipital; *EXS*—extrascapular; *FR*—frontal; *FS*—foramen for bone-enclosed sensory canal in base of parietal spine; *IC*—intercalar; *LAE*—lateral ethmoid; *ME*—mesethmoid; *NA*—nasal; *PD*—parasphenoid; *PL*—parietal; *PO*—prootic; *PTO*—pteric; *PTS*—pterosphenoid; *PTT*—posttemporal; *RC*—rostral cartilage; *SO*—supraoccipital; *SPH*—sphenotic; *VE*—first vertebra; *VO*—vomer. Cartilage open circles. Ligaments dashed.

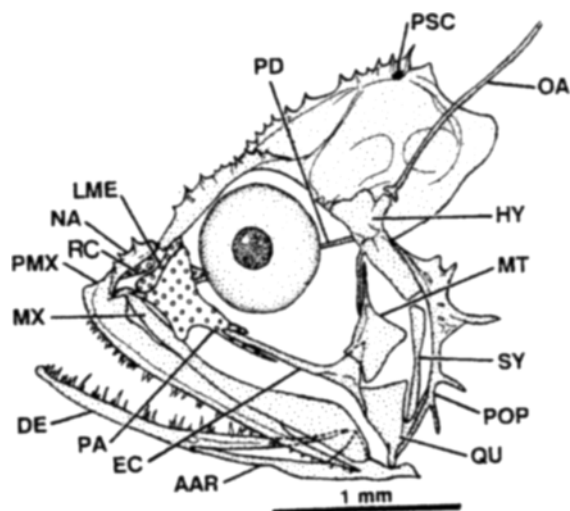


Fig. 3. Cranium and suspensorium of 7 mm SL *Champsodon* sp., AMS UN.91113-004. Note canal at base of parietal spine. *AAR*—anguloarticular+retroarticular; *DE*—dentary; *EC*—ectopterygoid; *HY*—hyomandibula; *LME*—lateral+medial ethmoids; *MX*—maxilla; *MT*—metapterygoid; *NA*—nasal; *OA*—opercular appendage; *PA*—palatine; *PD*—parasphe-noid; *PMX*—premaxilla; *POP*—preopercle; *PSC*—parietal spine canal; *QU*—quadrate; *RC*—rostral cartilage; *SY*—symplectic. Ventral opercular bones not shown. Cartilage open circles. Dashed lines show medial, hidden portions of select elements.

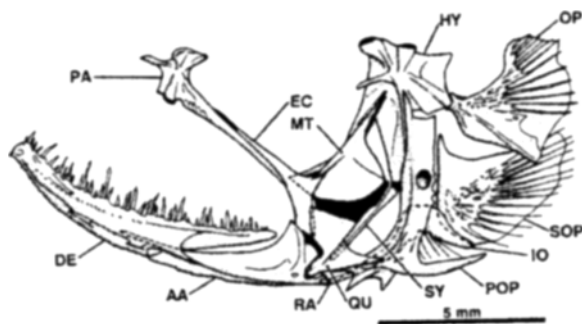


Fig. 4. Suspensorium of *Champsodon vorax*, USNM 245331, 50.1 mm SL. *AA*—anguloarticular; *IO*—interopercle; *OP*—opercle; *RA*—retroarticular; *SOP*—subopercle. Other abbreviations as in Fig. 3. Cartilage solid black. Dashed lines show medial, hidden portions of bones.

dentary teeth, all depressible (Type 4 of Fink, 1981), arranged in three main rows, except anteriorly: outer row of small, slightly hooked, conical teeth positioned laterally outside gape run-

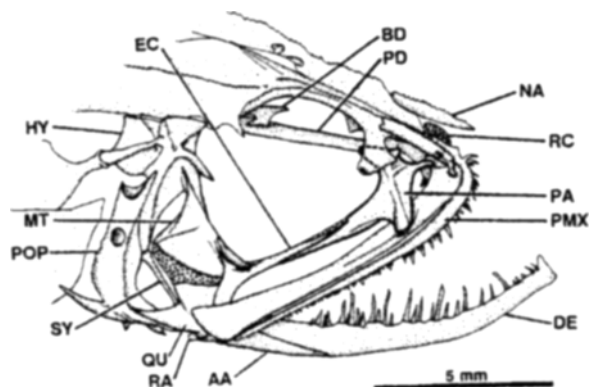


Fig. 5. Dorsolateral view of right suspensorium of *Champsodon vorax*, USNM 245331, 50.1 mm SL. *BD*—basisphenoid. Other abbreviations as in Figs. 2, 3, 4.

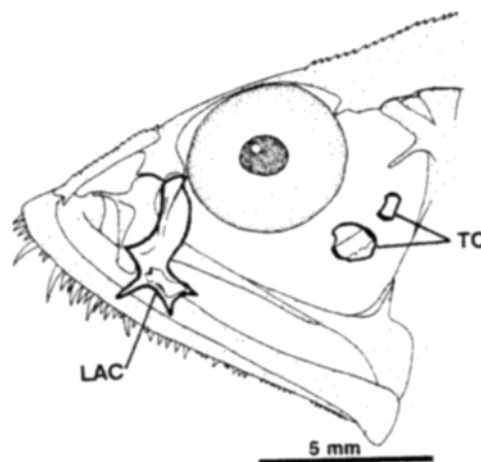


Fig. 6. Infraorbital series of *Champsodon vorax*, USNM 245331, 50.1 mm SL. *LAC*—lacrimal; *TO*—tubed ossicles.

ning over half dentary length; inner and middle rows adjacent and in gape, inner row with both long and short teeth interspersed, middle row with short teeth only. Long teeth with arrow-head-shaped tips. Anteriorly, many small teeth clustered about symphysis.

Maxilla broad, especially at neck of maxillary head forming articulation with ventral process of palatine. No supramaxilla. Premaxilla with very short ascending process closely attaching to rostral cartilage. In most species, notch lateral to symphysis particularly obvious in dorsal view. Premaxillary teeth depressible (Type 4 of Fink,

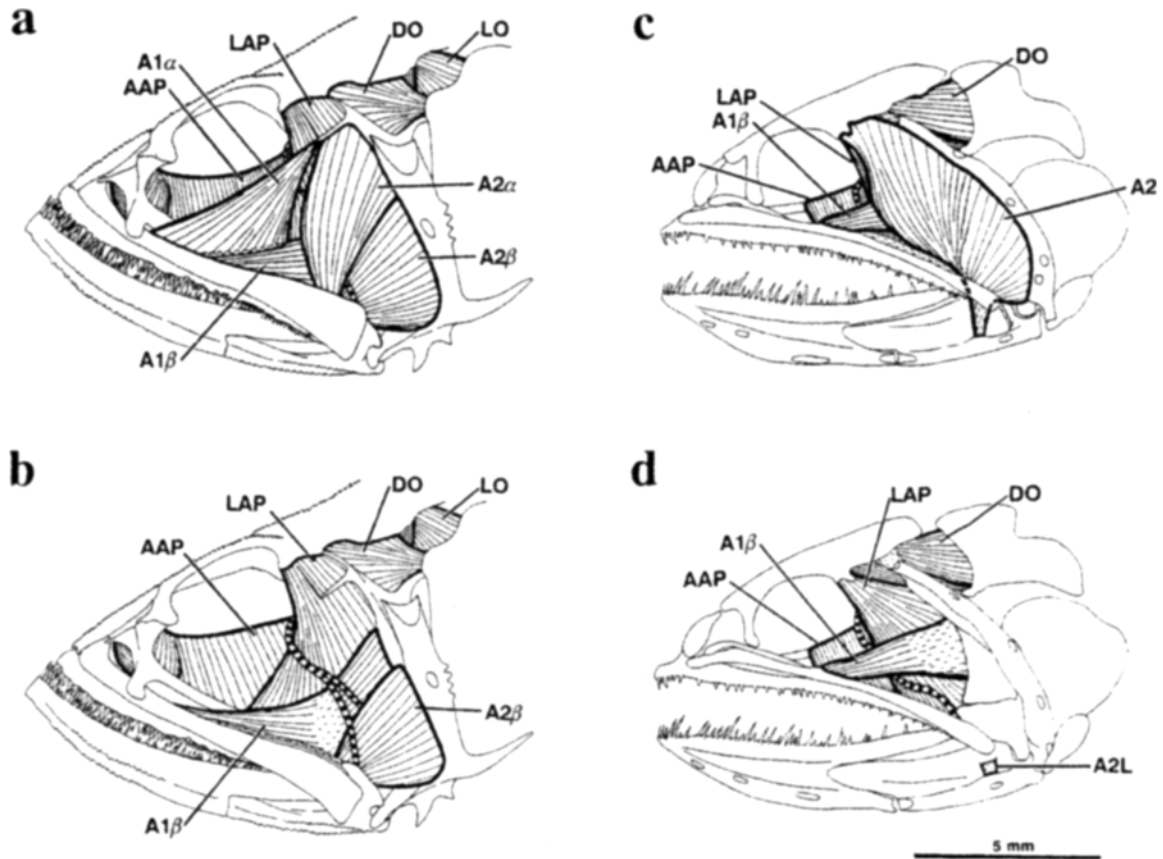


Fig. 7. Left lateral view of cheek musculature of champsodontids and chiasmodontids. a) *Champsodon vorax*, USNM 245331; b) as a) but with $A1\alpha$ and $A2\alpha$ removed to show $A1\beta$; c) *Pseudoscopus* sp., USNM 189130; d) as c) but with $A2$ and $A3$ (not shown) removed. *AAP*—adductor arcus palatini; $A1\alpha$, $A1\beta$, $A2$, $A2\alpha$, $A2\beta$ —sections of the adductor mandibulae; *A2L*—cut ligament of $A2$; *DO*—dilator operculi; *LAP*—levator arcus palatini; *LO*—levator operculi. Cartilage open circles.

1981) and in two rows (except anteriorly), the outer of small, closely spaced hooked teeth, the inner of longer curved teeth. Anteriorly, numerous small teeth clustered about symphysis.

Infraorbital series greatly reduced in number, including only large, spiny lacrimal and two or three posterior ossicles, all separate from one another. Lacrimal upright with strong articulation with lateral ethmoid acting as additional brace for maxilla. Ventral half of lacrimal (bearing the sensory canal) with four pointed processes, posterior three produced as external spines, anterior-most pointing anteroventrally or anteriorly and not visible externally. Two or three small tubular ossicles at or beyond posterior margin of orbit, but not closely associated with orbit; most poste-

rior ossicle overlying (or almost so) hyomandibular spur. Ossicles resemble modified scales found intermittently along lateral line.

Cheek musculature (Fig. 7a, b).—Adductor mandibulae divided into several recognizable sections. $A1\alpha$ thin, triangular sheet of muscle originating from tip of hyomandibular spur and inserting broadly along dorsal (lateral) edge of maxilla, some posterior fibers sharing tendinous insertion of $A1\beta$. $A1\beta$ medial to $A2$ sections and ramus mandibularis V, originating from lower arm of hyomandibula and head of symplectic as muscle fiber, narrowing to fascia only, and becoming fibers once again to insert via narrow tendon onto dorsal edge of maxilla; tendon shared by some posterior fibers of $A1\alpha$. Upper

portion of $A1\beta$ shares some fibers with $A2\beta$. $A2$ sections also share fibers with each other where ramus mandibularis nerve pierces muscle to run laterally before continuing to lower jaw, but sections clearly separate elsewhere. $A2\alpha$ originates from hyomandibular spur, posterior to origin of $A1\alpha$ and anterolateral surface of hyomandibula and inserts on lower jaw. $A2\beta$ originates from ventral arm of hyomandibula and preopercular angle and inserts on lower jaw.

Levator arcus palatini originates from sphenotic, with perhaps some fibers from pterotic. It inserts onto hyomandibular spur, anterolateral hyomandibular surface, ectopterygoid, and metapterygoid, particularly ecto-metapterygoid "pocket" formed at joint between these two bones. Adductor arcus palatini originates along length of parasphenoid and is continuous with anterior fibers from lateral ethmoid and vomer. These insert on medial surfaces of palatine, ectopterygoid, metapterygoid and hyomandibula. Origin of adductor arcus palatini from vomer unusual among perciforms (present in the cichlid genus *Trematocara* [Stiassny, 1981: 87, fig. 14]); antermost fibers that insert onto palatine and originate from median ethmoid and vomer do not appear referable to retractor arcus palatini as described in Winterbottom (1974: 241), a separate muscle occurring in acanthuroids and some tetraodontiforms.

Branchial and hyoid arches (Figs. 8–11).—Infrapharyngobranchial 1 absent. Uncinate process of epibranchial 1 in line with main shaft, and interarcual cartilage short, robust, and triangular. Epibranchial 1 with tip of main shaft displaced laterally and supporting ligament running to midventral edge of opercle bearing pseudo-branch. Ceratobranchials elongate, ceratobranchials 3 and 4 with gill rakers in form of flattened toothplates. Basibranchial 1 and anterior portion of basibranchial 2 ventrally expanded to form keel for articulation with urohyal.

Basihyal absent. Dorsal hypohyals with triangular processes meeting dorsal to basibranchial 1. Urohyal short with bifurcate articular head meeting cartilaginous keel of basibranchial 1. Posterior part of urohyal folded ventrally. Ceratohyals elongate and deeply interdigitated. Seven

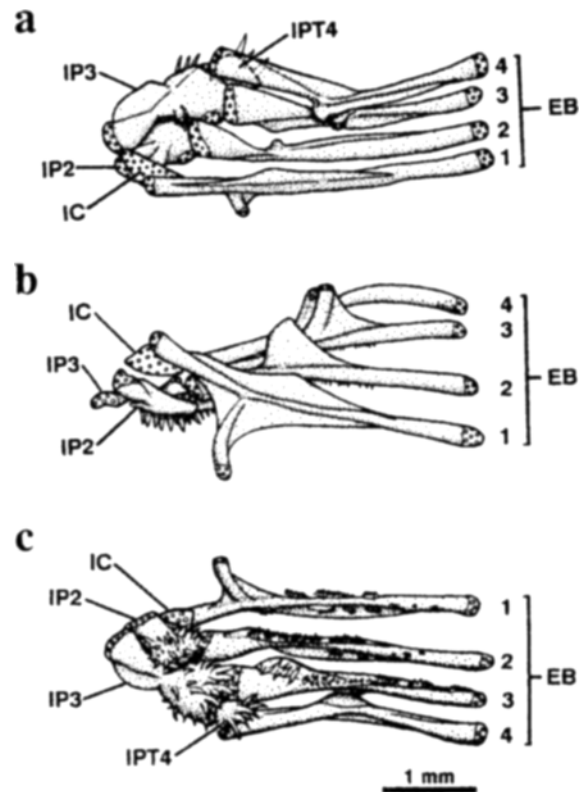


Fig. 8. Dorsal gill arches of *Champsodon vorax*, USNM 245331, 50.1 mm SL. a) Dorsal view; b) anterior view; c) ventral view. EB1–4—epibranchials; IC—interarcual cartilage; IP2–3—infrapharyngobranchials; IPT4—toothplate of infrapharyngobranchial 4. Cartilage open circles.

slender branchiostegal rays, four articulating with anterior ceratohyal, one with cartilaginous joint between anterior and posterior ceratohyals, and two with posterior ceratohyal; anterior three rays articulate medially, remaining laterally.

Dorsal gill arch musculature (Fig. 12).—Transversus dorsalis anterior originates from median septum, inserting on tip of epibranchial 1, proximal tip of interarcual cartilage, lateral surface of epibranchial 2. Transversus dorsalis posterior inserts on fourth epibranchials. Obliquus dorsalis originates from uncinata processes of epibranchials 3 and 4, inserting on dorsal surface of infrapharyngobranchial 3 with some fibers to interarcual cartilage. Anterior levator internus (=levator internus II of Winterbottom, 1974) inserts on lateral surface of large anterior process of infrapharyngobranchial 3,

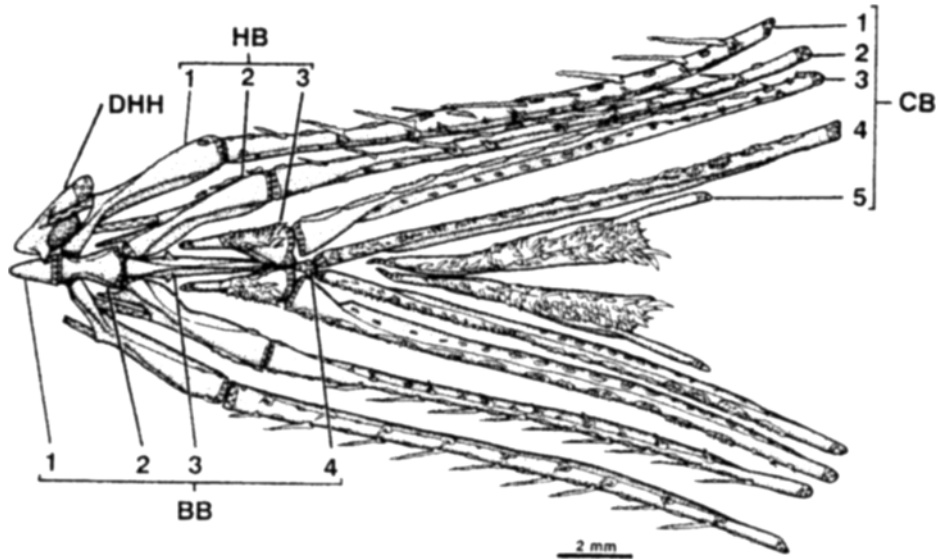


Fig. 9. Dorsal view of ventral gill arches of *Champsodon vorax*, USNM 245331, 50.1 mm SL. *BB1-4*—basibranchials; *CB1-5*—ceratobranchials; *DHH*—dorsal hypohyal; *HB1-3*—hypobranchials. Cartilage open circles. Ligaments dashed.

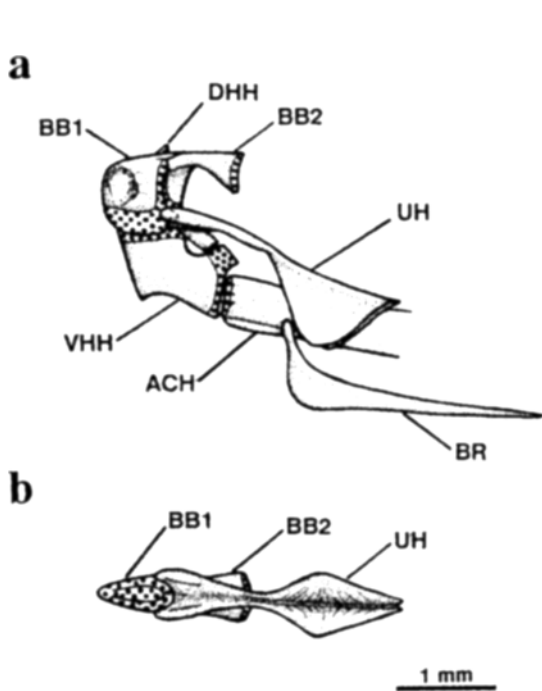


Fig. 10. Urohyal and anterior hyoid arch of *Champsodon vorax*, USNM 245331, 50.1 mm SL. a) Medial view of right side; b) ventral view. *ACH*—anterior ceratohyal; *BB1-2*—basibranchials; *BR*—first branchiostegal ray; *DHH*—dorsal hypohyal; *UH*—urohyal; *VHH*—ventral hypohyal. Cartilage closed circles.

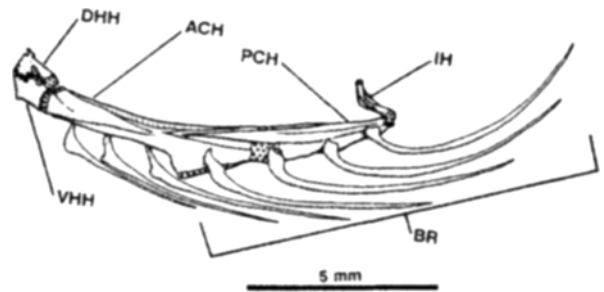


Fig. 11. Lateral view of left hyoid bar of *Champsodon vorax*, USNM 245331, 50.1 mm SL. *IH*—interhyal; *PCH*—posterior ceratohyal. Other abbreviations as Fig. 10. Cartilage closed circles.

perhaps with a few fibers to dorsal surface of infrapharyngobranchial 2. Posterior levator internus (=levator internus III of Winterbottom, 1974) inserts on lateral surface of anterior shaft of epibranchial 3 after passing through the obliquus dorsalis. Levatores externi 1 and 2 insert on uncinata process of first and second epibranchial, respectively. Third levator externus inserts onto closely applied uncinata processes of third and fourth epibranchial. Fourth levator externus inserts on dorsal and medial surface of posterior half of epibranchial 4. Levator posterior absent. Retractor dorsalis inserts on medial

surfaces of third infrapharyngobranchial and fourth infrapharyngobranchial toothplate.

Paired fins (Figs. 13–15). — Pectoral girdle narrow and reduced. Pectoral fin small, with accordingly small actinosts, scapula, and coracoid. Posttemporal with two serrate ridges on dorsal arm, ending in spine posteriorly. Cleithra elongate and extending far beyond coracoids to meet midventrally between posterior tips of anguloarticulars. Two robust postcleithra. Baudelot's ligament from first vertebra, bifid distally to pass on either side of cleithral process before inserting on supracleithrum.

Pelvic girdle and fins large. Ventral iliac spur and anterior pelvic process of each basipterygium very long and broad, almost meeting each other via angled tips. Posterior pelvic processes laminar and triangular, widely spaced. Pelvic rays share one large, autogenous, ball-like cartilaginous radial that is grooved for rotation about posterior edge of basipterygium. Dorsal half of medial (5th) ray with greatly expanded proximal articular head that serves as insertion point for hypaxial musculature and extensor proprius. Ventral half of medial ray with very large cartilage-tipped process at its base assumed to originate from fusion with elongate medial radial during ontogeny (Johnson, 1992) (Fig. 15a).

Pelvic-fin musculature (Fig. 16). — All dorsal muscles except arrector dorsalis originate from cleithrum. Extensor proprius inserts onto large dorsal process of medial (5th) ray only. Hypaxial fibers also insert onto posterior face of medial ray dorsal process. Adductor superficialis and profundus insert onto spine and all rays. Arrector dorsalis originates from lateral face of basipterygium. Ventral musculature not unusual compared to most percoids.

Vertebral column and unpaired fins (Figs. 17, 18). — Vertebrae 11–13+18–20=29–33, broadly overlapping among species. No epineural on first vertebra (contra Johnson and Patterson, 1995: 46), 6–8 ossified epineurals on 2nd through 9th vertebra, pleural ribs on third vertebra to last abdominal vertebra, large paraphophyses beginning on 4th vertebra. Neural spine on first vertebra very short or absent (Fig. 2b). Second centrum shorter than first or third; third neural spine broadened distally and closely associated

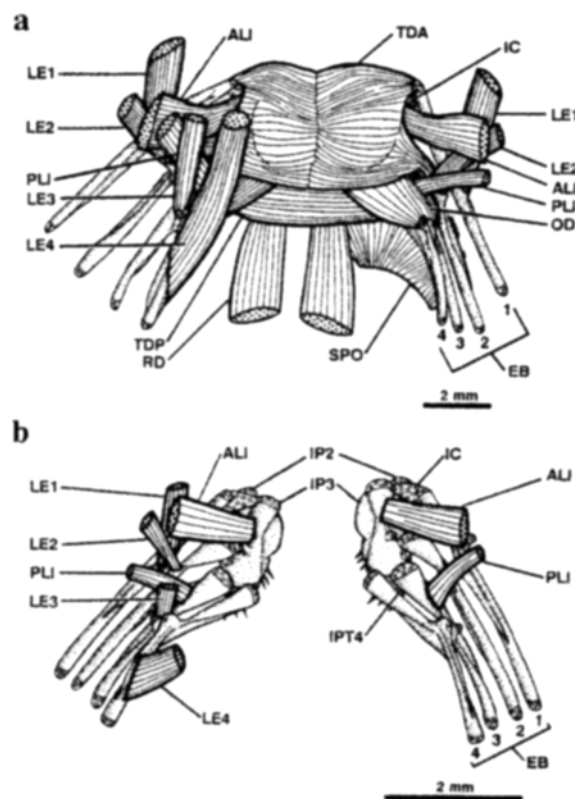


Fig. 12. Dorsal view of upper gill arch musculature. Anterior to top. a) *Champsodon nudivittis*, USNM 297753, 90.0 mm SL. All muscles intact on left side, LE3+4 removed from right side. Note PLI pierces OD. b) *C. vorax*, USNM 245331, 50.1 mm SL. Left side showing LE and LI insertions, right side LI only. ALI—anterior levator internus; EB1–4—epibranchials; IC—interarcual cartilage; IP2–3—infrapharyngobranchials; IPT4—toothplate of infrapharyngobranchial 4; LE1–4—levator externi; OD—obliquus dorsalis; PLI—posterior levator internus; RD—retractor dorsalis; SPO—sphincter oesophagi; TDA—transversus dorsalis anterior; TDP—transversus dorsalis posterior. Cartilage open circles. Cut muscle surfaces closed circles.

with first dorsal-fin pterygiophore (Fig. 17). Neural and haemal spines begin to broaden slightly at PU4, become broadly triangular on PU3, and extremely broad on PU2 (Fig. 18). Some species with vertically-ribbed expansions of anterior 5–10 haemal spines forming gradually narrowing tube surrounding posterior extension of the swimbladder (Matsubara et al., 1964: figs. 2a, 4a, 5c, 6c; Nemeth, 1994: fig. 3).

Caudal elements fused and reduced. Hypurals 1–4 fused to each other and to parhypural and

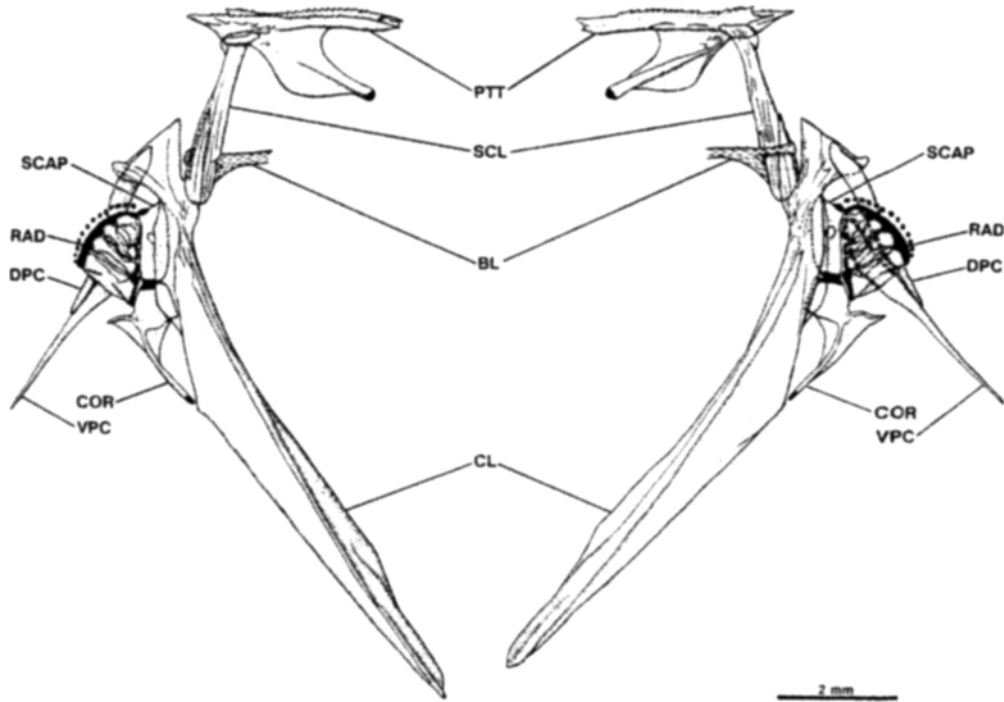
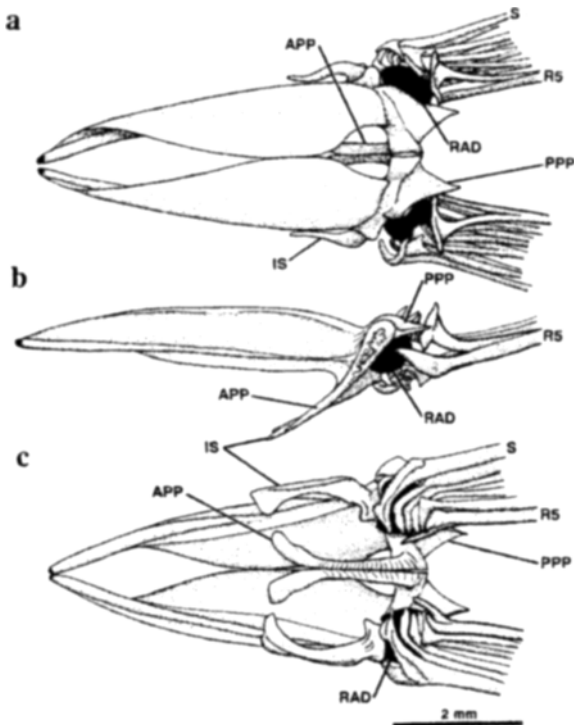


Fig. 13. Pectoral girdle osteology of *Champsodon vorax*, USNM 245331, 50.1 mm SL. Lateral view of right side (*left*); medial view of right side (*right*). *BL*—Baudelot's ligament; *CL*—cleithrum; *COR*—coracoid; *DPC*—dorsal postcleithrum; *PTT*—posttemporal; *RAD*—pectoral radials; *SCAP*—scapula; *SCL*—supracleithrum; *VPC*—ventral postcleithrum. Cartilage solid black. Hidden elements dotted. Ligaments dashed. Outlines of postcleithra overlying radials in medial view shown as open squares.



urostyler complex, with posteriorly directed "pockets" basally for muscle origins. Hypural 5 absent. Parhypural broad with horizontally expanded parhypurapophysis. No autogenous uro-neurals. Three epurals. Few autogenous cartilaginous elements, with only rodlike PU3 inter-haemal spine cartilage lying along ventro-posterior edge of PU2 spine and square PU2 post-haemal spine cartilage (Fig. 18; cf. Fujita, 1990: 616, fig. 435). Branched caudal rays 7+6, rays articulating with hypural plates 8+7, long proximal articulations on dorsal and ventral rays becoming progressively shorter on middle rays, two middle rays with relatively little hypural contact but with pointed lateral processes for

Fig. 14. Pelvic girdle osteology of *Champsodon vorax*, USNM 245331, 50.1 mm SL. a) Dorsal view; b) medial view of right basipterygium; c) ventral view. *APP*—anterior pelvic process; *IS*—iliac spur; *PPP*—posterior pelvic process; *RAD*—radial; *R5*—fifth or medial segmented ray; *S*—pelvic spine.

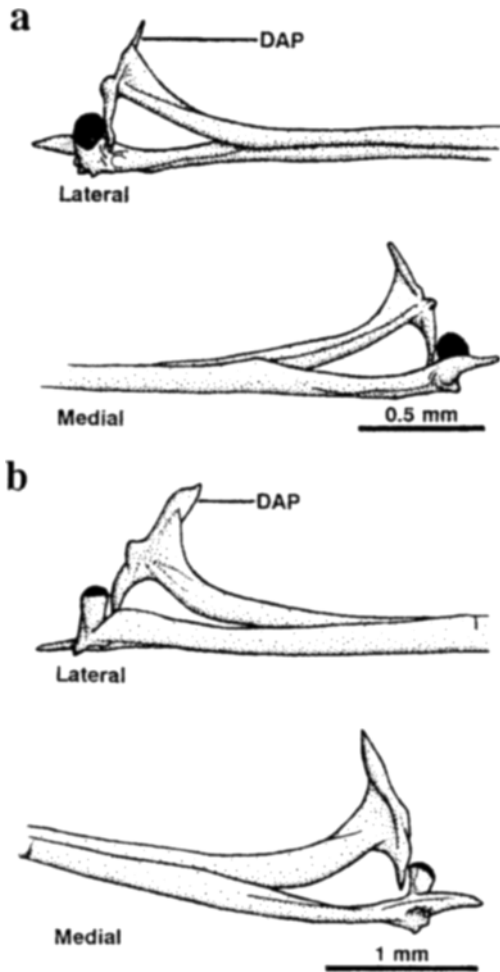


Fig. 15. Lateral and medial views of medial pelvic ray base of *Champsodon vorax*, USNM 245331. a) 17.2 mm SL; b) 50.1 mm SL. DAP—dorsal auxillary process for muscle insertion. Cartilage solid black.

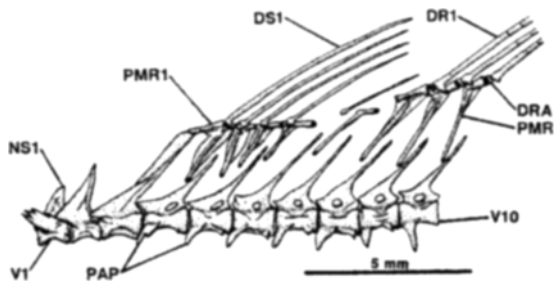


Fig. 17. First ten vertebrae and associated dorsal-fin elements of *Champsodon vorax*, USNM 245331, 50.1 mm SL. Pleural and epineural ribs not shown. DRA—distal radial; DR1—first dorsal segmented ray; DS1—first dorsal spine; NS1—first neural spine; PAP—parapophysis; PMR—proximal-middle radial; PMR1—first proximal-middle radial; V1—first vertebra; V10—tenth vertebra. Cartilage solid black.

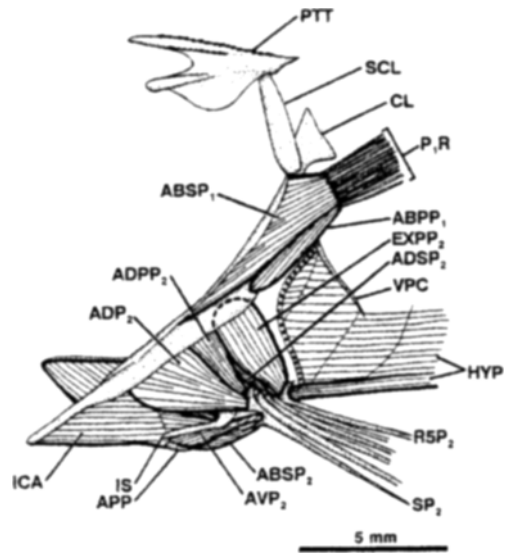


Fig. 16. Left lateral view of pelvic girdle musculature of *Champsodon vorax*, USNM 245331, 54.0 mm SL. Dotted line indicates origin of extensor proprius pelvius from the cleithrum. ABSP₁—abductor superficialis pectoralis; ABSP₂—abductor superficialis pelvius; ABPP₁—abductor profundus pectoralis; ADP₂—arrector dorsalis pelvius; ADPP₂—adductor profundus pelvius; ADSP₂—adductor superficialis pelvius; APP—anterior pelvic process; AVP₂—arrector ventralis pelvius; CL—cleithrum; EXPP₂—extensor proprius pelvius; HYP—hypaxialis; ICA—infracarinalis anterior; IS—iliac spur; PTT—post-temporal; P,R—pectoral rays; R5P₂—fifth pelvic segmented ray; SCL—supracleithrum; SP₂—pelvic spine; VPC—ventral postcleithrum.

muscle insertions. Procurrent rays 10+10 including 2+2 short segmented rays not associated with hypurals; anterior dorsal procurrent rays atypical in having broad, scalloped distal tips.

Dorsal fin normally with five weak spines (some authors report VI, e.g., Nemeth, 1994, but we have not seen this) (Fig. 17). No supraneurals. Spine-bearing pterygiophores without distal radials. Cartilage-tipped proximal-middle radials of first three pterygiophores insert into cup-shaped sockets of following pterygiophores. First pterygiophore with anterodorsal process that overlies distal tip of broadened third vertebral neural spine, bearing single supernumerary spine. Fifth pterygiophore not closely associated with other pterygiophores, and spineless. Fifth spine floats free in muscle, not closely associated with either its serially or secondarily associated

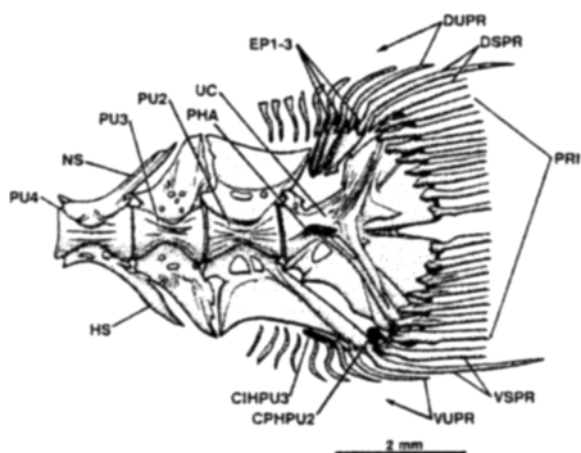


Fig. 18. Caudal osteology of *Champsodon vorax*, USNM 245331, 50.1 mm SL. *CIHPU3*—interhaemal spine cartilage between PU2 and PU3; *CPHPU2*—post-haemal spine cartilage after PU2; *DUSR*—dorsal segmented procurrent rays; *DUPR*—dorsal unsegmented procurrent rays; *EPI-3*—epurals; *HS*—haemal spine; *NS*—neural spine; *PRI*—principal caudal rays; *PHA*—parhypurapophysis; *PU2-4*—preural centra; *UC*—ural centrum complex of centra, hypurals, parhypural; *VSPR*—ventral segmented procurrent rays; *VUPR*—ventral unsegmented procurrent rays. Cartilage solid black.

pterygiophores (4th and 5th, respectively). Spines with open base rather than closed bony ring for articulation with pterygiophore.

Segmented ray portion of dorsal fin beginning with sixth pterygiophore, which does not bear supernumerary spine. First 2–4 ray-bearing pterygiophores (6th–9th pterygiophores) with fused proximal-middle elements and separate distal radials, following pterygiophores trisegmented with separate proximal, middle and distal radials. First 2–3 rays unbranched, remainder branched. Primarily 1:1 relationship of fin elements and vertebrae except in some species at 12th or 13th interneural space and/or 24th or 25th interneural space, where two pterygiophores may be present; these variable patterns determine number of segmented rays. Dorsal-fin formula of *Champsodon vorax*, V, 20: ///II/I+I/LP/1/1/1/1/1/1+1/1/1/1/1/1/1/1/1/1/1/1.

All anal fin-rays segmented (contra Nelson, 1994: 396), first two unbranched. First pterygiophore bears supernumerary ray and its associ-

ated distal radial. Anterior 2–4 pterygiophores with fused proximal-middle radials and autogenous distals, remaining pterygiophores trisegmented with separate proximal, middle, and distal radials. Three to four pterygiophores anterior to first haemal spine (anal-fin formula, first eight pterygiophores: 1+1+1/1/1+1/1/1 or 1+1+1+1/1+1/1/1).

Epaxial musculature.—Type 1 morphology of Mooi and Gill (1995). Separate slip of muscle to 2nd–4th pterygiophores, with additional insertions onto 5th and 6th pterygiophores (Fig. 19a).

Miscellaneous.—Head and body with series of superficial neuromasts (Fig. 1a). Head papillae densest dorsally with longitudinal and transverse rows on frontals and posterior skull, but also occurring on cheeks and dentaries. Those on body in two horizontal rows, one dorsal the other ventral, connected by intermittent vertical rows, often more prominent ventrally.

Scales not overlapping, each with a round, concave and embedded scale base, with a narrow, bony pedicel supporting and elevating a square or heart-shaped plate bearing robust spines on its lateral and posterior margins (Type 5 spinoid of Roberts, 1993: 86, fig. 19e, f). Some scales curved and kidney-shaped or otherwise modified in pairs or individually to form lateral-line tubes. Posterior ossicles of infraorbital series might be modified scales.

Nasal rosette usually vertically oriented with lamellae forming a crescent, sometimes horizontally oriented with lamellae radiating from a central rachis (Fig. 20).

Eye with dorsal lappet or cirrus, ventral margin of pupil indented by semicircular tab of iris in most species. Airbladder elongate and fusiform with bluntly rounded anterior end and tapering posterior end, the latter often penetrating haemal canal.

Larval features.—Unique attenuate and elongate opercular appendage of up to 40 per cent notochord length, which persists into postflexion stage (up to 10 mm SL) (Watson, 1989). Serrate ridges on head appear early in ontogeny (less than 4 mm notochord length). Prominent gas bladder and short, coiled gut.

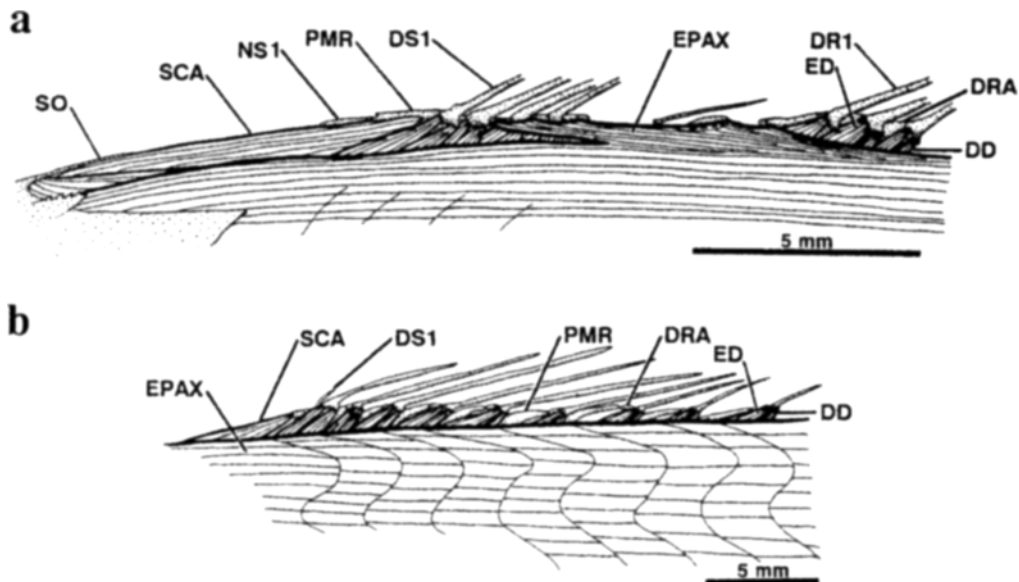


Fig. 19. Epaxial musculature. a) *Champsodon vorax*, USNM 245331, 54.0 mm SL; b) *Kali macroura*, USNM 207608, 111.5 mm SL. *DD*—depressores dorsales; *DRA*—distal radial; *DR1*—first dorsal segmented ray; *DS1*—first dorsal spine; *ED*—erectores dorsales; *EPAX*—epaxialis; *NS1*—third neural spine; *PMR*—proximal-middle radial; *SCA*—supracarinalis anterior; *SO*—supraoccipital. Bones stippled.

Discussion

Champsodontids are very unusual fishes. Their ambiguous systematic position is understandable given the impressive number of apparently unique morphological characteristics they possess. Indeed, the bizarre features are a distraction from the seemingly less impressive (but often unusual) characters shared with other taxa that might help resolve their phylogenetic relationships. In this discussion, we first provide a summary list of the autapomorphies of the family and then briefly examine some characters that vary among champsodontids. The latter should help determine intrarelationships when a sister taxon is more clearly identified. We then re-examine the evidence for the current position of the Champsodontidae within the Trachinoidei and as sister taxon to the Chiasmodontidae. Because we find this evidence unconvincing, we explore other possible relationships by focussing on the unusual champsodontid characters and on the taxonomic groups that share them.

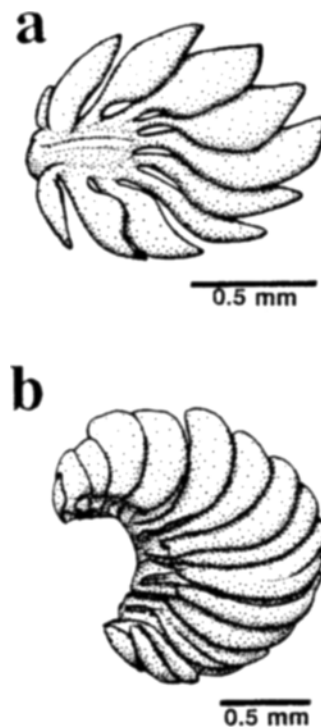


Fig. 20. Left lateral view of the two nasal rosette morphologies in *Champsodon*. a) *C. atridorsalis*, USNM 297752, 83.5 mm SL; b) *C. capensis*, USNM 307518, 93.0 mm SL.

Table 1. Distribution of select character states among *Champsodon* species, the "atridorsalis" group (5 species) followed by the "vorax" group (8 species). Vertebral and segmented dorsal- and anal-fin ray counts taken from Nemeth (1994: 370-1)

	Expanded haemal arches	Premaxillary notch	Nasal rosette orientation	Dorsal ray modal count > 20	Anal ray modal count > 18	Ant. lacrimal spine orientation	Iris tab	Eye cirrus	Fleshy eye tabs	Scaled chin	Scaled belly	Vertebral number (mode)
<i>atridorsalis</i>	+	shallow	H	+	+	+	+	+	+	+	-	30-33 (32)
<i>guentheri</i>	+	-	H	+	+	+	-	-	-	+	-	31
<i>longipinnis</i>	+	-	H	+	+	+	+	+	+	+	+-	31-32 (31)
<i>machaeratus</i>	+	-	?	+	+	+	-	-	-	+	-	30-31 (31)
<i>pantolepis</i>	+	-	?	+	+	+	-	-	-	+	+	31
<i>capensis</i>	-	+	V	-	-	-	+	+	-	-	+	30-32 (31)
<i>fimbriatus</i>	-	+	V	-	-	-	+	+	-	+	+	29-31 (30)
<i>nudivittis</i>	-	+	V	-	-	-	+	+	-	-	-	30-31 (31)
<i>omanensis</i>	-	+	V	-	-	-	+	+	-	+	+	31
<i>sagittus</i>	-	shallow	V	-	-	+	+	+	-	-	-	31
<i>sechellensis</i>	-	+	V	-	-	-	+	+	-	+	+-	31
<i>snyderi</i>	-	+	V	-	-	-	+	+	-	-	-	30-32 (31)
<i>vorax</i>	-	+	V	-	-	-	+	+	-	+	+-	31

+, present; -, absent; H, horizontally oriented nasal rosette; V, vertically oriented nasal rosette; ?, condition unknown.

Autapomorphies

The Champsodontidae possess a number of features that assure monophyly of the family because they are not presently known from any other perciform taxon or are sufficiently unusual to strongly suggest monophyly. These include: exoccipitals interdigitating with first vertebra, double-headed articulation of the palatine with the maxilla, distinctive $A1\alpha/A1\beta$ arrangement with the the triangular $A1\alpha$ originating from the hyomandibular spur sharing a tendinous insertion onto the maxilla with an $A1\beta$ that originates medial to $A2$, vomerine origin of a portion of the adductor arcus palatini that inserts onto the palatine, epibranchial I with uncinat process in line with main shaft and anterior end of main shaft directed ventrally and supporting a ligament to the opercle that bears the pseudobranch, a shift of the insertion of the posterior levator internus (=levator internus III of Winterbottom, 1974) from the third infrapharyngobranchial to the third epibranchial, a very large ball-like pelvic radial with a groove for rotation about the posterior edge of the basipterygium, hypaxial muscle insertion onto the medial pelvic-fin ray and a large process from the base of the dorsal half of ray for this insertion, no epineural on first vertebra, third neural spine broadened distally and closely associated with first dorsal-fin pterygiophore, very broad neural and haemal spines on PU2, horizontally expanded parhypurapophysis, anterior procurrent rays with broad and scalloped distal tips, spine-bearing pterygiophores without distal radials and cartilage-tipped proximal-middle radial of first three pterygiophores inserting into cup-shaped sockets of succeeding pterygiophores, first pterygiophore with forked anterodorsal process that surrounds distal tip of broadened third vertebral neural spine, larvae with opercular appendage.

Intrarelationships

Although intrarelationships of *Champsodon* are beyond the scope of this paper, we have noted a number of characters that vary among species and some of these exhibit correlated distributions (Table 1). Without a clearer hypothesis

of sister group relationships, polarization and application of these characters towards a phylogeny is not possible at present, but we offer them as a starting point for future champsodontid workers. The 13 species can be divided into two groups based on the presence or absence of expanded haemal arches, an "atridorsalis" group consisting of five species (*C. atridorsalis*, *C. guentheri*, *C. longipinnis*, *C. machaeratus*, and *C. pantolepis*) and a "vorax" group (8 remaining species) (Table 1). The following additional characters are consistent with these groupings: presence or absence of a premaxillary notch just lateral to the symphysis, nasal rosette lamellae orientation (Fig. 20), dorsal- and anal-fin segmented ray modal counts (which are not correlated with vertebral number, Table 1), and (possibly) orientation of the anterior lacrimal spine. These characters might support both or only one of these recognizable groups as monophyletic. The remaining characters listed in Table 1 could either support relationships within these two groups or suggest alternative hypotheses among the species. Other features that vary, but provide less clear-cut groupings, include patterns of scalation on the chin and ventral part of the abdomen, scalation around superficial neuromast rows, and the occurrence of elongate livers that extend posteriorly into the body cavity (the latter present in *C. guentheri* and *C. nudivittis* and absent in *C. atridorsalis* and *C. fimbriatus*, the four species examined for this feature). Larvae have been recognized as two types: a "robust" form with more head spination earlier in ontogeny, and a "slender" form that acquires fewer spines later in development (Watson, 1989). Although species identification of larvae is not possible, it appears that the slender form is consistent with the *atridorsalis* group and the robust form represents the larval type of the *vorax* group.

Interrelationships

Trachinoidei. — As outlined in the historical review, the Champsodontidae have been placed among the Trachinoidei for much of this century. The suborder has been used as a repository for morphologically unusual groups that could not be convincingly placed elsewhere, and as a result

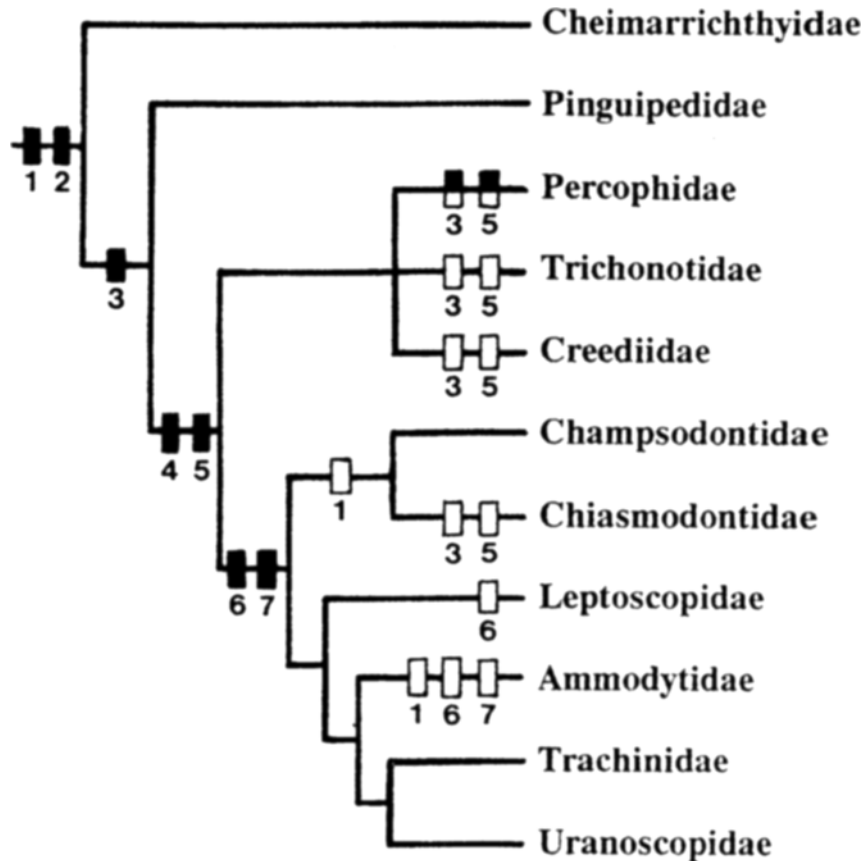


Fig. 21. Cladogram of proposed phylogenetic relationships of the trachinoids after Pietsch and Zabetian (1990: fig. 21) that is here re-evaluated. Closed rectangles are the seven characters used by Pietsch (1989) to support the first four nodes. Open rectangles indicate the necessary reversals. Half-open rectangles indicate reversals in all members of the Percophidae but *Percophis*. Numbers refer to characters described in the text, and follow the scheme of Pietsch (1989) and Pietsch and Zabetian (1990).

has had a variable and inconsistent membership during that period, gradually becoming less and less inclusive. In an attempt to identify an out-group for the Uranoscopidae, Pietsch (1989) defined a Trachinoidei with ten families. His cladogram included a sister group relationship of Champsodontidae and Chiasmodontidae embedded within the suborder. In a review of percormorph phylogeny, Johnson (1993) re-evaluated the characters defining the trachinoids found in Pietsch (1989; reiterated in Pietsch and Zabetian, 1990) and found them unconvincing. Mooi and Gill (1995) found that the Pietsch and Zabetian (1990) trachinoids exhibit a wide variety of epaxial muscle morphology regarding insertions on the dorsal-fin pterygiophores, which they felt

cast further doubt on the integrity of the group. Here we provide a more detailed re-examination of Pietsch's (1989) and Pietsch and Zabetian's (1990) evidence for trachinoid relationships as they pertain to a possible champsodontid/chiasmodontid grouping.

The Pietsch and Zabetian (1990: fig. 1) cladogram is reproduced here as Figure 21. There are seven characters nested at succeeding nodes of more basal taxa that place champsodontids and chiasmodontids among the trachinoids. Synapomorphies for all trachinoid families include small, short, wide pectoral radials (character 1) and the presence of a pelvic spur (character 2). As noted by Johnson (1993: 13), there is considerable variation in pectoral-fin radial morphol-

ogy among the Pietsch trachinoids (cf. *Bembrops*, *Trachinus*, and *Trichonotus*). A reversal to the primitive state must be hypothesized to account for the narrow pectoral-fin radials of chiasmodontids and champsodontids (Fig. 13). The short, wide radials typical of a number of other perciforms (e.g., all Notothenioidei, Trichodontidae) are not sufficiently different to exclude them from the trachinoids based on this feature (Hastings, 1993; Johnson, 1993).

Similarly, the morphology of the pelvic spur (character 2) is highly variable among trachinoids. The small bump in some taxa (e.g., *Cheimarrichthys*, *Hemerocoetes*, *Gnathagnus*) is indistinguishable from that found in the majority of perciforms (e.g., serranids, scorpaenoids), and a number of perciforms (e.g., Plesiopidae, some Pseudochromidae) exhibit a more developed pelvic spur than many trachinoids. An elongate spur is also found in some members of the Nototheniidae. A distinctive, elongate process is, indeed, found in some trachinoids (e.g., *Bembrops*, *Champsodon*; Fig. 14), but these taxa are not considered closely related in Pietsch's topology (Fig. 21), requiring this condition to have arisen independently. The pelvic spur provides no evidence of sister group relationship of champsodontids and chiasmodontids; it is a highly developed process in the former and only a small bump in the latter.

Characters 3 and 5 of the phylogeny (Fig. 21) are treated as steps of a transformation series in development of an elongate hyomandibular spur from a lateral, oblique crest on the hyomandibula (Pietsch, 1989: 299). These two structures appear to have no direct homology, their only similarity being a functional one involving muscle insertion/origin on the hyomandibula. Interpretation of the crest and spur as independent characters, along with the absence of either of these features in a number of taxa, strongly suggests that these characters cannot be used to define higher trachinoids. The morphology of the spur itself is variable, casting doubt upon its homology among those fishes bearing the feature. A hyomandibular spur is found in a number of taxa including gobioids, some notothenioids, and some blennioids. Champsodontids and chiasmodontids exhibit radically different conditions, with the for-

mer having a very well-developed hyomandibular spur and the latter having neither a crest nor spur.

The higher trachinoids purportedly share the derived state of scales being only partially ctenoid, reduced ctenoid, or cycloid (character 4, Fig. 21). The widespread reduction of ctenoid scales to cycloid among perciforms, and the frequent occurrence of variously ctenoid, reduced ctenoid, and cycloid scales in different species within the same family (e.g., Pempheridae), and even ontogenetically within the same species (e.g., some pseudochromids, A. C. Gill, pers. comm.) indicate this feature is of dubious value in establishing higher relationships in the absence of other corroborating evidence. As in other character descriptions (characters 1–3, 5), character 4 suffers from the inclusion of a broad variety of conditions that are treated as homologous without sufficient evidence (i.e., partially ctenoid, reduced ctenoid, cycloid); as presently defined, little confidence can be placed in this feature as support for higher trachinoid monophyly. Furthermore, champsodontids and chiasmodontids do not have cycloid scales and so do not fit the derived character definition. Chiasmodontids have either no scales or Type 4 spinoid scales (after Roberts, 1993) with a circular base bearing a central, slender, perpendicular spine (see Pietsch, 1989: fig. 5G, H). These spines are retained in the adults of only one of the four chiasmodontid genera (*Dysalotus*). Champsodontids have type 5 spinoid scales with a circular base and stout central pedicel bearing a bony plate having robust spines on its lateral and posterior margins (see Pietsch, 1989: fig. 5F; Roberts, 1993: fig. 19E, F). These two spinoid conditions are remotely similar, but have been classified as different types by Roberts (1993). Their homology has yet to be demonstrated.

The remaining two features used by Pietsch (1989) to support the placement of champsodontids among the trachinoids are highly sculptured and rugose cranium and shoulder girdle (character 6), and posteroventral expansion of the infraorbital series (character 7). In champsodontids, the nasals, frontals, parietals, pterotics and posttemporals bear serrated ridges that are confined to well-defined rows, with most of the bone sur-

faces smooth and unadorned (Fig. 2). In chiasmodontids, trachinids, and uranoscopids, the entire surface of these same bones are rugose and sculptured. In our opinion, there is no reason to consider the distinct, serrated ridges of champsodontids homologous with the overall rugosity of the skull in the remaining trachinoid taxa. Johnson and Cohen (1974: 14) observed that many midwater fishes such as chiasmodontids reduce the weight of the cranium with head bones that are vesicular in texture, having many caverns, bony struts, and braces. Given the difference in degree of rugosity between chiasmodontids and other higher trachinoids and its known recurrence in a number of unrelated midwater taxa, homology of the rugosity of bones among the remaining trachinoid taxa is also suspect.

The posteroventral expansion of the infraorbital series (character 7) as evidence for trachinoid relationships is problematical. The degree of expansion varies considerably among the taxa placed together by this feature: *Trachinus* has an infraorbital configuration that is indistinguishable from that of most perciforms, chiasmodontids have a slight posteroventral expansion, and leptoscopids have a large expansion. The homology of these conditions is questionable. For example, leptoscopids have seven elements with the posteroventral infraorbital expansion involving primarily an unusual and enlarged sixth element, whereas chiasmodontids have only a slight posteroventral expansion of the third infraorbital element. Uranoscopids have only four infraorbital bones, all very broad. In many uranoscopid species, there is little or no obvious posteroventral expansion other than by the broadening of the elements themselves; in those taxa with an expansion, it involves a long process on the lacrimal (first element) (Pietsch, 1989: figs. 16–17). It is difficult to conclude that these morphologies are homologous when they involve different elements. Furthermore, the character has no bearing on the inclusion of champsodontids which have greatly reduced the infraorbital series to a single, large lacrimal and two to three small tubular ossicles (Fig. 6).

For each of the seven basal characters employed by Pietsch (1989), an interpretation of

homology among states in trachinoids is highly questionable. For the conditions in champsodontids, in particular, our re-examination finds the family does not share the derived trachinoid condition (characters 1, 4, 7), the morphology of the derived condition is variable and/or shared with many other perciform taxa making the homology in *Champsodon* and trachinoids difficult or impossible to assess (characters 2, 3, 5), or the state is not homologous with that of other trachinoids (character 6). Winterbottom (1993: 407) reported a free cartilaginous pelvic radial in leptoscopids, a condition similar to that found in champsodontids, but we have not found such an element in leptoscopids available to us. Because we can find no additional features that indicate a close affinity with trachinoids sensu Pietsch, we conclude that champsodontid relationships lie elsewhere.

The lack of evidence to include Champsodontidae in the Trachinoidei seriously undermines the integrity of the suborder as presently recognized. Indeed, it is clear from a critical reinterpretation of the defining characters for Pietsch's (1989) trachinoids that there is little or no evidence for the inclusion of the seven basal families (Cheimarrichthyidae, Pinguipedidae, Percophidae, Trichonotidae, Creediidae, Champsodontidae, Chiasmodontidae). Derived states of basal characters are so inclusive that Hastings (1993: 102, fig. 1) was able to place the Notothenioidei in a trichotomy at the third node of Pietsch's topology (Fig. 21). Hastings (1993) noted, however, that derived states would have to have been lost repeatedly in both groups and concluded that "the homology of these character states requires further study" (p. 102). Ironically, the inclusion of the Ammodytidae as higher trachinoids by Pietsch and Zabetian (1990) further challenges the validity of the basal trachinoid characters; such a relationship requires additional reversals to a pre-trachinoid state in characters 1, 6, and 7. Only characters 2 and 4 of the seven basalmost trachinoid features escape reversal in higher taxa; as discussed previously, these two characters (pelvic spur and scales partially ctenoid, reduced ctenoid or cycloid) are of dubious value at this level of phylogenetic analysis. Excluding the seven basal taxa from Pietsch

and Zabetian's (1990) trachinoids, the remainder of their cladogram (including Leptoscopidae, Ammodytidae, Trachinidae, and Uranoscopidae) is more robust and provides an interesting and challenging template for further investigation (see Johnson, 1993: 15, for a brief review).

Chiasmodontidae. — The traditional alignment of the Champsodontidae and Chiasmodontidae, begun by Alcock (1899) and continued by Boulenger (1901), Weber (1913), and Jordan (1923) to the present day deserves attention. Among early workers, only Boulenger (1901: 269) listed a shared feature, a "complicated system of sensory organs on the body," but the superficial neuromasts of champsodontids bear little resemblance to the open pits and naked neuromasts found in chiasmodontids. The only character linking the two taxa in Pietsch's (1989) analysis was a reversal to the primitive condition of elongate, narrow pectoral radials, and it becomes uninformative (symplesiomorphic) if chiasmodontids and champsodontids are no longer considered trachinoids *sensu* Pietsch. With the dismantling of the basal trachinoid assemblage that we recommend, there remains evidence for neither the chiasmodontids and champsodontids to be included as members of the suborder, nor for the two families to be considered closely related.

The Champsodontidae and Chiasmodontidae are superficially similar in having two dorsal fins, large head, huge mouth with long teeth, and high numbers of vertebrae. Dissimilarities between chiasmodontids and champsodontids begin with habitats, with the former a pelagic, midwater family, and the latter deep benthic. Differences in anatomy are too numerous to list in detail, but some of the major systems will be noted here. Johnson (1993: 14) mentioned two: typical spinous dorsal-fin pterygiophore in chiasmodontids vs. a lack of distal radials in champsodontids (Fig. 17), and attenuate, horizontally oriented infrapharyngobranchials in chiasmodontids vs. short and more dorsally oriented elements in champsodontids (Fig. 8). The dorsal surfaces of the crania bear little resemblance, with champsodontids having serrated ridges confined to one or two distinct rows on nasals, frontals, parietals and pterotics, and chi-

asmodontids having a generally rugose skull that is vesicular in nature. The suspensoria are structurally quite different (cf. Fig. 4 and Johnson and Cohen, 1974: fig. 4). Cheek musculature is very divergent (Fig. 7), e.g., A2 with a lateral tendon to the anguloarticular in chiasmodontids, triangular A1 α from a large hyomandibular spur and large adductor arcus palatini in champsodontids. Upper jaws of chiasmodontids have a robust premaxilla larger than the maxilla, contrary to the condition in champsodontids. The first centrum of chiasmodontids is smaller than the second, has a well-developed neural spine, and a narrow articulation with skull, but in champsodontids the first centrum is longer than the second centrum, has a very short or no neural spine, and is sutured broadly to the exoccipitals (Fig. 2). Pectoral girdle elements in chiasmodontids are of regular proportions, whereas champsodontids have a greatly reduced pectoral fin, scapula and coracoid (Fig. 13). In chiasmodontids, the pelvic girdle is flattened, without an enlarged pelvic spur, and is not closely associated with its opposite member or the pectoral girdle (to accommodate a hugely expandable stomach); in champsodontids the basipterygia are concave, associated closely with each other and the pectoral girdle, and bear elongate pelvic spurs and very large pelvic fins (Fig. 14). As noted by Mooi and Gill (1995), champsodontids have epaxial muscle insertions onto the distal ends of the pterygiophores of the spinous dorsal fin (Type 1) whereas chiasmodontids have no such insertions (Type 0) (Fig. 19).

Of course, differences might be explained by autapomorphic features derived in each lineage. However, we find no features shared between chiasmodontids and champsodontids that could be considered strongly indicative of relationship. One unusual feature in common is the association of a separate distal radial with the supernumerary element of the first anal pterygiophore, although the element is a spine in chiasmodontids and a segmented ray in champsodontids. A supernumerary element (spine or ray) with a separate distal radial on the first anal-fin pterygiophore is also found in gobioids (usually a spine), cheimarrichthyids (spine), some percophidids (present in *Pterosaron* and *Hemero-*

coetes with ray, supernumerary completely absent in *Bembrops*), creediids (ray), ammodytids, leptoscopids (ray), uranoscopids (ray). A supernumerary distal is not found in trichonotids (contra Johnson and Brothers, 1993: 461), and no supernumerary elements are found in trachinids or trichodontids. *Champsodon* and chiasmodontids both have a relatively large cartilage-tipped process on the ventral half of the the medial pelvic-fin ray. As noted by Johnson (1992), this process results from fusion of the medial radial with the medial pelvic-fin ray, a character of the Eurypterygii. A similar process characterizes perciforms in general, but its large size in *Champsodon* and chiasmodontids is unusual and reminiscent of the condition seen in more primitive eurypterygians. An enlarged process is also found in the scorpaenoid *Anoplopoma* (but not *Normanichthys*, *Hoplichthys*, *Myoxocephalus*, *Icelus*, or *Sebastes*) and the "trachinoid" *Gnathagnus* (but not *Cheimarichthys*, *Parapercis*, *Bembrops*, *Hemerocoetes*, or *Trachinus*). The distributions of these two characters make their homology among the taxa difficult to assess.

Another feature that might suggest a relationship is the shape of the anterior ends of the premaxillae. In *Chiasmodon* (but no other chiasmodontid), there is an anteriorly directed process that bears large, hooked teeth and gives the appearance of a lateral notch in the premaxilla. In some species of *Champsodon*, there is a very obvious notch in the premaxilla just lateral to the symphysis. However, these superficially similar conditions are not homologous; in champsodontids the notch is an indentation that does not involve an additional process, whereas in *Chiasmodon* it is an extension of the bone that gives only the impression of indentation. Even if treated as an unreversed synapomorphy, the inconsistent distribution of the conditions within each family would render one or both of the families nonmonophyletic, and clearly both families have sufficient autapomorphies to support their monophyly.

The scales could be argued to be similar, both taxa having spinoid types (Roberts, 1993). But chiasmodontids have Type 4 with a simple, perpendicular spine that occurs in larvae and juve-

niles that disappear in adults (except in *Kali* where they are retained), whereas all adult champsodontids have Type 5 with a stout pedicel bearing a bony plate with robust spines on its posterior edges. The similarity is not any more striking than that with other taxa that have spinoid scales (see below).

With no obvious shared derived characters, and in light of the more promising alternatives for champsodontid sister taxa explored below, we do not further consider a close relationship between champsodontids and chiasmodontids.

Paracanthopterygii. — Could champsodontids be paracanthopterygians? Champsodontids have always been placed among the Perciformes in the Acanthopterygii, (the hypothesized sister to Paracanthopterygii; Johnson and Patterson, 1993), but evidence for such an alignment has not been examined, due at least in part to a paucity of characters diagnosing these higher taxa. Most recently, Johnson and Patterson (1993) set forth 19 characters (their characters 15–33) to define the Percomorpha (including Perciformes) or nest them among the Acanthopterygii. Among these, three are equivocal because of independent derivation among paracanthopterygians, and one does not apply to champsodontids: (20) anterior epineurals displaced ventrally on to ribs (found in many paracanthopterygians); (23) supraneurals ossified distally (champsodontids do not have supraneurals); (29) fewer than six pelvic-fin rays (true of many paracanthopterygians); (32) all but first two epineurals displaced ventrally (found in some paracanthopterygians). Of the remaining 15 characters, we find that champsodontids have eight: (15) pelvic spine; (17) anteromedial process of the pelvic bone or anterior pelvic process; (19) advanced dorsal fin; (21) complex pelvic spine; (25) ligament from ventral postcleithrum to posterolateral pelvic girdle; (27) second ural centrum absent; (28) five or fewer hypurals; (33) 17 or fewer principal caudal-fin rays. Johnson and Patterson (1993) discussed two additional characters for defining percomorphs: sutured anterior and posterior ceratohyals, and larvae with ornamented skull bones. Both are present in champsodontids and provide possible corroboration of percomorph member-

ship, although, as noted by Johnson and Patterson, the ceratohyal suturing is also found among numerous paracanthopterygians.

Contrary to percomorph membership, champsodontids do not have: (16) free pelvic radials reduced in size; (18) Baudelot's ligament originating from occiput (from the first vertebra in champsodontids); (22) chain-link articulation of the dorsal-fin spines; (24) proximally shortened ventral procurrent ray; (26) rod-like interarcual cartilage (short, triangular in champsodontids); (30) transforming ctenoid scales (spinoid in champsodontids); (31) loss of free pelvic radials. Some of the apparent reversals required to include champsodontids among percomorphs are striking enough to justify the exploration of a paracanthopterygian relationship.

Patterson and Rosen (1989: fig. 16) hypothesized monophyly of the Paracanthopterygii based on four characters: (1) full neural spine on PU2; (2) two epurals; (3) single supraneural; (4) enlarged intercalar containing glossopharyngeal foramen. Champsodontids exhibit only the first of these characters, making the case for their inclusion in paracanthopterygians appear weak. However, all four of the characters have been shown to be of dubious value for defining paracanthopterygians or determining higher relationships of any taxa because of their variability or their wide distribution among acanthomorphs (Gill, 1996). This opens the possibility that some, or all, of Patterson and Rosen's (1989) paracanthopterygians might be related to champsodontids (or other acanthomorphs). Of the remaining 15 morphological character states listed by Patterson and Rosen (1989: 33, character 20 is an allozyme feature not scored here), champsodontids share six: (5) second centrum shorter than both first and third; (6) forward extension of "prezygapophyses" on first centrum; (9) parapophyses absent on first three vertebrae; (10) interarcual cartilage small or absent; (13) first neural arch "in close articulation" with occipital crest; (15) pharyngobranchial 1 absent and tip of epibranchial 1 withdrawn laterally and remote from remaining pharyngobranchials. The last is the most striking feature of similarity between champsodontids and paracanthopterygians, found outside of these groups only among some

blennioids (*Gibbonsia*, Rosen and Patterson, 1990: fig. 33A). The shortened second vertebra (5) is also of interest. In addition, champsodontids share a condition similar to that of some pediculates and gadiforms, having the first epineural absent (Patterson and Rosen, 1989: 33, character 18, no epineurals on first two vertebrae). However, the homology of none of these characters has been strongly demonstrated. For example, paracanthopterygians with the epibranchial feature do not have an interarcual cartilage and exhibit other differences (cf. Fig. 8 and Patterson and Rosen, 1989: fig. 10), and the shortening of the second vertebra is not striking in champsodontids. Furthermore, champsodontids have neither the more convincing paracanthopterygian features of the premaxillary "gadoid notch" (character 7), lost myodome (character 8), "cod-like" exoccipital condyles (character 11), and "bear's paw"-shaped pharyngobranchial 3 (character 12), nor four others that are unique to pediculates or gadiforms (characters 14, 16–17, 19) listed in Patterson and Rosen (1989).

If champsodontids are to be considered paracanthopterygians, the Batrachoidiformes appear to form the most likely (and surprising) candidate for close relationship. At least some members have a ball-like radial associated with the pelvic-fin rays reminiscent, though much smaller, than that of champsodontids, and have reduced the number of infraorbitals, retaining only a large lacrimal. Batrachoidiforms also have an anteriorly placed dorsal fin and have no supraneurals. Of course, batrachoidiforms and champsodontids share several of the paracanthopterygian characters listed by Patterson and Rosen (1989: fig. 16; characters 5, 6, 9, 10 and 13). Most impressively, though, some batrachoidiforms possess an epibranchial 1 morphology very similar to that of champsodontids with its tip withdrawn laterally (cf. Fig. 8 with Patterson and Rosen, 1989: fig. 10C). Additionally, batrachoidiforms are unique among paracanthopterygians (and non-perciform acanthomorphs, *sensu* Mooi and Gill, 1995) in having a Type 1 epaxial muscle morphology, a condition shared by champsodontids (Mooi and Gill, 1995).

However, because of trenchant differences between champsodontids and batrachoidiforms (strong head spination vs. none; cranial osteology—e.g., intercalar present vs. absent; 1st epineural absent vs. enlarged; ribs present vs. absent; numerous aspects of pectoral and pelvic osteology), we think a relationship is unlikely despite the possible interpretation of these differences as autapomorphies. And, except for the unusual epibranchial 1 morphology (found only in some batrachoidiforms, others exhibit an essentially unmodified epibranchial 1; Patterson and Rosen: fig. 10A, B), most of their shared characters can be found among higher acanthopterygian groups, rendering them unconvincing as evidence of a sistergroup relationship between champsodontids and batrachoidiforms.

We believe that any interpretation of similarities between Champsodontidae and Paracanthopterygii as homologies reflects the poor definition of characters considered synapomorphies for members of the latter taxon rather than a close relationship. With this recognition comes the possibility that taxa currently considered paracanthopterygian might be more closely aligned with the acanthopterygian lineage. Gill (1996) examined the characters of the Paracanthopterygii in more detail and concluded that some taxa currently considered paracanthopterygians share several of Johnson and Patterson's (1993) percomorph features, and, conversely, that relationships of some taxa currently included among percomorphs have not had possible paracanthopterygian relationships adequately tested.

For example, rather than postulating a paracanthopterygian placement for champsodontids to explain their many similarities with batrachoidiforms, it might be more reasonable to postulate an acanthopterygian relationship for batrachoidiforms, although we are not in a position to propose such a relationship in this paper. Batrachoidiforms lack several of the features used by Patterson and Rosen to define the Paracanthopterygii, or have been sufficiently modified to make them inapplicable (e.g., no supraneurals, no intercalar, some species without "gadoid notch," no ribs; affecting, respectively, Patterson and Rosen's characters 3, 4, 7, and 9). Reviewing

Johnson and Patterson's (1993) characters defining the Percomorpha or nesting them within the Acanthopterygii, we find that batrachoidids have eight of 19 derived features: (15) pelvic spine; (16) pelvic radials reduced in size; (19) advanced dorsal fin; (21) complex pelvic spine; (28) five or fewer hypurals; (29) fewer than six pelvic-fin rays; (32) all but first two epineurals displaced ventrally; (33) 17 or fewer principal caudal-fin rays. Of the remaining eleven characters, seven are either not applicable to the batrachoidiforms due to possible secondary modification or equivocal because some percomorphs (by current classifications) exhibit a reversed or modified condition similar to that found in batrachoidiforms: (18) Baudelot's ligament from occiput (ligament absent in batrachoidiforms by our observations, although Markle [1989: 72] reports the ligament from the occiput in some batrachoidiforms); (20) anterior epineurals displaced ventrally onto ribs (ribs absent in batrachoidiforms); (23) supraneurals ossified distally (supraneurals absent in batrachoidiforms); (24) proximally shortened ventral procurrent ray (absent in batrachoidiforms and many percomorphs); (26) rod-like interarcual cartilage (absent in batrachoidiforms and many percomorphs); (30) transforming ctenoid scales (scales cycloid or absent in batrachoidiforms and many percomorphs); (31) loss of free pelvic radials (pelvic radials found in batrachoidiforms, callionymids and gobiesocids). Only four features argue strongly against an acanthopterygian relationship because they do not occur in batrachoidiforms: (17) anteromedial process of the pelvic bone or anterior pelvic process; (22) chain-link articulation of the dorsal-fin spines; (25) ligament from ventral postcleithrum to posterolateral pelvic girdle; (27) second ural centrum absent. Two more characters that might define percomorphs discussed by Johnson and Patterson (1993) include ornamented skull bones in larvae and sutured anterior and posterior ceratohyals; in batrachoidiforms, the first is absent and the second is present. Considering this evidence and the questionable monophyly of the Paracanthopterygii (see Gill, 1996 for a brief review), an acanthopterygian (and even perciform) relationship for batrachoidiforms deserves con-

sideration and could explain some of their similarities to champsodontids.

The nature of characters defining our current notions of Paracanthopterygii and Acanthopterygii makes unproductive a "check-list" parsimony approach where the features summarized by Patterson and Rosen (1989) and Johnson and Patterson (1993) are simply scored for the taxon in question without careful determination of homology. As noted previously, champsodontids exhibit only eight of the 15 applicable characters provided in Johnson and Patterson (1993) to establish percomorph membership (characters 15, 17, 19, 21, 25, 27, 28, 33), but the remaining seven that seem to oppose this are open to reinterpretation or are hypothesized to have reversed in other taxa currently accepted as percomorphs. The presence of a large, autogenous pelvic-fin radial appears to contradict the nested transformation of characters 16 (reduction in size and number of pelvic-fin radials) and 31 (loss of free pelvic-fin radials). But this large element supports all of the pelvic rays and is grooved for articulation with the basipterygium, bearing no resemblance to the primitive condition; the pelvic radial morphology of champsodontids can be interpreted as having arisen *de novo*. Baudelot's ligament originating from the first vertebra (contra 18) is known to occur in some scorpaenoids, some zoarcoids, and some gobioids. The absence of the chain-link articulation of the dorsal-fin spines (contra 22) can be reinterpreted as a secondarily derived condition through modification of pterygiophore morphology. The loss of a proximally shortened ventral procurrent ray (contra 24) is the common character state in most non-basal percomorphs. Percomorphs usually have a rod-like interarcual cartilage (26), but it is absent in blennioids, zoarcoids and short or absent in some scorpaenoids. That champsodontids do not have transforming ctenoid scales (contra 30) can be explained as a reversal or modification as it is for many percomorphs. Overall, the weight of evidence strongly favors the traditional acanthopterygian and specifically percomorph alignment of champsodontids, particularly given the propensity for homoplasy among characters defining higher taxa (see Johnson and Patterson, 1993). There is no evidence

to suggest that champsodontids are smegmamorphs (see Johnson and Patterson, 1993), so the remainder of the discussion focusses on possible perciform relationships (excluding the Trachinoidei sensu Pietsch and Zabetian, 1990, which has been dealt with above).

Gobioidei. — Winterbottom (1993) surveyed 23 characters he considered gobioid apomorphies in an attempt to align the suborder with a plausible sister taxon. Of these, champsodontids share: (1) reduced infraorbital series; (2) a large gap between the symplectic and preopercle; (3) cleithral notch; (4) pelvic radials; (5) no supra-neurals; (6) superficial neuromasts on the head (head papillae of Winterbottom, 1993). The first of these characters is so widespread among perciforms that it is not useful as an apomorphy at this taxonomic level. The "large" symplectic gap, as noted by Winterbottom (1993: 399), is difficult to quantify and exists to a greater or lesser degree in a number of other perciform taxa, and even some smegmamorphs. The cleithral notch is found in many percomorphs to various degrees. Among gobioids there is some variation in cleithral condition (cf. figs. 5, 6 in Winterbottom, 1993 and fig. 3 in Hoese and Gill, 1993), with *Micropercops* not being greatly different from a number of perciform families (e.g., Callanthiidae, Grammatidae, Plesiopidae, at least some blennioids, some serranids). Pelvic radials in gobioids were reported by Springer (1988) and included by Winterbottom (1993) as a gobioid apomorphy, but Johnson and Patterson (1993: 615) noted that the original report was in error. The absence of free pelvic radials in gobioids removes this character from consideration as a synapomorphy with champsodontids. Supra-neurals are absent in many of the other groups examined here as possible alternative champsodontid relatives (e.g., scorpaenoids, trachinoids). Superficial neuromasts on the head are uncommonly found among perciforms, but occur in taxa that have not been considered closely related (see Kurtoidei, below) and further work on their ultrastructure and innervation is needed to establish homologies. These character distributions suggest that these features do not support a champsodontid/gobioid relationship without more convincing corroborative evi-

dence. Champsodontids exhibit none of the more striking gobioid apomorphies listed by Winterbottom (1993): absence of parietals, cartilaginous basibranchial 1, pelvic intercleithral cartilage, ventral intercleithral cartilage, parhypural reduction. Two of Winterbottom's included apomorphies were not examined in champsodontids, the shape of otolith primordia (elongate in gobioids) and presence of sperm duct glands in the testes.

Johnson and Brothers (1993: 465) restricted their list of gobioid apomorphies to twelve, five of which were not included by Winterbottom (1993): (3) hypurals one and two are fused to one another, and hypurals three and four fused to one another and to urostyle; (4) first centrum elongate and no shorter than succeeding centra; (5) first neural arch fused to first centrum at its initial appearance in ontogeny; (6) single supernumerary ray (usually a spine) on the first anal pterygiophore embraces a separate distal radial; (7) dorsalmost pectoral ray articulates with the posterior margin of the dorsalmost actinost rather than with the scapula; the medial half of this ray does not have an enlarged articular base and, in early ontogeny, does not embrace an ovoid cartilage lying at the posterodorsal corner of the scapulocoracoid cartilage. Characters 4 and 7 do not occur in champsodontids, and 5 could not be determined with the material available to us. Champsodontids exhibit characters 3 and 6, but both of these features have wide distributions among perciforms; similar caudal fusion is common among many perciform groups (e.g., blennioids, pseudochromoids and many others), and, as discussed previously, a number of other taxa share the presence of a supernumerary distal radial on the first anal pterygiophore (Cheimarrichthyidae, some Percophididae, Creediidae, Chiasmodontidae, Leptoscopidae, and Uranoscopidae). These features can not be realistically used to hypothesize relationship without additional corroborative evidence from uniquely shared apomorphies. Additionally, the supernumerary distal radial on the first anal-fin pterygiophore supports a segmented ray element in champsodontids and a spinous element primitively in gobioids.

One other relatively unusual morphological

feature not examined by Winterbottom (1993) or Johnson and Brothers (1993) is shared by champsodontids and at least some gobioids: absence of distal radials on spine-bearing dorsal-fin pterygiophores. Unfortunately, this is of dubious value as evidence for hypothesizing relationships for several reasons. Distal radials are primitively present in gobioids (e.g., *Rhyacichthys*, A.C. Gill, pers. comm.), and are occasionally present as cartilage in some species of eleotridids. Distal radials are absent (i.e., do not form or are resorbed during development) in the spine-bearing portion of the dorsal fin in a number of other perciform taxa including some scorpaenoids, Opistognathidae, some Grammatidae, and callionymoids (free distal radials are "absent" in other groups, e.g., blennioids, labrids, plesiopids, but this is due to incorporation of the distal element into the succeeding pterygiophore and not a failure to develop or persist in the adult as in other taxa noted here) (Mooi, 1993; Gill and Mooi, 1993; Nakabo, 1983). Furthermore, the morphology of champsodontid pterygiophores is unusual in that the distal tips are inserted into sockets of the subsequent element, a condition not found in gobioids, although such a morphology could be interpreted as an autapomorphy of *Champsodon*.

Callionymoidei. — Gill (1996) summarized the apomorphies that suggest a relationship of callionymoids and gobiesocids. Champsodontids share five of the 14 characters listed: highly reduced infraorbital series, no supraneurals, large gap between the symplectic and preopercle, first epineural absent, free cartilaginous pelvic radials. The first three characters have been discussed previously and have been discarded as uninformative at this level. Epineurals are absent on the first vertebra of gadiforms, lophiiforms and bythitoids of the Paracanthopterygii (Patterson and Rosen, 1989; Gill, 1996). Gill (1996) used this feature, among others, to suggest a possible relationship between the paracanthopterygians, callionymoids and gobiesocids (although epineurals are absent from the first vertebra of other taxa, e.g., Trichodontidae), and champsodontid relationships with paracanthopterygians have been explored previously. Free pelvic radials in adult percomorphs are

uniquely found in callionymoids and champsodontids, but the morphology of the radials in these groups is very different; a relatively small element found nestled between the articular tips of each spine or first segmented ray in the former (Johnson and Patterson, 1993: 614; Gill, 1996) vs. a very large element grooved for articulation with the posterior basipterygium that supports all the segmented rays and barely penetrates between the articular tips of the spine in the latter. The presence of the pelvic radials in callionymoids was employed by Gill (1996), along with other lines of evidence, to challenge the traditional percomorph alignment of this group. Here, we have argued that the pelvic radial of champsodontids is a uniquely derived structure because it bears little resemblance to the primitive condition.

The hypothesis of a callionymid/gobiesocid relationship would have to include champsodontids if the epineural and pelvic radial characters were deemed sufficient, an unreasonable consideration in our opinion, although there are additional similarities between champsodontids and callionymoids. Nakabo (1983: figs. 44–48) illustrated the anterior dorsal-fin pterygiophores of callionymoids. He reported (p. 57) that “each proximal pterygiophore fuses with each distal pterygiophore to form one bone” suggesting that the distal radials are fused with the proximal-middle radials for both spine-bearing and segmented ray-bearing pterygiophores. Without ontogenetic data, such a supposition is unfounded, and among the segmented ray-bearing elements the absence of distals is highly unlikely—a lack of cartilage staining might have contributed to such a misinterpretation. Our observations contradict those of Nakabo (1983). We find that the anterior four or five dorsal-fin pterygiophores are very closely associated and exhibit the champsodontid condition of anterior pterygiophores inserting into a socket of the succeeding element. Like champsodontids, distal radials for these anterior elements appear to be truly absent rather than having been fused to the proximal-middle radial (see also Gobioidei, above). For pterygiophores bearing segmented rays in callionymids, we found separate (though reduced) distal radials following the usual pattern (except

that there is no distal radial on the last pterygiophore—character 13 of Gill, 1996). (Gobiesocids do not have spine-bearing dorsal fins, but have a unique absence of distal radials on the ray-bearing pterygiophores. The reduced distals of callionymoids and their absence in gobiesocids might be additional evidence of a close relationship.)

The caudal skeletons of callionymoids and champsodontids are also similar in their extreme fusion and/or reduction, and in having exceedingly broad neural and haemal spines on PU2 (=first preural vertebra of Nakabo, 1983: fig. 57). They also share a very broad parhypurapophysis, although this process points anteriorly in callionymoids (Nakabo, 1983: figs. 57–59) and posteriorly in champsodontids (Fig. 18). Both taxa have lost the endopterygoid, have large preopercular spines, and have fimbriate or striated opercular elements. Callionymoids have highly modified suspensoria with no metapterygoid (well-developed in champsodontids, Figs. 3–5) and a large symplectic (a thin strut in champsodontids). Clearly, the callionymoid condition is derived and must at some juncture be related to more “standard” suspensorial morphologies, but the champsodontid suspensorium has been modified in a different direction and seems an unlikely model from which to derive the callionymoid form (or vice versa). Many perciform taxa have enlarged preopercular spines, so this feature in itself is not reliably indicative of relationship. The opercular fimbriations of callionymoids are restricted to the subopercular element (Nakabo, 1983: figs. 28–29), whereas these are found on all opercular bones in champsodontids (Fig. 4). Opercular fimbriations are found in many perciform families (e.g., Ammodytidae, Creediidae, Dactyloscopidae, Notograptidae, Opistognathidae, Trichonotidae).

Most of the conditions shared between champsodontids and callionymoids are found among other taxa and are not sufficient in themselves to suggest a relationship, or are parts of highly modified complexes that seem unlikely to be homologous at the appropriate level. The similarity of the dorsal spine-bearing pterygiophores and caudal osteology is intriguing, and in and of themselves are not easily explained as indepen-

dent derivations. But differences in the osteology of the pelvic girdle (extreme lateral orientation of basipterygia and rays vs. medial position), suspensorium (as noted above), cranium (myodome absent vs. present), gill arches (infra-pharyngobranchial 4 toothplate and interarcual cartilage absent vs. present), and epaxial muscle insertion onto the pterygiophores (Type 2 vs. Type 1; Mooi and Gill, 1995) all suggest that the Callionymoidei is an unlikely candidate as sister group for the Champsodontidae.

Kurtoidei and Apogonidae. — Champsodontids, kurtids and apogonids have series of horizontal and vertical rows of superficial neuro-masts on the head and body, a feature also found among gobioids. Johnson (1993: 14) implied that this might be an avenue for exploring champsodontid relationships, although he noted that more work is necessary to evaluate homology. However, other than the unusual sensory papillae, few features of kurtoid or apogonid morphology suggest close relationship. Many striking differences include, for example, dorsal gill arch osteology (the first epibranchials are not at all similar, and, in contrast with champsodontids, the second epibranchial has no direct articulation with the second infrapharyngobranchial in either kurtids or apogonids), and kurtid and apogonid eggs bear filaments and are guarded by the male whereas champsodontids have unadorned, pelagic eggs. Apogonids and champsodontids do share an apparently derived epaxial muscle morphology, Type 1 of Mooi and Gill (1995) (kurtids exhibit Type 0), but without additional corroborative evidence a relationship seems remote.

Trichodontidae. — The relationships of this family are little understood. Trichodontids have been traditionally placed in the Trachinoidei, but were excluded from this group by Pietsch (1989). Standard references maintain their position among trachinoids because their placement remains unresolved (e.g., Eschmeyer, 1990: 484; Nelson, 1994: 397). The trichodontids share the following with champsodontids: no distal radials on the spine-bearing dorsal-fin pterygiophores (although questionable because specimens available to us were of poor quality), spine bases open anteriorly (but closed on more posterior

spines, unlike champsodontids; this character varies considerably among perciforms, see "Scorpaenoidei" below), no epineural on first vertebra, short neural spine on first vertebra, similar spiny lacrimal (but complete infraorbital series), parietal with an enclosed sensory canal. The latter is derived feature of scorpaenoids, and might suggest that trichodontids are scorpaenoids; below, we argue for a champsodontid/scorpaenoid relationship based in part on an unusual modification of this feature. Although not further explored here, a trichodontid/scorpaenoid relationship might be a hypothesis worth testing. We note, however, that trichodontids exhibit a Type 2 epaxial muscle morphology as opposed to the Type 1 morphology found exclusively among scorpaenoids (Mooi and Gill, 1995).

Despite a possible common relationship with scorpaenoids, the other characters shared by trichodontids and champsodontids are not convincing evidence of sister group status because of their wide distribution among other perciforms. A number of differences between trichodontids and champsodontids also might weaken a hypothesis of relationship: very broad, short pectoral-fin radials (vs. more elongate and typical perciform radials), first infrapharyngobranchial present (vs. absent), no interarcual cartilage (vs. triangular cartilage), no supernumerary distal radial on first anal pterygiophore (vs. present), ceratohyals not interdigitated (vs. interdigitated), Baudelot's ligament from basioccipital (vs. from first vertebra), Type 2 epaxial muscle morphology (vs. Type 1), dernersal mass of large eggs (vs. small, pelagic eggs) (Watson et al., 1984). In dorsal gill-arch musculature, though both have the obliquus dorsalis embracing the posterior levator internus, the insertion of the posterior levator internus remains to the third infrapharyngobranchial in *Trichodon* (vs. to third epibranchial). Additionally, the osteology of the dorsal gill arches is so divergent that a close relationship between the two seems unlikely.

Blennioidei. — Johnson (1993: 14) noted the shared condition of a short or absent first neural spine in blennioids and champsodontids. Blennioids (along with a few other perciform taxa) also share with champsodontids a Type 1

epaxial morphology with insertions onto the dorsal-fin pterygiophores, although the blennioid condition is unique in having a fan-shaped anterior slip inserting onto the anterior dorsal-fin pterygiophores and skull (Mooi and Gill, 1995: table 1, fig. 14). Blennioids, excepting most tripterygiids, have a bone enclosed supratemporal sensory canal as do champsodontids, although it is not associated with a parietal spine. A bone-enclosed supratemporal canal is also found in scorpaenoids, some zoarcoids, some pseudochromids, and several other perciforms (see Mooi and Gill, 1995: 128; these authors also suggest a possible scorpaenoid relationship for blennioids). *Gibbonsia* (Clinidae) has a first epibranchial similar to that of champsodontids, with a laterally displaced and ventral process on epibranchial 1, although this process is not cartilage-tipped (Rosen and Patterson, 1990: fig. 33A). *Gibbonsia*, however, is a relatively derived blennioid, so that the homology of the epibranchial process is doubtful. Champsodontids and the basal blennioid family Dactyloscopidae possess fimbriate opercular elements. Similarly fimbriate opercles can be found in several percormorph taxa (e.g., Notograptidae, and those listed in Nelson, 1985: 288), and seem to be associated with groups that burrow or are found on soft substrates. In many of these taxa, the fimbriations differ in morphology or are restricted to different bony elements, making their homology unlikely. Winterbottom (1993: 407) reported a free cartilaginous pelvic radial in dactyloscopids, a condition found in champsodontids, but we can find no free radial in dactyloscopids or any other blennioid in material available to us.

Springer (1993: 476–483) listed five major specializations to define the Blennioidei: (1) infrapharyngobranchials 2 and 4 lost, no interarcual cartilage; (2) caudal complex composed of autogenous ventral hypural plate of fused parhypural+hypural 1 and 2, dorsal hypural plate of hypurals 3 and 4 fused to urostyle complex, autogenous hypural 5, no autogenous uroneurals, no parhypurapophysis, two epurals, fewer than 16 segmented rays with fewer than 12 branched, haemal spines of PU2 and PU3 fused to their respective centra, short PU2 neural spine; (3) pelvises convex forming a nut-like pod, four or

fewer pelvic rays; (4) anal fin with fewer than three (0–2) non-pungent spines and only simple segmented rays; (5) large pectoral radials with reduced scapula and coracoid. Among these, champsodontids share only a few components of the caudal-fin morphology (2) and anal-fin composition (4). The caudal complex differs in having a single highly fused caudal complex that lacks an autogenous 5th hypural, a large parhypurapophysis, three epurals, and more segmented rays. While these differences do not exclude a champsodontid/blennioid relationship, there are several groups that exhibit a pattern of caudal morphology more similar to that of champsodontids (e.g., callionymoids, some creediids). It is clear that caudal element fusion/reduction has occurred independently in several groups (Gill and Mooi, 1993), and can not be considered conclusive evidence of relationship. Champsodontid anal fins, as in blennioids, are derived in having fewer than three pungent spines (replaced by 2 unbranched segmented rays in champsodontids), but remaining segmented elements, unlike in blennioids, are primitive in being branched. Loss of pungent anal spines occurs in many perciform groups (e.g., some scorpaenoids, cottoids, notothenioids, some zoarcoids, creediids, leptoscopids, uranoscopids, ammodytids, channids, some pseudochromids), suggesting this character, too, is insufficient to convincingly hypothesize relationship. Despite recent suggestions that blennioids might be scorpaenoids (Mooi and Gill, 1995: 128), a relationship we suggest below for champsodontids, we do not consider blennioids a likely candidate for a champsodontid sister group.

Scorpaenoidei. — The monophyly of the Scorpaenoidei (sensu Mooi and Gill, 1995 = Scorpaeniformes of Nelson, 1994 minus Dactylopteridae and perhaps Bathylutichthyidae) has not been well corroborated. The suborbital stay, a posterior extension of the third suborbital that usually attaches to the preopercle, is usually listed as the only defining characteristic. The homology of this feature has been questioned by numerous authors (e.g., Greenwood et al., 1966; Johnson, 1993). Secondary loss of the stay is common in groups presently included among the

scorpaenoids, indicating that there is little evidence to exclude from scorpaenoid membership the many other perciforms that have reduced or lost suborbital bones (e.g., Gobioidae as suggested by Winterbottom, 1993).

Johnson (1984, 1993) suggested a second unusual feature that deserves attention as a possible synapomorphy of scorpaenoids: presence of distinct parietal spines in larvae associated with a bone-enclosed supratemporal canal. In many scorpaenoids, the parietal spine is retained in adults and the supratemporal canal passes through the spine base. A bone-enclosed supratemporal canal on the parietal is known from most scorpaenoids, exceptions being the Psychrolutidae (a free tubular bone; Yabe, 1985), Abyssocottidae (Sideleva, 1982), and some members of the Liparidae (loss of parietal; Kido, 1988). However, a spine is not always associated with the parietal canal (e.g., Anoplomatidae, Hexagrammidae, Zaniolepididae, Normanichthyidae, Comephoridae, Cottocomephoridae, Cyclopteridae, Liparidae, and some cottids) (Washington et al., 1984). Regardless, among non-scorpaenoid acanthomorphs, distinct parietal spines in larvae are known only in some beryciforms (Johnson, 1984) and these do not persist in adults. Thus the canal-bearing parietal spine is unique at some level among scorpaenoids. Either this feature corroborates scorpaenoid monophyly and several families have secondarily lost the parietal spine (and occasionally the canal), or it is evidence for monophyly of the subgroup of scorpaenoids sharing it. Based on the lack of parietal spines and a bone-enclosed supratemporal canal, Johnson (1993) doubted the inclusion of the Dactylopteridae in the Scorpaenoidei.

Mooi and Gill (1995) reported that all but one scorpaenoid they examined (Bathylutichthyidae) exhibited Type-1 epaxial muscle morphology with well-defined slips of muscle to the distal tips of the dorsal spine-bearing pterygiophores. This epaxial morphology is uncommon among acanthomorphs, and they suggested possible relationships among the scorpaenoids and the few other perciform groups (blennioids, most cirrhitoids, Apogonidae, Centrogeniidae, Champsodontidae, Cheimarrichthyidae, Grammatidae, Haemulidae, Percidae, Serranidae) with this ap-

parently derived feature. Because Dactylopteridae and Bathylutichthyidae have Type 0 epaxial musculature, Mooi and Gill (1995) argued that these two groups should be excluded from the Scorpaenoidei, supporting Johnson's (1993) hypothesis concerning the former. They also assigned subordinal status within the Perciformes to the scorpaeniforms (as Scorpaenoidei) based on epaxial musculature and other evidence.

The Champsodontidae have a distinct parietal spine in the larvae that is pierced by a supratemporal sensory canal (Fig. 3); the spine and canal are retained in the adults (Fig. 2a, b). Whether the presence of a parietal spine and canal is interpreted as a synapomorphy for the Scorpaenoidei following Johnson (1984, 1993) or as a synapomorphy of a subset of scorpaenoids, this apparently unique feature provides strong evidence for a champsodontid/scorpaenoid relationship. As noted by Mooi and Gill (1995), the Champsodontidae are one of only a few perciform taxa to have Type 1 epaxial morphology (Fig. 19a). This feature is held in common with the Scorpaenoidei and, while not providing direct evidence for a relationship, does not contradict one. Both champsodontids and several scorpaenoids have Baudelot's ligament originating from the first vertebra rather than the basioccipital (Yabe, 1985; pers. obs.), an uncommon condition among percomorphs. The Type 5 spinoid scales are known from champsodontids and few other taxa (Roberts, 1993: appendix 1); some cottids have scales remarkably similar to those of champsodontids (e.g., *Icelinus*, *Rastrinus*; D.W. Nelson, 1984). The short or absent neural spine on the first vertebra of champsodontids is shared with blennioids, and Mooi and Gill (1995) have provided some characters that suggest a blennioid/scorpaenoid relationship. Cottids also have a short neural spine on the first vertebra.

Champsodontids cannot have the scorpaenoid suborbital stay because they lack the element that normally bears it, the third infraorbital (Fig. 6). Therefore, its absence is not in conflict with the hypothesis of a scorpaenoid relationship. Champsodontids and at least some scorpaenoids share open spine bases on the first dorsal fin, perhaps a primitive condition compared to the

bony ring found on the bases of dorsal-fin spines among most perciforms. However, this character varies considerably in some groups, even intraspecifically in some pseudochromids (A. C. Gill, pers. comm.). Like champsodontids, most members of the Scorpaenoidei lack supraneural elements (most scorpaenids and cottoids) and some have relatively posteriorly placed dorsal fins such as *Anoplopoma* (beginning in the 5th interneural space) and some cottoids (Yabe, 1985; Ishida, 1994); the homology of these two conditions is questionable given their variation among acanthomorphs. The scorpaenoid families Apistidae, Aploactinidae, and Pataecidae have a posterior levator internus (=levator internus 3) that passes through the obliquus dorsalis ("obliquus dorsalis sandwiching levator internus 3," Ishida, 1994: 20, table 3, fig. 10E) which is very similar to the condition in champsodontids (Fig. 12a). The homology of this shared muscle arrangement is perhaps questionable because the insertion of the posterior levator internus is on infrapharyngobranchial 3 in the three scorpaenoid families (Ishida, 1994; pers. obs.) and (uniquely to our knowledge) on epibranchial 3 in champsodontids (Fig. 12b).

Against the inclusion of champsodontids among scorpaenoids are the following: no ramus lateralis accessorius (RLA) vs. RLA Type 11 or 12 uniquely in scorpaenoids (except triglids with none) (Freihofer, 1963); enlarged medial cartilage tip on pelvic ray vs. no cartilage tip in most scorpaenoids (known exception *Anoplopoma*); air bladder thin and without muscles vs. thick and with muscle attachments in most scorpaenoids. All of these differences could be attributed to autapomorphic conditions occurring in either champsodontids or scorpaenoids.

Conclusions

There is no convincing evidence to include the Champsodontidae in the Trachinoidei. Indeed, there is no support for a close relationship of Cheimarrichthyidae, Pinguipedidae, Percophidae, Trichonotidae, Creediidae, Champsodontidae, and Chiasmodontidae with the remaining trachinoids of Pietsch and Zabetian (1990) or

with each other (an exception being trichonotids, creediids, and some percophids which share a unique suspensorium morphology, see Johnson, 1993: 14). Chiasmodontids and champsodontids are very different in all major character complexes, and no features were found to support sister-group status.

Looking elsewhere for relatives, no convincing evidence can place champsodontids among the Paracanthopterygii. Although seven of 15 applicable characters listed by Johnson and Patterson (1993) appear to contradict a percomorph and even acanthopterygian affinity for champsodontids, these are either open to reinterpretation as nonhomologous to the primitive condition or are known to reverse in other groups presently considered percomorphs. We conclude that the weight of evidence clearly favors the traditional perciform relationship for champsodontids. Several perciform groups were surveyed as potential relatives. Although unusual characters are shared by champsodontids, kurtoids and apogonids, and champsodontids and blennioids, there seems little to indicate a close relationship. Champsodontids share a number of character states with gobioids, with callionymoids, and with trichodontids, but none of these taxa prove satisfactory as sister groups. Based on the presence of an enclosed sensory canal on the parietal of the Trichodontidae, a relationship of this problematic taxon with the Scorpaenoidei is worthy of consideration.

With many scorpaenoids, champsodontids share a parietal spine enclosing a supratemporal canal, a condition that is not known elsewhere in the Percomorpha. Other derived characters shared by champsodontids and at least some scorpaenoids, but not uniquely so among perciforms, include: a Type 1 epaxial muscle morphology, a Type 5 spinoid scale, Baudelot's ligament originating from the first vertebra. We hypothesize that the Champsodontidae is a member of the Scorpaenoidei (sensu Mooi and Gill, 1995=Scorpaeniformes sensu Nelson, 1994 minus Dactylopteridae), and recommend that classifications reflect this relationship by placing champsodontids as incertae sedis within the scorpaenoids.

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