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On the Interrelationships of the Genera of Creediidae (Perciformes: Trachinoidei)

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Abstract An osteological study of representatives of the seven genera of creediids supports the view that the family is monophyletic. New diagnostic characters include the form of the pelvis, mesopterygoid, and ectopterygoid. Characters are given which distinguish members of Creediidae from other fishes. Three lineages of creediids are recognized on the basis of osteological and external characters, with *Schizochirus insolens*, the least derived and the most distinctive species, comprising the first lineage, the species of *Creedia* the second, and those of *Limnichthys*, *Tewara*, *Crystallodytes*, *Chalixodytes*, and *Apodocreedia* the third.

The family Creediidae is recognized with 7 genera and 16 species. These small fishes occur in the Indian and Pacific oceans from the Red Sea and South Africa to Hawaii and Easter Island. They occur primarily in tropical and subtropical waters at shallow depths, although *Limnichthys rendahli* is known from off Auckland Island, south of 50°S latitude and at depths of over 100 m. Probably all are sand-diving fishes. The species are keyed in Nelson and Randall (1985).

The interrelationships of the genera have not previously been studied. In addition, the osteology of the group is poorly known although Gosline (1963) describes many osteological characters for *Crystallodytes cookei*. This paper lists characters which support the view that the family is monophyletic and which distinguish creediids from all other fishes. It also presents a hypothesis on the interrelationships of creediids based on a limited study of their osteological and external characters. The interrelationships and taxonomic problems of the 5 species of *Limnichthys* are not explored here.

Materials and methods

Material for examination from the following institutions was cleared and stained for bone with alizarin red-S: Australian Museum, Sydney—AMS; Bernice P. Bishop Museum, Honolulu—BPBM; J. L. B. Smith Institute of Ichthyology, Grahamstown—RUSI; University of Alberta Museum of Zoology, Edmonton—UAMZ; National Museum of Natural History, Smithsonian Institution, Washington, D. C.—USNM. The cleared and stained material employed with number of specimens and size range in standard length (with standard length of figured specimens, measured in glycerin, in parentheses) is as follows: *Schizochirus insolens*, 1, (52 mm), AMS 1B. 514; *Creedia haswelli*, 2, (42) and 47 mm, AMS IB. 1114; *C. partimsquamigera*, 2, 52 and 55 mm, I. 21420-006; *Limnichthys donaldsoni*, 1, (25.5 mm), BPBM 9261—1, 19 mm, BPBM 13952; *L. fasciatus*, 3, 24–(32) mm, UAMZ 3765; *L. nitidus* 3, 28–(34) mm, UAMZ 5517 (formerly RUSI 76-21); *Tewara cranwellae*, 9, 43–67(57)mm, UAMZ 3761; *Crystallodytes cookei*, 2 paratypes, 46 and (58.5) mm, USNM 116087; *Chalixodytes chameleontoculis*, 2, 35 and (43) mm, UAMZ 5518 (formerly RUSI 74-95); *C. tauensis*, 2, (42.5 mm), BPBM 17745—2, 31 and 41 mm, BPBM 18447—1 paratype, 36 mm, USNM 116084—2, 31 and 39 mm, USNM 140903; *Apodocreedia vanderhorsti*, 3, 56–81(78) mm, UAMZ 5519 (formerly RUSI 76-21). In addition, as representatives of the families thought to have the closest affinity to creediids, *Trichonotus setiger* (Trichonotidae) was examined from unstained material (10 specimens, AMS IA. 6238) and cleared and stained material (2 specimens, USNM 265627) and several species of *Hemerocoetes* (Percophidae) were utilized from cleared and stained specimens. Information was utilized from Nelson (1978, 1979, 1983) and Nelson and Randall (1985) for Creediidae.

Family limits

The family Creediidae is a relatively compact group whose species are quite distinct from those of all other families currently recognized in the heterogeneous suborder Trachinoidei (Nelson, 1984). It is postulated here that its affinities come closest to the Percophidae and Trichonotidae; however, there is not sufficient comparative information to argue convincingly which perciform family Creediidae is most closely related to.

The family is thought to be monophyletic on the basis of the characters listed below; these are shared by all species examined, except as noted, of

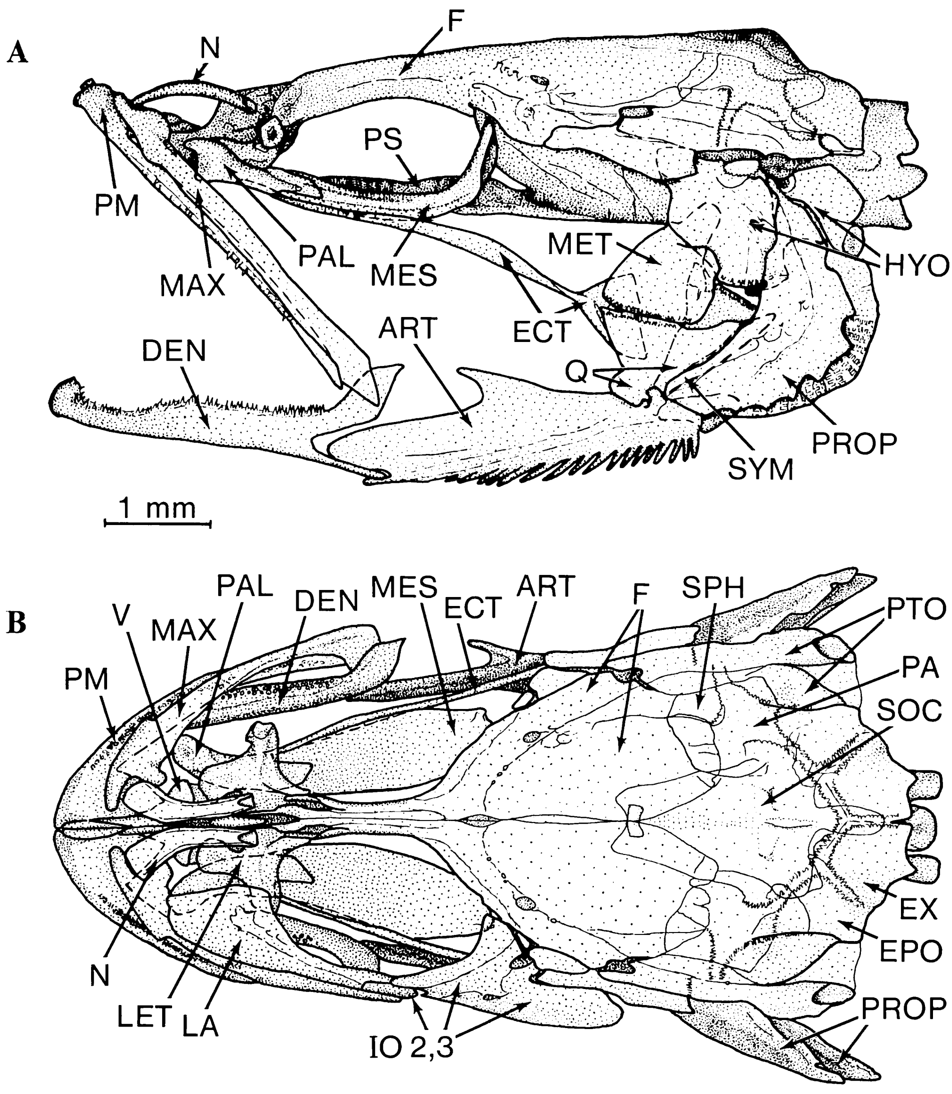

Fig. 1. *Tewara cranwellae* showing skull in lateral view (right side in reverse image with infraorbital bones removed) (A) and skull in dorsal view (B). Abbreviations: ART, articular; DEN, dentary; ECT, ectopterygoid; EPO, epiotic; EX, exoccipital; F, frontal; HYO, hyomandibular; IO, infraorbitals; LA, lachrymal (=first infraorbital); LET, lateral ethmoid; MAX, maxilla; MES, mesopterygoid; MET, metapterygoid; N, nasal; PA, parietal; PAL, palatine; PM, premaxilla; PROP, preopercle; PS, parasphenoid; PTO, pterotic; Q, quadrate; SOC, supraoccipital; SPH, sphenotic; SYM, symplectic; V, vomer. The margins of some bones are indefinite and the identification of some bones is uncertain.

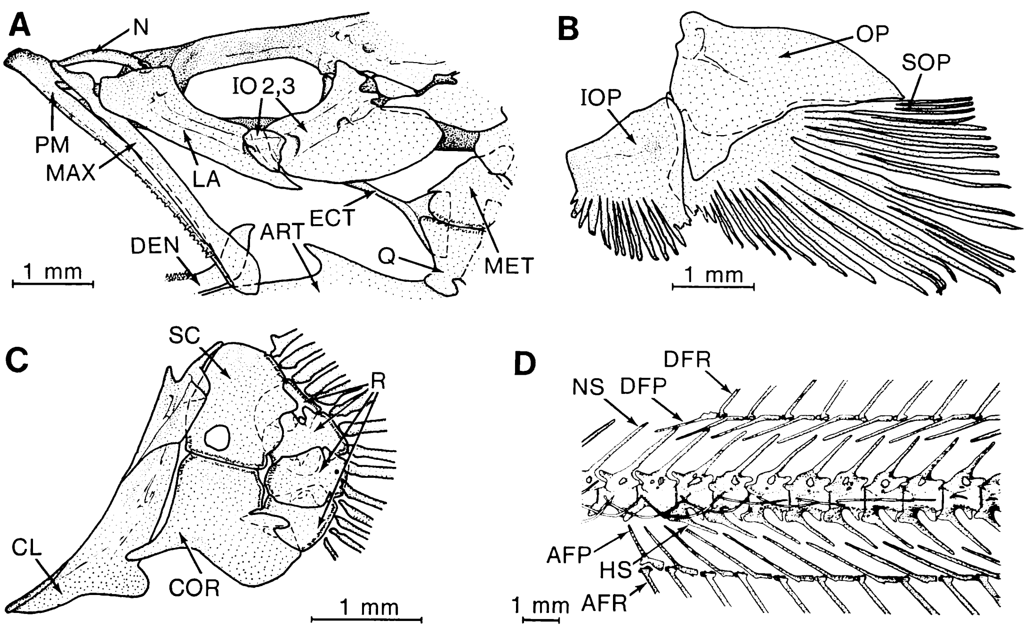

Fig. 2. *Tewara cranwellae* showing infraorbital area (A), opercular bones (B), pectoral skeleton (C), and portion of vertebral column (D). Abbreviations for A in Fig. 1; others are: AFP, anal fin pterygiophore (first); AFR, anal fin ray (first); CL, cleithrum; COR, coracoid; DFP, dorsal fin pterygiophore (first); DFR, dorsal fin ray (first); HS, haemal spine (first); IOP, interopercle; NS, neural spine; OP, opercle; R, radials of pectoral fin; SC, scapula; SOP, subopercle.

the genera *Schizochirus, Creedia, Limnichthys, Tewara, Crystallodytes, Chalixodytes,* and *Apodocreedia.* There appears to be a marked morphological gap between creediids and other families relative to the degree of differences within the creediids. Although many trachinoids variously possess some of these characters (comment to this effect is given for a few), the majority of the characters are absent in any one species, of those known to me, of other fish families. Most of the following characters are probably derived, relative to other trachinoid groups. Characters 7, 10, and 19 are probably primitive; character 14, although derived, has been achieved independently in many teleost lineages (although, in general, the splintering of the gill cover differs in detail between families); 16 may be unique to creediids; 17 and 18, although similar in *Trichonotus setiger,* may in detail be unique to creediids.

1. Upper jaw with fleshy extension (little so in *Schizochirus insolens*); bony jaws protruding about equally far forward.
2. Symphysis of lower jaw with dorsal projection or knob (Fig. 1A).
3. Lower jaw bordered by row of cirri.
4. Lateral line descends (abruptly or gradually) from upper edge of gill cover to ventral surface.
5. Premaxilla with weakly developed postmaxillary process in *S. insolens* and *Creedia haswelli,* otherwise present only as a trace (e.g., *C. partimsquamigera*) or absent.
6. Eye with infolding of the cornea at orbit margin and eyes slightly protruding and probably capable of independent movement; bony interorbital space very narrow.
7. Eye without darkish dorsal iris flap. This structure is present in trichonotids and most species of the percophid subfamily Hemerocoetinae and is also present in some other unrelated benthic fishes.
8. Orbit and infraorbital series placed anteriorly, well in advance of point of articulation of lower jaw with the quadrate (Figs. 1A, 2A).
9. Infraorbital series completely encasing lower margin of orbit with three bones (including the lachrymal), the middle of which is smallest (Fig. 2A) except in *Creedia* spp. A fourth infraorbital or a dermosphenotic may be present

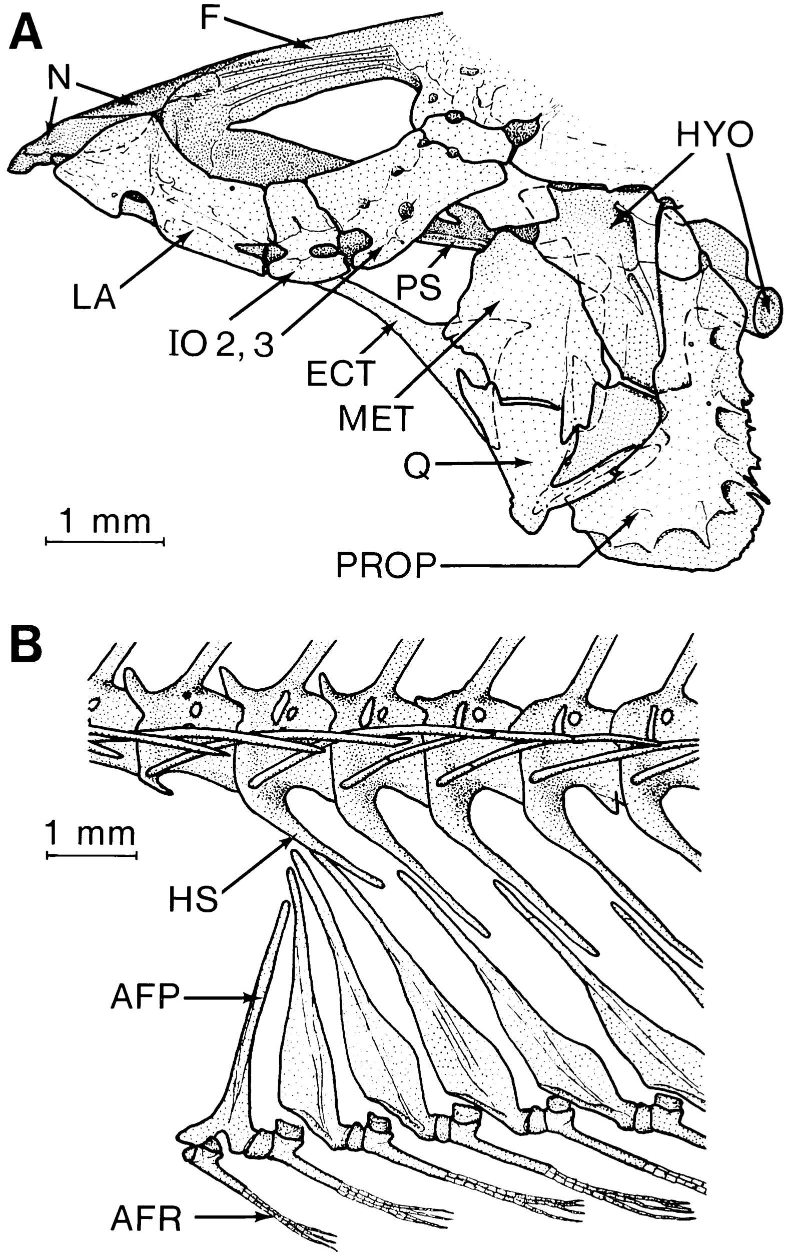

Fig. 3. *Schizochirus insolens* showing portion of skull (A) and anterior anal fin pterygiophores (B). Abbreviations for A in Fig. 1 and for B in Fig. 2.

in at least *S. insolens*. The third infraorbital in most species has a well-developed posterior lobe (but not in *S. insolens* where the bones are more rectangular than in the other species—Fig. 3A); posterior lobe especially large in *C. partimsquamigera* and third infraorbital larger than the others.

10. Gill rakers short, as multi-spined stubs.

11. Dorsal fin single, without spines, branched rays, or elongated rays.

12. Pectoral fin rays 9–17 (excluding the uppermost splintlike ray); *S. insolens* has the highest number and most of the others fall between 11

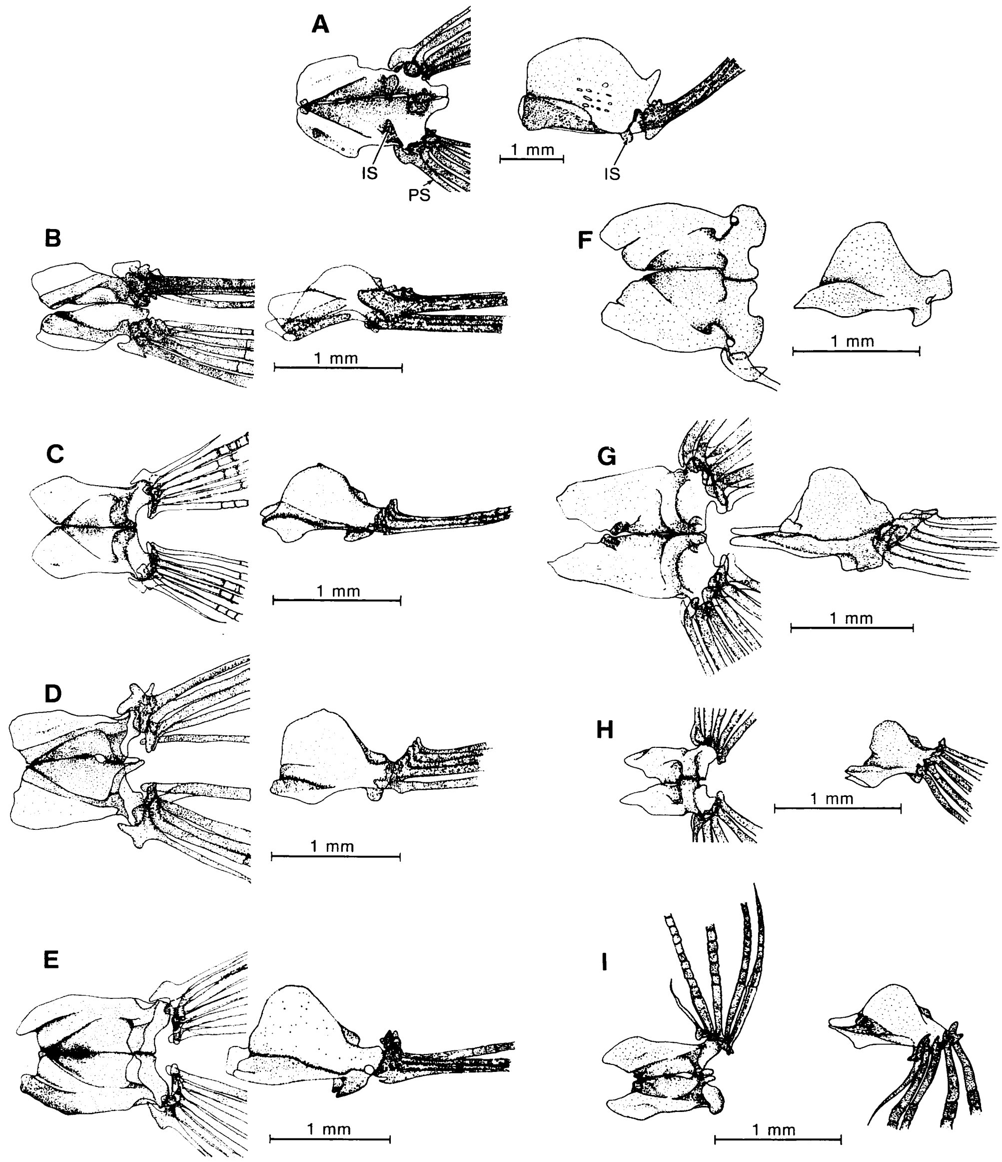

Fig. 4. Pelvic skeleton in ventral view and lateral view (left side) of *Schizochirus insolens* (anterior margin in lateral view may be deformed) (A), *Creedia haswelli* (B), *Limnichthys donaldsoni* (C), *L. fasciatus* (D), *L. nitidus* (E), *Tewara cranwellae* (F), *Crystallodytes cookei* (G), *Chalixodytes chameleontoculis* (H), and *C. tauensis* (I). Abbreviations: IS, iliac spur; PS, pelvic spine. See text for note on orientation.

and 14; rays unbranched except in *S. insolens* and male *C. partimsquamigera*.

13. Postcleithrum absent, except two elements on each side in *S. insolens*. The two elements in the latter species are as follows: the upper and longest bladelike (of uniform width), originating above dorsal fin base on scapula, and extending ventrally beneath the actinosts; the lower element relatively small and with broad base overlapping upper element and with elongate and pointed tip extending to just beneath insertion of lowermost pectoral ray.

Distinct spine fused to cleithrum, originating beneath dorsal tip, projecting medially and pos-

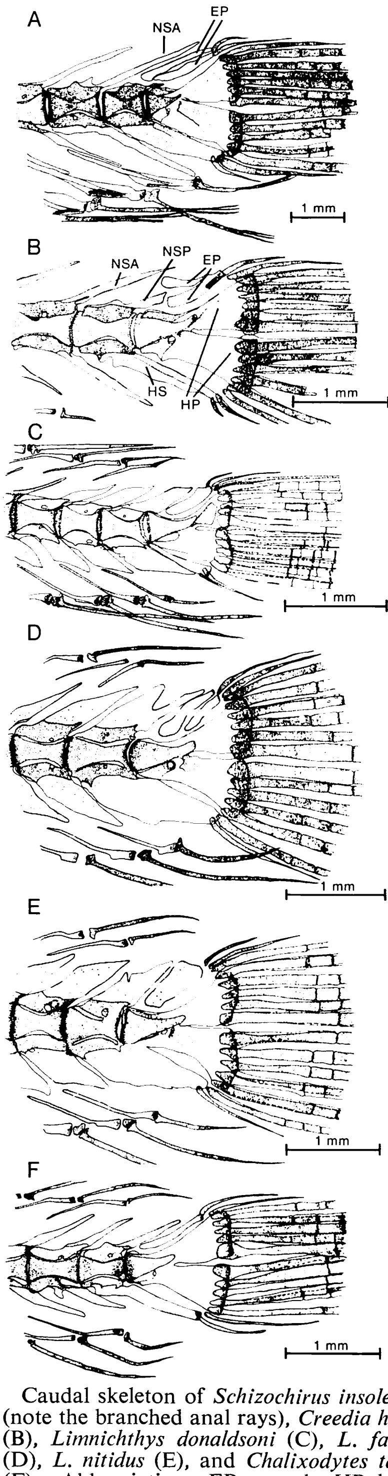

Fig. 5. Caudal skeleton of *Schizochirus insolens* (A) (note the branched anal rays), *Creedia haswelli* (B), *Limnichthys donaldsoni* (C), *L. fasciatus* (D), *L. nitidus* (E), and *Chalixodytes tauensis* (F). Abbreviations: EP, epurals; HP, hypural plates; HS, haemal spine; NSA, neural spine of antepenultimate vertebra; NSP, neural spine of penultimate vertebra.

teriorly (not examined for in *S. insolens, Creedia* spp., and *Crystallodytes cookei*). This projection was not observed in *Trichonotus setiger*.

14. Bone of gill cover highly splintered (Fig. 2B); the subopercle and interopercle are always heavily incised while the opercle, preopercle, and articular may be variously incised.

The incised gill cover, while present in all creediids, is also present in certain members of many other groups, both trachinoid and not. For example, it is variously developed in specimens of the following perciform species examined at Scripps Institution of Oceanography: *Champsodon capensis* (Champsodontidae), *Dactylagnus mundus, Dactyloscopus fimbriatus* (Dactyloscopidae), *Ammodytes hexapterus* (Ammodytidae), *Synchiropus atrilabiatus* (*Callionymus atrilabiatus*) (Callionymidae), and *Gobiesox fulva* (Gobiesocidae); several species of *Opistognathus* (Opistognathidae) have the dorsal projection of the subopercle deeply incised. In *Trichonotus setiger* the subopercle, interopercle, and preopercle are incised. Springer and Freihofer (1976) show an incised opercle in the only species of Pholidichthyidae; Roberts (1984) shows a deeply incised opercula and a partially incised subopercle in the only species of the salmoniform family Lepidogalaxiidae and refers to literature reports which show that at least some galaxiids have a variously incised opercle, usually weakly so. Various opercular bones in some but not all syngnathiforms and gasterosteiforms are deeply incised; in *Culaea inconstans* the opercle and subopercle in specimens of some populations are solid while in others they are incised. The subopercle of a fossil gonorynchid figured in Wilson (1980) may exhibit a weak development of the splintered opercle of creediids. All percophids that I have examined have a solid operculum (although the edge may be jagged). An incised operculum seems to be commonest in benthic and burrowing species and species sucking in water pipette style, although a broad survey is necessary before accepting any such generalization of occurrence. The functional significance of an incised operculum is unknown; however, in discussions with J. E. Randall it is suggested that this flexible operculum may provide a tighter fit than would otherwise be possible between the opercular edge and the body and thereby make any sucking action more efficient.

15. Interpelvic distance, when fins present,

small, less than or about equal to the length of each pelvic fin base except in *S. insolens* where the interpelvic distance is slightly larger than the pelvic fin base length.

16. Pelvis shaped like an inverted bowl, with the opening ventral and the apex, which may be keel-like or rounded, dorsal (Fig. 4); in *S. insolens* there is a paired set of median spurs projecting dorsally from the posterior portion of the bowl just above the rim (Fig. 4A). Each basipterygium with a widened anterior flange which is much larger than the reduced opening in *Creedia partimsquamigera* and almost so in *Crystallodytes cookei*. The flanges of the two basipterygia are separated from each other anteriorly, and each basipterygium is attached to its respective cleithrum dorsal to the cleithral symphysis and on or near a small posterior extension of the cleithrum. The base of the inverted bowl forms an oblique angle with the ventral profile (e.g., see fig. 2 of Nelson, 1979) with base where pelvic rays articulate being approximately horizontal. Iliac spurs arise near the pelvic spine articulation. I do not know of a similarly shaped pelvis in any other group of fishes.

Only the anterior flanges and a variable trace of other parts of the pelvis present in *Apodocreedia vanderhorsti*; one specimen had a trace of a pelvic spine.

17. Mesopterygoid largely free, attached anteriorly to palatine and extending posteriorly as a flattened, wide bone forming the floor of the orbit, narrowing as it curves dorsally, medial to the posterior infraorbitals and contacting, or nearly so doing, the neurocranium adjacent and medial to the contact point of the last infraorbital (Fig. 1A). Posterior end only slightly upturned in *S. insolens*.

18. Ectopterygoid toothless, highly elongate, and rod-like, not attached nor adjacent to other bones for most of its length, extending from palatine and running adjacent to ventral portion of mesopterygoid for part of its length to a fan-like base overlapping the quadrate and metapterygoid (Fig. 1A); the fan-like base not evident in *C. partimsquamigera* but end portion running adjacent to lower margin of metapterygoid and bone ending at anterior corner of quadrate.

19. Generally in each species a one-to-one relation between the number of dorsal and anal fin rays with the pterygiophores and vertebrae; the first two anal rays articulate with the first pterygiophore (Figs. 2D, 3B). In *S. insolens*, unlike other creediids, the first four anal fin pterygiophores converge to the first haemal arch (Fig. 3B) while the remaining ones are parallel and generally contiguous to the anterior surface of their associated haemal spine. In other creediids the anal fin pterygiophores interdigitate with the haemal spines (the first few pterygiophores commence anteriorly to the development of the haemal spines, considerably so in *A. vanderhorsti* and *Crystallodytes cookei*); they penetrate the haemal spine space least (as do the dorsal fin pterygiophores with the neural spine space) in *A. vanderhorsti* where they are relatively short and oblique (the pterygiophores form a sharp angle with the neural and haemal spines in *T. cranwellae*—Fig. 2D).

20. One set of ribs only (epipleurals), well developed.

21. Hypurals fused with well-developed diastema separating the dorsal and ventral halves of the hypural plate; hypurapophysis absent (Fig. 5).

Some earlier workers placed creediids in the "catch-all" family Trichonotidae (see Nelson, 1978, for a brief review of the family placement of various species of creediids and Nelson, 1982, for reasons for excluding *Squamicreedia obtusa*). The genera recognized herein under Creediidae are quite different from *Trichonotus setiger*, the type species of the type genus of Trichonotidae, and are not close enough to be placed in the same family (see Nelson, ms). In addition, according to Leis and Rennis (1983), in at least the three species of creediids for which the pelagic larvae are known, two species of *Limnichthys* and *Crystallodytes cookei*, the preopercle is spined and the swim bladder is absent; known trichonotid larvae lack preopercular spination and have a small swim bladder. In the adult material examined in this study, distinct, but very short spines are evident only on the preopercle of *S. insolens*.

Interrelationships of the genera

Of the various creediids, *Schizochirus insolens* most closely resembles the percophid condition (e.g., in having a deeper body than other creediids, more similar to that of percophids; pectoral, pelvic, and anal fin rays branched; a relatively wide interpelvic distance; lateral line scales resembling those of some of the species of the percophid subfamily Hemerocoetinae which lack protruding maxillary spines). It is, therefore, assumed to be the most primitive species; it is also the most distinctive creediid (e.g., in being the only creediid having a large second suborbital, a postcleithrum, a spur on the dorsal part of the pelvis bowl, and converging anal fin pterygiophores). For purposes of proposing at least a preliminary family tree, character states are assumed to be primitive in *S. insolens* with the extreme condition in other species assumed to be derived. The genera given in Table 1 are listed in order of the postulated phylogenetic sequence based on the conclusions of this simple character analysis. Of course, all the character states in *Schizochirus insolens* need not in fact be primitive and when we have a more thorough knowledge of character states in other trachinoid families than we do at present, it may be possible to polarize character trends and offer a more rational basis for postulating the interrelationships of the genera. The characters employed and the character states recognized in Table 1 in postulating interrelationships are given below.

1. Body depth. Species vary from having a relatively deep body with body depth over 150 thousandths (‰) of standard length (SL) (D), to moderately deep with body depth over or in most specimens of the taxon over 100‰ but under 150‰ (M), relatively slender with body depth between 90–105‰ (R), to slender with body depth under 90‰ (S).

2. Lateral line. The lateral line descends either gradually from the upper edge of the gill opening to the end of the anal fin base (G) or descends abruptly near the tip of the pectoral fin to run parallel, or nearly so, to the ventral profile (P).

3. Body scales. Scales may cover the body (C), be present only along the lateral line, on the caudal peduncle region, and in a predorsal row, either in a paired row (P) or a single row (S), or may be present only along the lateral line (V).

4. Lateral-line scales behind the pectoral fin. In general, the posterior margin of scales along the lateral line is trilobed, with the central lobe large but not extended beyond the general curvature of the scale (C), trilobed and with the central lobe extended (T), or weakly trilobed, if at all, but with a variously developed posterior extension (Y).

5. Maxilla. Posterior portion greatly expanded and tip forked, ventral lobe most pronounced (F) (Fig. 6A, B); expanded but tip only weakly forked (E); moderately expanded, tip rounded or pointed (M); slender with little or no expansion, tip rounded or pointed (S) (Fig. 6C–F).

6. Teeth. All species possess short teeth along the premaxilla and dentary; they are generally absent, except as noted below, along the anteriormost portion of both bones. In addition, two clusters may exist at the head of the vomer (V) and teeth may occur on an expansion at the anterior tip of the premaxilla (P). Most specimens of *Tewara cranwellae* lack teeth on the vomer and at the tip of the premaxilla (A). In *S. insolens* there are also teeth on the palatine (observed on one side only) and relatively elongate teeth on the posterior portion of the dentary followed by a gap and with the short teeth extending almost to the symphysial knob.

7. Urohyal. The urohyal may be elongate, reaching the cleithral junction (E), moderately

Table 1. Character states in Creediidae. See text for explanation of character number. For *Crystallodytes* spp. the data apply only to *C. cookei* for most osteological characters.

	Character number														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Schizochirus insolens	D	G	C	C	F	VP	E	C	R	2	18–20	28–29	I, 5	9	36–41
Creedia alleni	S	P	C	Y	F	V?P	?	?	R	2	12–13	24	I, 3	9	40–42
Creedia haswelli	S	P	C	Y	F	V?P	E	C	R	2	13–16	24–26	I, 4	8, 9	42–45
Creedia partimsquamigera	S	P	P	Y	E	VP	E	C	R	2	14–16	25–28	I, 4	8, 9	44–47
Limnichthys spp.	M	G	C	T	S	V	S	C–T	T	1 or 2	21–33	25–34	I, 5	8	36–47
Tewara cranwellae	R	G	C	T	M	A–V	M	C	T	1	34–36	37–40	I, 5	8	49–55
Crystallodytes spp.	S	G	V	Y	S	V	S	T	T	1	30–43	34–41	I, 5	8	48–60
Chalixodytes spp.	S	G	S	Y	S	V	S	H	T	1	35–40	36–40	I, 4	7, 8	55–59
Apodocreedia vanderhorsti	S	P	C	Y	S	V	S	—	T	1	35–40	32–36	0	8	56–58

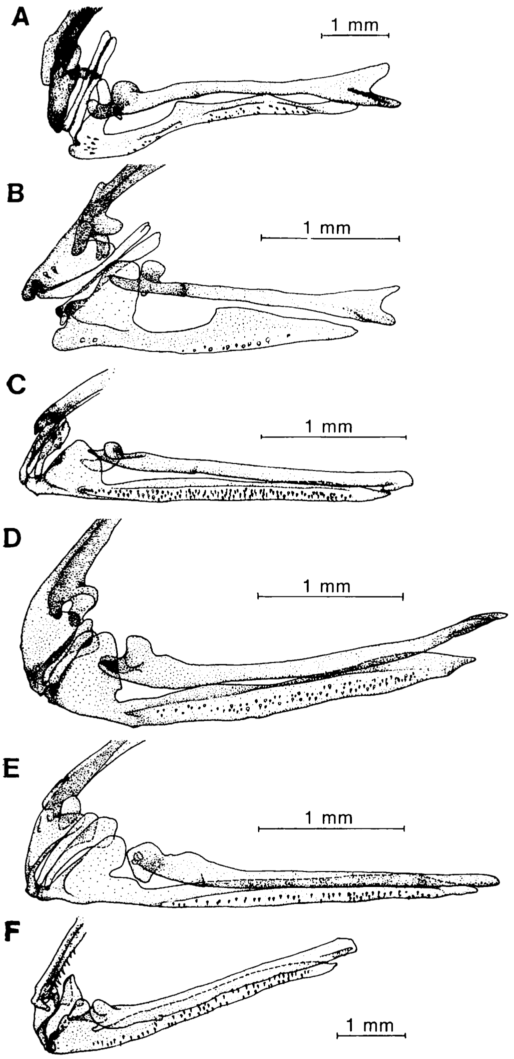

Fig. 6. Maxilla and premaxilla in anterio-dorso-lateral view of *Schizochirus insolens* (A), *Creedia haswelli* (B), *Limnichthys donaldsoni* (C), *L. nitidus* (D), *Chalixodytes tauensis* (E), and *Apodocreedia vanderhorsti* (F). Right side in reverse image for A, E, and F.

elongate, with a relatively small gap between it and the cleithra (M), or be relatively short (S).

8. Iliac spur. The iliac spurs of the pelvis may be short, not meeting in the midline (C), be extended and meet in the midline but with little or no posterior extension (H), or meet in the middle and extend posteriorly (T). The full range of variation exists within the species of *Limnichthys* with the two New Zealand species having short iliac spurs (Nelson, 1979).

9. Last neural spine. The neural spine on the penultimate vertebrae may be reduced to a relatively short stub (R) or be elongate and similar to the other neural spines (T). Considerable variation exists in the width of this bone within the species of *Limnichthys* (see also Nelson, 1979).

10. Epurals. There may be one or two epurals. The shape of the epural is highly variable. In *A. vanderhorsti* it is curved. The single one in *T. cranwellae* and in three species of *Limnichthys* is broad and in some specimens shows evidence of a split. The two epurals in the species of *Creedia* are quite distinctive, unlike the two elongate and parallel ones in *S. insolens*, *L. fasciatus*, and *L. rendahli*.

11. Number of dorsal fin rays.

12. Number of anal fin rays. Only in *S. insolens* are the rays, including the first one, branched.

13. Number of pelvic fin rays. Only in *S. insolens* and perhaps in some *C. partimsquamigera* are at least some of the soft rays branched.

14. Number of branched caudal fin rays. *Creedia partimsquamigera* usually has nine branched rays and *Chalixodytes* spp. usually have eight.

15. Number of vertebrae or lateral scales. There is close agreement in the number of these

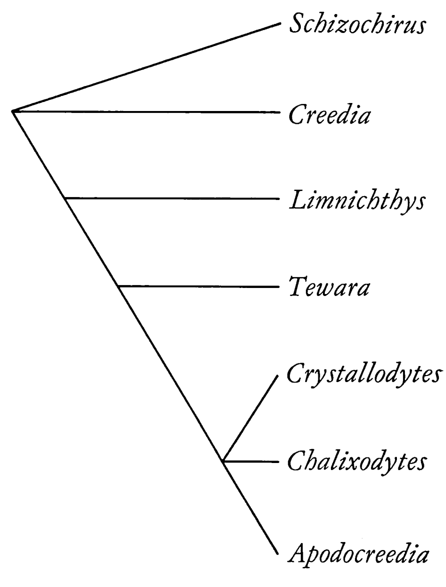

Fig. 7. Postulated relationships of the genera of Creediidae.

two characters; the counts given represent the extremes of both.

The postulated relationships of the genera of creediids, based primarily on the similarities and differences given in Table 1 and the assumption that *Schizochirus insolens* represents the most primitive or least derived species, are shown on the tree in Fig. 7. Three basal lineages are recognized. *Creedia* would seem to form a distinct but diversified group characterized by having a reduced number of dorsal fin rays. It is thought to form a separate radiation from the remaining groups comprising the genera *Limnichthys, Tewara, Crystallodytes, Chalixodytes*, and *Apodocreedia*; the interrelationships of the latter three are uncertain and *Apodocreedia* may very well be closer to *Tewara cranwellae* than are the species of the two other genera. Within the family, if the postulated relationships are correct, there is a general trend toward having a more elongate body, a shorter urohyal, and an increase in the number of dorsal and anal fin rays, lateral-line scales, and vertebrae. The abrupt drop in the lateral line has probably been independently acquired in *Creedia* and *Apodocreedia*, and the pelvic fin rays independently reduced in *Creedia* and the *Chalixodytes-Apodocreedia* branch. Also, the failure to develop all body scales appears to have been independently evolved in *Creedia partimsquamigera* and the species of *Crystallodytes* and *Chalixodytes*. Squamation is also incomplete in the Japanese species of *Trichonotus elegans* (Shimada and Yoshino, 1984).

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トビギンポ科の属の類縁関係

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トビギンポ科の全属を対象に骨格系の比較研究をおこない，21形質によって本科の単系統性が支持された．これらの中には，腰帯，中翼状骨および外翼状骨の性状から新たに見出された標徴形質も含まれる．

骨格系と外部形態の特徴に基づいて属間の類縁関係を検討した結果，*Schizochirus* をもっとも原始的な属と考え，これを第1系群に，*Creedia* を第2系群に，残りの5属—*Limnichthys*, *Tewara*, *Crystallodytes*, *Chalixodytes* および *Apodocreedia*—を第3系群に位置づける体系を提唱した．