New Phylogenetic Proposal for the Family Leptoscopidae
(Perciformes: Trachinoidei)

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Abstract

Examination of taxa closely related to the family Leptoscopidae resulted in 61 apomorphic characters recognized within the family, based on morphological comparisons with the suborder Percoidei, the following being determined as autapomorphic for the former: U-shaped arrangement of infraorbitals; dermosphenotic fused with sphenotic; laminar process present on dorsal surface of ethmoid; medially-directed palatine process; and adductor mandibulae section A1 with two tendons inserted laterally and medially onto maxilla. In addition, presence of the rectus dorsalis 3 muscle (rare among Perciformes), is also considered to support leptoscopid monophyly. The trachinoid family Creediidae was the inferred sister group of Leptoscopidae, based on the sharing of 43 apomorphies, including two rare perciform characters (absence of pterosphenoid and presence of rectus dorsalis 2). It was also inferred that Leptoscopidae plus Creediidae form a monophyletic group with Trichonotidae and the percophid subfamily Hemerocoetinae, an inference supported by 17 apomorphies, including four rare characters found in only several perciform taxa (ligament present between lower jaw and hyoid arch, ectopterygoid rod-like, ligament present between posttemporal and epiotic, and pelvic bone anterior cartilages fused), although the taxa most closely-related to the group have not yet been determined.

Key words: Leptoscopidae, Morphology, Phylogeny, Creediidae, Sister group

Introduction

The family Leptoscopidae (sensu Nelson, 2006), belonging to the perciform suborder Trachinoidei, includes three genera and five species, inhabiting the coastal zone to the continental shelf in Australasian waters, including estuaries and lowland rivers in New Zealand (McDowall, 1978; Paulin et al., 1989; Glover, 1994; Last, 2001; Nelson, 2006; Gomon and Last, 2008).

Pietsch (1989) inferred the phylogenetic relationships of the suborder Trachinoidei, suggesting that Leptoscopidae comprised a monophyletic group with Trachinidae and Uranoscopidae. Subsequently, Pietsch and Zabetian (1990) inferred that Ammodytidae was nested within that group. However, Johnson (1993) and Mooi and Johnson (1997) questioned such hypotheses of trachinoid relationships and the synapomorphies supposedly supporting each clade. Since then, no candidate groups have been proposed as having a close relationship with Leptoscopidae. After a detailed morphological examination of Leptoscopidae and extensive consideration of many other perciforms, we concluded that Leptoscopidae has a sister-group relationship with Creediidae. In addition, Trichonotidae and the percophid subfamily Hemerocoetinae were recognized as forming a monophyletic clade. The latter hypothesis partially supports the close relationships of Creediidae, Trichonotidae and Hemerocoetinae, suggested by several authors (e.g., Nelson, 1986; Johnson, 1993; Odani et al., 2006; Smith and Johnson, 2007). The present study provided evidence for the newly-proposed relationships of Leptoscopidae and related taxa.

Materials and Methods

The specimens used for osteological examination were dissected after staining with alcian blue and/or alizarin red-S, and observed under a stereomicroscope. Osteological characters of whole specimens were determined from radiographs. Anatomical illustrations of the morphology of Leptoscopidae, Creediidae and Trachinidae are shown as mirror images of the right side in the figures. Specimen lengths are expressed as standard length (SL, mm). Terminology generally follows recent perciform studies (e.g., Baldwin and Johnson, 1993; Odani et al., 2006) for osteology and Winterbottom (1974) for myology. Institutional abbreviations follow Leviton et al. (1985), except for the Hokkaido University

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Museum, Hakodate (HUMZ).   For determination of character polarity, the Percoidei (sensu Nelson, 2006), which has been considered as the most primitive group within Perciformes, was employed.   Typical or primitive percoid characters were determined by examination and from previous reports on percoid characters (e.g., Tominaga, 1968; Kusaka, 1974; Vari, 1978; Johnson, 1984; Imamura, 1996, 2000; Kim, 2002).   Apomorphies common to all leptoscopids were recognized as leptoscopid apomorphies.

The trachinoid family Percophidae includes three subfamilies, Bembropinae, Hemerocoetinae and Percophinae (Nelson, 2006).   However, the family definition is unclear because its monophyly has not been evaluated by phylogenetic analysis.   In addition, several authors, including Nelson (1986), Johnson (1993) and Odani et al. (2006), have noted the possibility of percophid polyphyly and the close relationships of Hemerocoetinae, Creediidae and Trichonotidae.   Therefore, the family Percophidae was herein divided into three subfamilies for morphological comparisons.

Materials examined.   *Crapatalus angusticeps*, MNHN A-3080 (2 specimens, 171.6-236.0 mm, partial osteology examined from radiographs); *Leptoscopus macropygus*, NMNZ P. 5268, 21822 (105.6-119.0 mm); *Lesueurina platycephala*, AMS I.15731-014 (44.9 mm).

Comparative materials. Blennioidei.—Blenniidae: *Entomacrodus stellifer*, HUMZ 195698 (87.6 mm).   Callionymoidei.—Callionymidae: *Repomucenus curvicornis*, HUMZ 110544 (139.0 mm).   Draconettidae: *Draconetta xenica*, HUMZ 178466 (84.2 mm).   Gobioidei.—Gobiidae: *Acanthogobius flavimanus*, HUMZ uncat. (105.4 mm); *Suruga fundicola*, HUMZ uncat. (66.0 mm).   Labroidei.— Labridae: *Pseudolabrus eoethinus*, HUMZ 97042 (102.2 mm).   Scombroidei.—Gempylidae: *Promethichthys prometheus*, HUMZ 117433 (158.0 mm).   Scombridae: *Gymnosarda unicolor*, HUMZ 39256 (202.4 mm).   Percoidei.—Acropomatidae: *Acropoma japonicum*, HUMZ 39772 (106.0 mm); *Malakichthys wakiyae*, HUMZ 79412 (106.0 mm).   Ambassidae: *Ambassis vachelii*, HUMZ 198820 (47.2 mm).   Apogonidae: *Apogon semilineatus*, HUMZ 107056 (83.5 mm).   Cheilodactylidae: *Goniistius zebra*, HUMZ 36355 (113.6 mm); Epigonidae: *Epigonus denticulatus*, HUMZ 135064 (118.5 mm).   Gerreidae: *Gerres japonicus*, HUMZ 119392 (98.2 mm).   Haemulidae: *Hapalogenys mucronatus*, HUMZ 143107 (98.8 mm).   Lutjanidae: *Lutjanus fulvus*, HUMZ 80518 (102.2 mm).   Pempheridae: *Pempheris schwenkii*, HUMZ 62960 (103.1 mm).   Plesiopidae: *Plesiops coeruleolineatus*, HUMZ 119731 (53.4 mm); Polyprionidae: *Stereolepis doederlieni*, HUMZ 71230 (106.0 mm).   Teraponidae: *Terapon theraps*, HUMZ 105799 (116.0 mm).   Scorpaenoidei.—Serranidae: *Chelidoperca hirundinacea*, HUMZ 62574 (125.0 mm); *Diploprion bifasciatum*, HUMZ 87231 (124.3 mm); *Epinephelus latifasciatus*, HUMZ 36511 (113.2 mm).

Trachinoidei.—Ammodytidae: *Ammodytes personatus*, HUMZ 131165 (170.7 mm).   Champsodontidae: *Champsodon longipinnis*, HUMZ 149645 (113.6 mm); *Champsodon snyderi*, HUMZ 109313 (87.6 mm).   Chiasmodontidae: *Chiasmodon boulengeri*, HUMZ 124516 (154.0 mm).   Creediidae: *Creedia haswelli*, AMS I.26397-002 (38.9 mm); *Limnichthys fasciatus*, AMS I.17363-002 (33.0 mm); *Tewara cranwellae*, NMNZ P. 3136 (60.6 mm).   Percophidae: *Acanthaphritis barbata*, HUMZ 178034, 178035 (78.4-88.0 mm); *Bembrops curvatura*, HUMZ 37322, 75324, 79900 (134.0-141.0 mm); *Chrionema furunoi*, HUMZ 178348 (137.8 mm); *Enigmapercis reducta*, AMS I.21420-007 (75.6 mm); *Hemerocoetes monopterygius*, HUMZ 67065, 67066 (180.0-184.1 mm); *Matsubaraea fusiforme*, KSHS 24375, 24376 (51.2-56.2 mm); *Osopsaron verecundum*, HUMZ 178322, 178323 (39.6-47.0 mm); *Percophis brasiliensis*, MNHN 1975-330 (2 specimens, 213.8-243.0 mm); *Pteropsaron evolans*, HUMZ 189885 (62.2 mm).   Pinguipedidae: *Parapercis multifasciata*, HUMZ 65563 (117.8 mm).   Trachinidae: *Trachinus draco*, USNM 198840 (114.0 mm).   Trichonotidae: *Trichonotus filamentosus*, URM-P 18701 (98.9 mm); *T. setiger*, URM-P 6453 (120.3 mm).   Uranoscopidae: *Uranoscopus bicinctus*, HUMZ 131756 (90.0 mm); *Xenocephalus elongatus*, HUMZ 63654 (176.4 mm).

In addition, 47 perciforms, including 24 percoid species, were also examined, such being listed in Imamura (2000) and Imamura and Yabe (2002).

Apomorphies of the family Leptoscopidae

As a result of comparisons between the Leptoscopidae and representative percoids, the following 61 apomorphic characters (AC) were recognized in the former.

AC 1.   U-shaped arrangement of infraorbitals (Fig. 1).— The infraorbitals are arranged in a U-shape in Leptoscopidae, such being considered as an autapomorphy, supporting the monophyly of the family, because those elements are typically arranged in a semicircle in percoids, as well as in other perciforms.

AC 2.   Absence of suborbital shelf.—The suborbital shelf is absent in leptoscopids, but primitively present in percoids (e.g., Smith and Bailey, 1962; Shinohara, 1994).   Absence of the shelf is also a characteristic of several other perciforms, such as the trachinoids Creediidae, Pinguipedidae and Trichonotidae, and the callionymoids Callionymidae and Draconettidae.

AC 3.   Dermosphenotic and sphenotic fused (Fig. 2B).— Fusion of the dermosphenotic (= sixth infraorbital sensu Imamura, 2004) with the sphenotic in leptoscopids is an autapomorphy, supporting the monophyly of the family, due to the bone being only primitively attached to the sphenotic in percoids and other perciforms.   Definition of "fusion" and
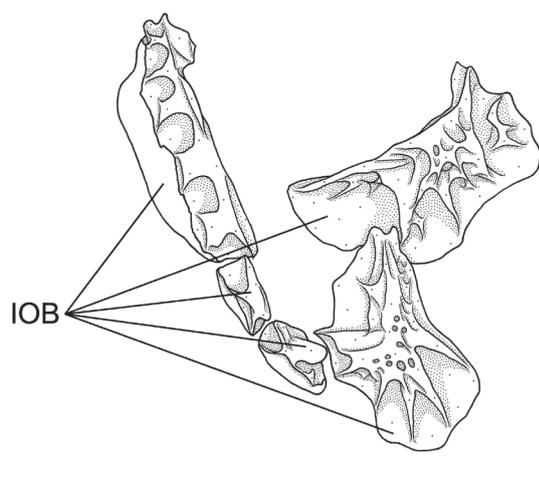
Fig. 1.   Lateral aspect of infraorbital bones of *Leptoscopus macropygus,* NMNZ P. 5268, 119.0 mm SL.   Scale indicates 5 mm.   IOB, infraorbital bones.   Posteriormost infraorbital (= dermosphenotic) not figured.
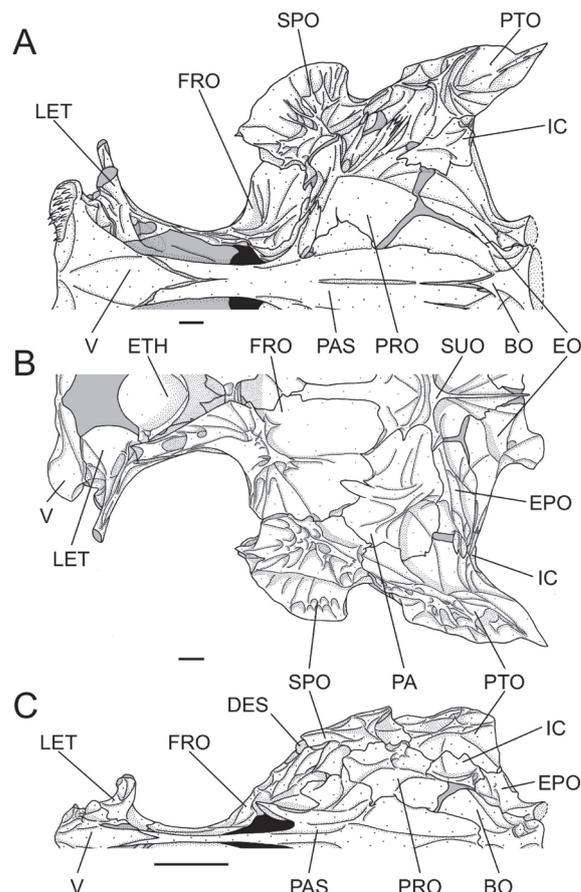

Fig. 2.   Ventral (A and C) and dorsal (B) aspects of cranium.   A and B, *Leptoscopus macropygus*, NMNZ P. 5268, 119.0 mm SL;   C, *Tewara cranwellae*, NMNZ P. 3136, 60.6 mm SL. Scales indicate 1 mm.   BO, basioccipital; DES, dermosphenotic;   EO, exoccipital;   EPO, epiotic; ETH, ethmoid;   FRO, frontal;   IC, intercalary;   LET, lateral ethmoid;   PA, parietal;   PAS, parasphenoid; PRO, prootic;   PTO, pterotic;   SPO sphenotic;   SUO, supraoccipital;   V, vomer.

"attachment" of these bones follows Imamura (2004).

AC 4.   Opening of dermosphenotic (continuous with sensory canal of adjacent infraorbital) directed anteriorly (Fig. 2A, C).—The dermosphenotic opening, being continuous with the adjacent infraorbital, is directed anteriorly in leptoscopids.   This is regarded as apomorphic because the opening is typically directed laterally in percoids (e.g., Fraser, 1968; Otero, 2004).   The apomorphic condition also occurs in several other perciforms, including trachinoids in the percophid subfamily Hemerocoetinae and the creediids *Limnichthys* and *Tewara*.

AC 5.   Two tooth plates on vomer (Fig. 2A, C).—Leptoscopids possess two tooth plates on the vomer, whereas percoids primitively have a single plate (e.g., Tominaga, 1968; Imamura, 1996).   The apomorphic condition also occurs in the trachinoids Champsodontidae, Creediidae and Trichonotidae.

AC 6.   Presence of laminar process on dorsal surface of ethmoid (Fig. 2B).—A laminar process on the dorsal surface of the ethmoid in leptoscopids is absent in all other perciforms.   Accordingly, the leptoscopid condition is regarded as an autapomorphy, strongly supporting the monophyly of the family.

AC 7.   Frontal and parasphenoid connected (Fig. 2A, C).—The frontal and parasphenoid are connected in leptoscopids, but primitively separated in percoids (e.g., Fraser, 1972; Sasaki, 1989).   The apomorphic condition also occurs in several other perciforms, including the trachinoid families Creediidae and Percophidae (*Enigmapercis* and *Percophis*).

AC 8.   Absence of an autogenous pterosphenoid (Fig. 2A, C).—An autogenous pterosphenoid is absent in Leptoscopidae, although it is unclear whether or not such absence has resulted from fusion of the element with an adjacent bone

(frontal or parasphenoid) or simply its non-development.   Absence of the pterosphenoid among perciforms elsewhere occurs only in the Creediidae (e.g., Fraser, 1968; Rosen and Patterson, 1990; this study).   Thus the condition can be regarded as a rare apomorphy.

AC 9.   Absence of basisphenoid.—Whereas percoids primitively possess the basisphenoid, that element is absent in leptoscopids (e.g., Tominaga, 1968; Vari, 1978).   It is absent also in several other perciforms, such as the trachinoids Creediidae, Uranoscopidae and the percophid subfamily Hemerocoetinae, and the gobioid Gobiidae.

AC 10.   Exoccipital condyles on both sides separated.— The exoccipital condyles on both sides are separated on the midline in leptoscopids.   Odani et al. (2006) regarded this condition to be apomorphic, because the condyles are typically connected in percoids.   Separation of the condyles also occurs in several other perciforms, including the trachinoids

Creediidae, Percophidae and Trichonotidae, the gobioid Gobiidae, and the callionymoid Callionymidae.

AC 11. Lower jaw and hyoid arch connected by ligament.—The presence of a ligament (typically absent in percoids) connecting the lower jaw and hyoid arch is regarded as an apomorphy (e.g., Fraser, 1968; Kim, 2002). Several other perciforms, including the trachinoids Creediidae, Trichonotidae and the percophid subfamily Hemerocoetinae also possess the ligament.

AC 12. Absence of supramaxilla.—The supramaxilla is absent in leptoscopids, but primitively present in percoids (e.g., Tominaga, 1968; Fraser, 1972), as well as in many other perciforms, including the trachinoids Creediidae, Percophidae, Trichonotidae and Trachinidae, and the scombroids Gempylidae and Scombridae.

AC 13. Presence of medially-directed process on palatine (Fig. 3A).— A medially-directed process on the palatine in leptoscopids is autapomorphic. Because all other perciforms lack such a process, its presence in Leptoscopidae supports the monophyly of the family.

AC 14. Ectopterygoid rod-like (Fig. 3A, B).—A rod-like

ectopterygoid is the apomorphic condition, since the bone is typically triangular in percoids (e.g., Sasaki, 1989; Otero, 2004). A rod-like ectopterygoid is found in several other perciforms, including the trachinoids Creediidae, Trichonotidae and the percophid subfamily Hemerocoetinae.

AC 15. Absence of metapterygoid lamina (Fig. 3A, C).—Leptoscopids lack the metapterygoid lamina typically present in percoids (e.g., Greenwood, 1976; Johnson, 1980), and several other perciforms, including the trachinoids Ammodytidae, Champsodontidae and Chiasmodontidae.

AC 16. Absence of beryciform foramen (Fig. 4).—A beryciform foramen is absent in leptoscopids, but primitively present in percoids (e.g., Fraser, 1968; Imamura, 1996). Several other perciforms, including the trachinoids Creediidae Percophidae and Trichonotidae, the scombroid Gempylidae, and the labroid Labridae also lack the foramen.

AC 17. Presence of small laminar process on ceratohyal (Fig. 4A).—A small laminar process on the ceratohyal receiving the protractor hyoidei in leptoscopids is typically absent in percoids (e.g., Sasaki, 1989; Mooi, 1993). Regarded as apomorphic, the laminar process is also present in other perciforms, such as the trachinoids Creediidae and Pinguipedidae, and the gobioid Gobiidae.

AC 18. Single branchiostegal ray on epihyal (Fig. 4).—A single branchiostegal ray is present on the epihyal in leptoscopids, compared with two in typical percoids (e.g., McAllister, 1968; Vari, 1978). A single ray on the epihyal occurs in several other perciforms, including the trachinoids Creediidae, Pinguipedidae and Trichonotidae, the blennioid Blenniidae, and the labroid Labridae.
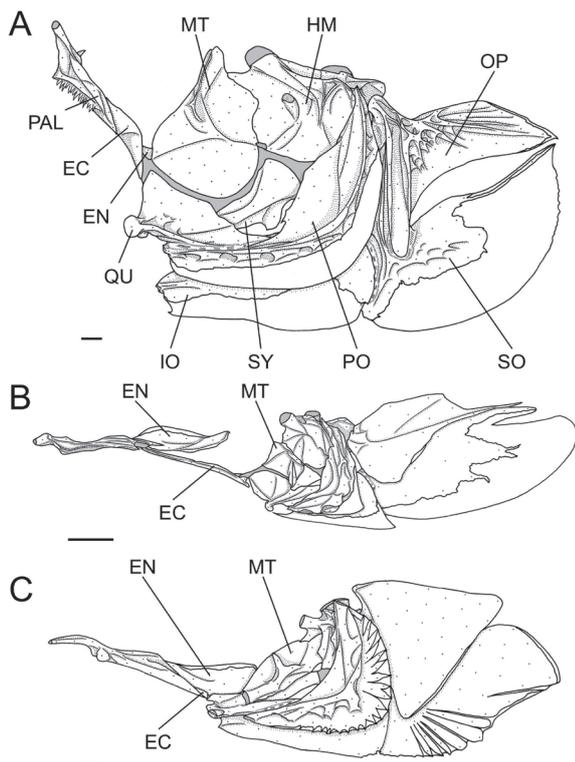

Fig. 3. Lateral aspect of suspensorium of *Leptoscopus macropygus*, NMNZ P. 5268, 119.0 mm SL (A), *Matsubaraea fusiforme*, KSHS 24376, 51.2 mm SL (B) and *Ammodytes personatus*, HUMZ 131165, 170.7 mm SL (C). Scales indicate 1 mm. EC, ectopterygoid; EN, endopterygoid; HM, hyomandibula; IO, interopercle; MT, metapterygoid; OP, opercle; PAL, palatine; PO, preopercle; QU, quadrate; SO, subopercle; SY, symplectic.
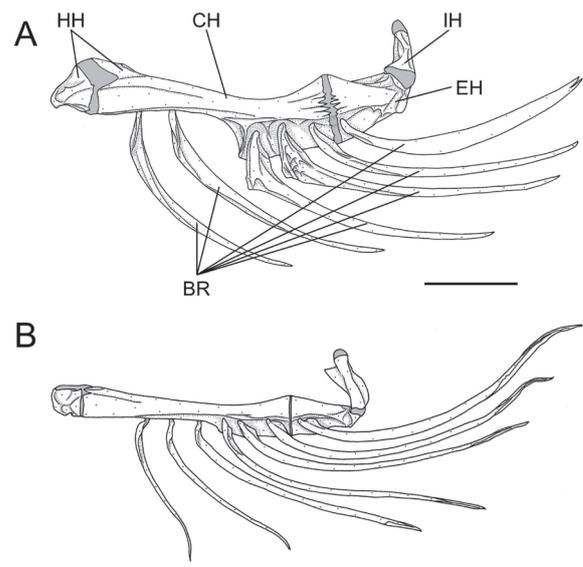

Fig. 4. Lateral aspect of hyoid arch of *Leptoscopus macropygus*, NMNZ P. 5268, 119.0 mm SL (A) and *Trichonotus setiger*, URM-P 6453, 120.3 mm SL (B). Scales indicate 5 mm. BR, branchiostegal ray; CH, ceratohyal; EH, epihyal; HH, hypohyal; IH, interhyal.
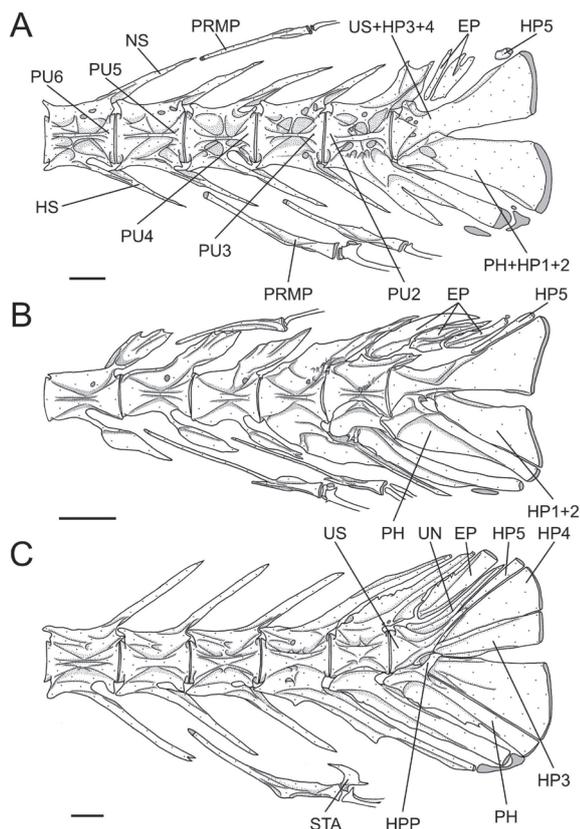
Fig. 5. Lateral aspect of caudal fin skeleton of *Leptoscopus mac-ropygus,* NMNZ P. 5268, 119.0 mm SL (A), *Pteropsaron evolans*, HUMZ 189885, 62.2 mm SL (B) and *Trachinus draco*, USNM 198840, 114.0 mm SL (C). Scales indi-cate 1 mm. EP, epural; HP, hypural; HPP, hypurapo-physis; HS, hemal spine; NS, neural spine; PH, parhypural; PRMP, proximal-middle pterygiophore; PU, preural centrum; STA, stay; UN, uroneural; US, urostyle.

AC 19. Six branchiostegal rays (Fig. 4A).—Six bran-chiostegal rays are present in Leptoscopidae, the percoids primitively possessing seven rays (e.g., McAllister, 1968; Shinohara, 1994). The apomorphic condition also occurs in several other perciforms, including the trachinoids Pinguipe-didae and Trachinidae, the callionymoid Draconettidae, and the labroid Labridae.

AC 20. Absence of gill rakers and/or tooth plates on hypobranchial.— Hypobranchial gill rakers and/or tooth plates are absent in leptoscopids, but primitively present in percoids (e.g., Tominaga, 1968; Johnson, 1993). They also occur in the trachinoids Chiasmodontidae and Uranoscopidae, the blennioid Blenniidae, and the labroid Labridae.

Although Pietsch (1989) and Pietsch and Zabetian (1990) distinguished between gill rakers and tooth plates on the gill arches, the shape of the gill rakers is variable (e.g., comb-like, rod-like, triangular, conical, hemispherical or knob-like). In addition, the anterior rakers are more rudimentary and diffi-cult to distinguish from tooth plates in several perci-

forms. However, the aforementioned authors failed to provide criteria separating the two conditions. Gill rakers and tooth plates were treated as serial elements in this study.

AC 21. Absence of interarcual cartilage.—Leptoscopids lack an interarcual cartilage, which is a primitive character of percoids (e.g., Imamura, 1996; Kim, 2002). Several other perciforms, including the trachinoids Chiasmodontidae, Cree-diidae and Trichonotidae, the blennioid Blenniidae, and the callionymoid Callionymidae, also lack the cartilage.

AC 22. Third basibranchial cartilaginous.—The carti-laginous third basibranchial is apomorphic in leptoscopids, because the element is primitively centrally ossified in per-coids (e.g., Johnson and Fritzsche, 1989; Rosen and Patter-son, 1990). In the perciforms examined, only the uranoscopid genus *Uranoscopus* also possessed a cartilagi-nous third basibranchial

AC 23. Autogenous tooth plate absent on ventromedial part of second epibranchial.—Absence of an autogenous tooth plate on the ventromedial part of the second epibran-chial is apomorphic in leptoscopids, being primitively present in percoids (e.g., Fraser, 1968; Johnson, 1980). The apo-morphic condition occurs in several other perciforms, includ-ing the trachinoids Chiasmodontidae, Creediidae, Percophidae and Trichonotidae, the labroid Labridae, and the scombroid Gempylidae.

AC 24. Absence of tooth plate on third epibranchial.—The absence in leptoscopids, of a tooth plate which is typi-cally fused with the ventral surface of the third epibranchial in percoids (e.g., Fraser, 1972; Imamura, 1996), is regarded as an apomorphy. Several other perciforms, including the trachinoids Ammodytidae and Uranoscopidae, and the calli-onymoids Callionymidae and Draconettidae also lack the plate.

AC 25. Absence of first pharyngobranchial (Fig. 7).—Leptoscopids lack the first pharyngobranchial, the presence of which is a primitive condition in percoids (e.g., Tominaga, 1968; Johnson and Fritzsche, 1989). The apomorphic con-dition also occurs in other perciform taxa, including the trachinoids Creediidae, Trichonotidae and the percophid sub-family Hemerocoetinae, the blennioid Blenniidae, and the gobioid Gobiidae.

AC 26. Absence of medial supratemporal (Fig. 6).—The medial supratemporal is absent in leptoscopids. Because the element is present in typical percoids (e.g., Tominaga, 1968; Johnson, 1980), absence of the bone is considered to be apomorphic. The apomorphic condition is also found in other perciforms, including the trachinoids Creediidae, Trachinoid and the percophid subfamily Hemerocoetinae, the scombroid Scombridae, and the blennioid Blenniidae.

AC 27. Presence of ligament connecting posttemporal and epiotic (Fig. 6).— A ligament connecting the posttempo-ral and epiotic is considered apomorphic in leptoscopids, being absent in typical percoids which have the posttemporal
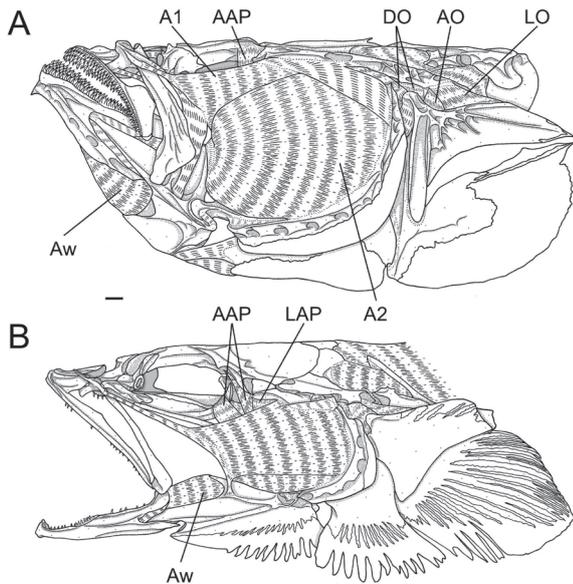
Fig. 6. Lateral aspect of cheek and other cephalic muscles of *Leptoscopus macropygus,* NMNZ P. 5268, 119.0 mm SL (A) and *Tewara cranwellae*, NMNZ P. 3136, 60.6 mm SL (B). Scales indicate 1 mm. A1–2 and Aw, adductor mandibular sections A1–2 and Aw; AAP, adductor arcus palatini; AO, adductor operculi; DO, dilatator operculi; LAP, levator arcus palatini; LO, levator operculi.
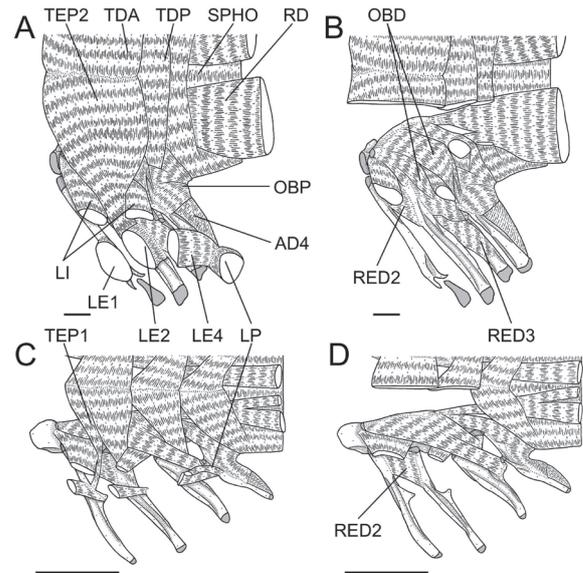

Fig. 7. Dorsal aspect of branchial muscles of *Leptoscopus macropygus,* NMNZ P. 5268, 119.0 mm SL (A and B) and *Tewara cranwellae*, NMNZ P. 3136, 60.6 mm SL (C and D). Scales indicate 1 mm. Superficial muscles partially removed in B and D. AD, adductor; LE, levator externus; LI, levator internus; LP, levator posterior; OBD, obliquus dorsalis; OBP, obliquus posterior; RD, retractor dorsalis; RED, rectus dorsalis; SPHO, shincter oesophagi; TDA, transversus dorsalis anterior; TDP, transversus dorsalis posterior; TEP1, transversus epibranchialis 1; TEP2, transversus epibranchialis 2. Adductores 1–3 not figured.

directly connected with the epiotic (e.g., Greenwood, 1976; Kim, 2002). Presence of the ligament, regarded as an apomorphy, occurs also in the perciform trachinoids Creediidae, Trichonotidae and the percophid subfamily Hemerocoetinae.

AC 28. Absence of postcleithra.—Postcleithra are absent in leptoscopids, but primitively present in percoids (e.g., Sasaki, 1989; Otero, 2004). Postcleithra are also absent in the trachinoid Creediidae and gobioid *Acanthogobius*, among other perciforms.

AC 29. Anterior cartilages of pelvic bones fused.—The anterior cartilaginous caps of the pelvic bones on both sides are fused in the Leptoscopidae. The fusion of these cartilages is an apomorphy, because they are primitively separated in the percoids (e.g., Stiassny and Moore, 1992; Imamura, 1996). The fusion is also observed in other perciforms, such as the trachinoids Creediidae, Trachinidae and the percophid subfamily Hemerocoetinae.

AC 30. Neural spine and centrum of first abdominal vertebra fused.—The neural spine and centrum of the first abdominal vertebra are fused in leptoscopids, but primitively separated in percoids (e.g., Otero, 2004; Odani et al., 2006). The apomorphic condition is also found in several other perciforms, such as the trachinoids Creediidae, Trichonotidae and Uranoscopidae, the blennioid Blenniidae, and the callionymoid Draconettidae.

AC 31. Absence of pleural ribs.—Pleural ribs are absent

in Leptoscopidae, but primitively present in percoids (e.g., Vari, 1978; Sasaki, 1989). Several other perciforms, including the trachinoids Creediidae, Trichonotidae and the percophid subfamily Hemerocoetinae, and the callionymoids Callionymidae and Draconettidae, also lack pleural ribs.

AC 32. Absence of supraneurals.—Whereas leptoscopids lack supraneurals, percoids primitively possess three such elements (e.g., Johnson, 1984; Imamura, 1996). The apomorphic condition also occurs in perciforms, such as the trachinoids Champsodontidae, Creediidae and Pinguipedidae, and the scombroids Gempylidae and Scombridae.

AC 33. Ventral margin of first proximal-middle pterygiophore of anal fin with single soft ray.—The first proximal-middle pterygiophore of the anal fin supports a single soft ray ventrally in leptoscopids, compared with two spines supported in percoids (e.g., Imamura, 1996; Odani et al., 2006). This leptoscopid apomorphy also occurs in other perciforms, including the trachinoids Creediidae, Trachinidae and the percophid subfamily Hemerocoetinae.

AC 34. Ventral margin of second proximal-middle pterygiophore of anal fin with single soft ray.—The ventral support of a single soft ray is considered an apomorphy in leptoscopids, because the anal fin second proximal-middle pterygiophore supports a spine ventrally in typical percoids

(e.g., Tominaga, 1968; Odani et al., 2006). The apomorphic condition is also found in several other perciforms, including the trachinoids Creediidae, Percophidae and Trichonotidae, the callionymoid Callionymidae, and the gobioid Gobiidae.

AC 35. Absence of middle pterygiophores of dorsal and anal fins.—The middle pterygiophores of the dorsal and anal fins are absent in leptoscopids, but primitively present in percoids (e.g., Johnson, 1980; Otero, 2004). Several other perciforms, including the trachinoids Creediidae, Trichonotidae and percophid subfamily Hemerocoetinae, the callionymoid Draconettidae, and the labroid Labridae, also lack these elements.

AC 36. Absence of stays of dorsal and anal fins (Fig. 5A, BB).—Leptoscopids lack dorsal and anal fin stays, in contrast to the primitive condition in percoids (e.g., Johnson, 1984; Imamura, 1996). The apomorphic condition also occurs in the trachinoids Creediidae, Trichonotidae and Uranoscopidae, and the callionymoids Callionymidae and Draconettidae.

AC 37. Last dorsal fin soft ray comprised of single element (Fig. 5A, B).—The last dorsal fin soft ray is comprised of a single ray element in leptoscopids, compared with the primitive condition of two elements in percoids (e.g., Fraser, 1968; Imamura and Matsuura, 2003). Among other perciforms, the trachinoids Ammodytidae and Creediidae, the blennioid Blenniidae and the scombroid Scombridae also have a single ray element.

AC 38. Last anal fin soft ray comprised of single ray element (Fig. 5A).— A single ray element in the last anal fin soft ray is apomorphic, since the ray primitively comprises two ray elements in the percoids (e.g., Tominaga, 1968; Imamura and Matsuura, 2003). The apomorphic condition also occurs in the trachinoids Ammodytidae and Creediidae, the blennioid Blenniidae and the callionymoid Draconettidae.

AC 39. Hemal spine and second preural centrum fused (Fig. 5A).—The hemal spine on the second preural centrum is fused with the centrum in leptoscopids, while it is autogenously connected with the centrum in typical percoids (e.g., Fraser, 1968; Fujita, 1990). Fusion of the spine, the apomorphic condition, also occurs in several other perciforms, including the trachinoids Champsodontidae and Creediidae, the blennioid Blenniidae and the gobioid Gobiidae.

AC 40. Hemal spine and third preural centrum fused (Fig. 5).—The hemal spine and third preural centrum are fused in leptoscopids, but are primitively attached in most percoids (e.g., Johnson, 1984; Shinohara, 1994). The apomorphic condition also occurs in the trachinoids Creediidae, Trichonotidae and the percophid subfamily Hemerocoetinae, the gobioid Gobiidae and the labroid Labridae.

AC 41. Urostyle and hypurals fused (Fig. 5A, B).—The urostyle is fused with the hypurals in leptoscopids, whereas percoids primitively possess an autogenous urostyle and hypurals (e.g., Gosline, 1961; Greenwood, 1976). Fusion

of these elements also occurs in other perciforms, including the trachinoids Ammodytidae, Creediidae and Uranoscopidae, the callionymoid Callionymidae and the scombroid Scombridae.

AC 42. First and second hypurals fused (Fig. 5A, B).—Fusion of the first and second hypurals is apomorphic, since they are primitively autogenous in percoids (e.g., Vari, 1978; Fujita, 1990). The apomorphic condition also occurs in other perciforms, including the trachinoids Creediidae, Trichonotidae and the percophid subfamily Hemerocoetinae, the callionymoid Draconettidae and the labroid Labridae.

AC 43. Third and fourth hypurals fused (Fig. 5A, B).—The third and fourth hypurals are fused in leptoscopids, but primitively autogenous in percoids (e.g., Shinohara, 1994; Kim, 2002). The apomorphic condition also occurs in other perciforms, including the trachinoids Ammodytidae, Creediidae and Uranoscopidae, the scombroid Scombridae and the gobioid Gobiidae.

AC 44. Absence of hypurapophysis (Fig. 5A, B).—Leptoscopids lack the hypurapophysis, which occurs in percoids (e.g., Gosline, 1961; Johnson, 1984). Several other perciforms, including the trachinoid Creediidae, the blennioid Blenniidae and the gobioid Gobiidae, also lack the hypurapophysis.

AC 45. Absence of uroneural (Fig. 5A, B).—Absence of the uroneural is the apomorphic condition, since that bone is present in percoids (e.g., Sasaki, 1989; Fujita, 1990). The apomorphic condition also occurs in other perciforms, including the trachinoids Creediidae, Trichonotidae and the percophid subfamily Hemerocoetinae, and the callionymoids Callionymidae and Draconettidae.

AC 46. Two epurals (Fig. 5A).—Leptoscopids possess two epurals, whereas most percoids possess three (e.g., Kim, 2002; Odani et al., 2006). The apomorphic condition also occurs in other perciforms, including the trachinoids Ammodytidae and the creediid *Limnichthys*, the blennioid Blenniidae and the gobioid Gobiidae.

AC 47. Four branched rays on upper caudal lobe.—Four branched rays are present on the upper caudal lobe in leptoscopids. In contrast, percoids primitively possess eight branched rays (e.g., Johnson, 1984; Fujita, 1990). The former character also occurs in several other perciforms, including the trachinoids Creediidae and the percophid subfamily Hemerocoetinae, the callionymoid Callionymidae and the labroid Labridae.

AC 48. Four branched rays on lower caudal lobe.—Four branched rays are present on the lower caudal lobe in leptoscopids, compared with seven primitively in percoids (e.g., Greenwood, 1976; Odani et al., 2006). The apomorphic condition also occurs in the trachinoids Creediidae and the percophid subfamily *Acanthaphritis*, the blennioid Blenniidae and the callionymoid Draconettidae.

AC 49. Adductor mandibulae section 1 with two tendons

inserted onto maxilla laterally and medially (Fig. 6A).—The adductor mandibulae section 1 (A1) has two anterior tendons in leptoscopids, one being inserted onto the posterior aspect of the premaxillary condyle on the maxilla and the other onto the anterolateral part of the maxilla.   In contrast, A1 has a single tendon inserted onto the posterior aspect of the premaxillary condyle on the maxilla in all other perciforms examined.   Therefore, the former character is recognized as auta- pomorphic for Leptoscopidae, thereby supporting the monophyly of the family.

AC 50.   Posterior part of A1 connected with lateral por- tion of cranium (Fig. 6).—Whereas the posterior part of A1 is connected with the lateral portion of the cranium in leptoscop- ids, it is typically connected with the hyomandibula, metapter- ygoid and preopercle in percoids (e.g., Johnson and Fritzsche, 1989; Imamura, 2000).   Accordingly, the former condition is considered to be apomorphic.   The condition is also found in other perciforms including the trachinoids Creediidae and Trichonotidae, and the gobioid Gobiidae.

AC 51.   Presence of rectus dorsalis 2 (Fig. 7B-D).—Rec- tus dorsalis 2 is recognized in Leptoscopidae, although not so in percoids (e.g., Winterbottom 1974; Sasaki 1989).   Also observed only in the trachinoid Creediidae and the calliony- moid Callionymidae among other perciforms, the character is considered a rare apomorphy in perciforms.

AC 52.   Presence of rectus dorsalis 3 (Fig. 7B).—Rectus dorsalis 3 is present in Leptoscopidae, but absent in all per- coids (e.g., Shinohara, 1994; Springer and Johnson, 2004).   Found elsewhere in perciforms, only in the calliony- moid Callionymidae, the condition is a rare perciform apo- morphy.

AC 53. Absence of levator externus 3 (Fig. 7).—Leptoscop- ids lack levator externus 3, which is a primitive character in percoids (e.g., Sasaki, 1989; Springer and Johnson, 2004).   The apomorphic condition occurs also in several other perciforms, including the trachinoids Uranoscopidae and the creediid genera *Limnichthys* and *Tewara*, and the cal- lionymoid Callionymidae.

AC 54.   Posterior element of levator internus penetrating obliquus dorsalis (Fig. 7B).—The condition wherein the pos- terior element of levator internus penetrates peretrates the middle portion of the obliquus dorsalis is apomorphic, due to the muscle primitively passing through the lateral margin of the obliquus dorsalis in percoids (e.g., Imamura, 2000; Springer and Johnson, 2004).   The apomorphic con- dition occurs also in the percophids *Enigmapercis* and *Matsubaraea*.

AC 55.   Transversus dorsalis anterior comprising only transversus epibranchialis 2 (Fig. 7A).—Comprising only the transversus epibranchialis 2 in leptoscopids, the transversus dorsalis anterior is primitively comprised of the transversus pharyngobranchialis 2 and transversus epibranchialis 2 in per- coids (e.g., Stiassny and Jensen, 1987; Imamura,
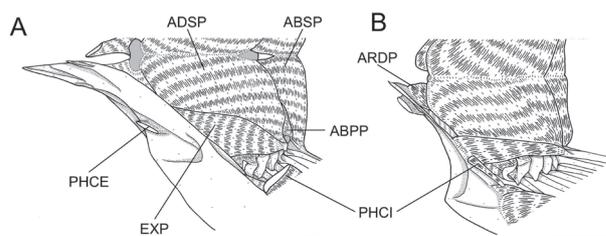

Fig. 8.   Dorsal aspect of pelvic fin muscles of *Leptoscopus mac- ropygus,* NMNZ P. 5268, 119.0 mm SL (A) and *Osopsa- ron verecundum*, HUMZ 189322, 39.6 mm SL (B). Scales indicate 1 mm.   ABPP, abductor profundus pelvicus; ABSP, abductor superficialis pelvicus; ADSP, adductor superficialis pelvicus; ARDP, arrector dorsalis pelvicus; EXP, extensor proprius; PHCE, pha- ryngoclaviclaris externus; PHCI, pharyngoclaviclaris internus.

1996).   The apomorphic condition occurs also in other perci- forms, including the trachinoids Trichonotidae, the percophid subfamily Hemerocoetinae and creediid genus *Creedia*, the blennioid Blenniidae and the labroid Labridae.

AC 56.   Presence of adductores 1-3.—Leptoscopids pos- sess adductores 1-3, whereas percoids primitively lack them (e.g., Imamura and Yabe, 2002; Imamura and Matsuura, 2003).   Several other perciforms, including the trachinoids Creediidae, Pinguipedidae and Trichonotidae, the blennioid Blenniidae and the gobioid Gobiidae, also have adductores 1-3.

AC 57.   Absence of adductor radialis.—Absence of the adductor radialis is apomorphic, because it occurs primitively in percoids (e.g., Kim, 2002).   The apomorphic condition also occurs in other perciforms, including the trachinoids Champsodontidae, Creediidae and Trichonotidae, the callio- nymoid Draconettidae and the gobioid Gobiidae.

AC 58.   Extensor proprius connecting with cleithrum (Fig. 8).—The extensor proprius connects with the cleithrum anteromedially in leptoscopids, compared with the dorsolat- eral edge of the pelvic bone in percoids (primitive condition) (e.g., Shinohara, 1994; Imamura and Matsuura, 2003).   The apomorphic condition occurs also in other perciforms, includ- ing the trachinoids Creediidae, Percophidae and Trichonot- idae, the blennioid Blenniidae and the callionymoid Callionymidae.

AC 59.   Presence of cirri on upper lip.—Leptoscopids possess cirri on the upper lip, an apomorphic condition since they are absent in percoids (e.g., Pietsch, 1989).   The former condition occurs also in the trachinoids Trachinidae and Ura- noscopidae, and the blennioid Blenniidae.

AC 60.   Presence of cirri on lower lip.—Presence of cirri on the lower lip is apomorphic in leptoscopids, the condition being primitively absent in percoids (e.g., Nelson, 1985).   The trachinoids Creediidae, Trichonotidae and Ura- noscopidae also possess lower lip cirri.

AC 61.   Body scales completely covered with skin and not

forming discrete oblique rows.—The skin-covered body scales in leptoscopids do not form discrete oblique rows (contrary to Pietsch, 1989 and Pietsch and Zabetian, 1990), unlike similarly skin-covered scales in Ammodytidae, Trachinidae and Uranoscopidae.   Both conditions are apomorphic, the scales being only partially covered by skin and not forming rows in typical percoids.   The condition found in Ammodytidae, Trachinidae and Uranoscopidae is interpreted as a further-derived character from the leptoscopid condition.

Discussion

Pietsch and Zabetian (1990) considered Leptoscopidae as having close relationships with Ammodytidae, Trachinidae and Uranoscopidae (Fig. 9), inferring that the suborder Trachinoidei, including the aforementioned four and seven other families, was monophyletic (the suborder is provisionally treated by Wiley and Johnson, 2010 as order "Trachiniformes" incertae sedis, included in their Percomorphacea). The latter proposed the following seven synapomorphies supporting the successive nodes of more basal taxa (i.e., Cheimarrhichthyidae, Pinguipedidae, Percophidae, Trichonotidae, Creediidae, Champsodontidae and Chiasmodontidae) leading to Leptoscopidae, Ammodytidae, Trachinidae and Uranoscopidae: short wide actinosts [Pietsch and Zabetian's (1990) character (PZ) 1]; presence of a pelvic spur (PZ 2); presence of a lateral crest or spur on the hyomandibula (PZ 3); squamation of partially ctenoid, reduced ctenoid, or cycloid scales (PZ 4); presence of a lateral spur, being a more derived condition of PZ 3 (PZ 5); cranial and shoulder portions rugose and highly sculptured (PZ 6); and infraorbitals expanded posteroventrally (PZ 7).   However, Johnson (1993) and Mooi and Johnson (1997) had questioned the validity of these characters, criticisms which we also have for

similar reasons, which will not be further discussed here.

Pietsch and Zabetian (1990) also considered that Leptoscopidae and the three related families shared the following nine synapomorphies: actinosts sutured with the scapula and coracoid, but separated from each other by small narrow foramina (PZ 8); skin covering of scales united between adjacent scales (PZ 9); cranium greatly depressed dorsoventrally (PZ 10); width of cranium equal to or greater than cranial length (PZ 11); vomer large, laterally expanded (PZ 12); basihyal short, broad (PZ 13); first pharyngobranchial greatly reduced or absent (PZ 14); hypobranchial tooth plates absent (PZ 15); and eyes directed dorsolaterally or dorsally (PZ 16).   However, as pointed out by Johnson (1993), the optimizations for PZ 10, 11, 12, 14 and 16 were incorrect, because a more parsimonious interpretation is their independent acquisition in Leptoscopidae and Uranoscopidae.   Because PZ 8 is also observed in more basal trachinoid taxa, such as the Creediidae and percophid subfamily Hemerocoetinae, the validity of the character as a synapomorphy of the clade including the four families is doubtful.   Although Pietsch and Zabetian (1990) considered that Leptoscopidae had a skin covering of scales united between adjacent scales (PZ 9), we found the family possesses body scales completely covered with skin and not forming discrete oblique rows (AC 61).   However, we agree with Pietsch and Zabetian (1990) in that the Ammodytidae, Trachinidae and Uranoscopidae are characterized by PZ 9.   We consider that PZ 13 is also unavailable, because the basihyal shape is highly variable in perciforms (e.g., spatulate, fan-like, plate-like, or rod-like) (e.g., Fraser, 1968; Stiassny and Jensen, 1987; this study) and polarity for the shape of the element is difficult to determine.   Although Leptoscopidae lacked tooth plates on the hypobranchial (PZ 15) (recognized also in the present study), we were unable to clearly distinguish between gill rakers and tooth plates in several perciforms, and redefined the character as "absence of gill rakers and/or tooth plates on hypobranchial" (see also discussion under AC 20).   Accordingly, Ammodytidae is not characterised by AC 20, because the family has long "gill rakers" on the hypobranchial.   Therefore, AC 20 does not support the monophyly of Leptoscopidae, Ammodytidae, Trachinidae and Uranoscopidae.

In summation, Pietsch and Zabetian's (1990) "monophyletic group" comprising Leptoscopidae, Ammodytidae, Trachinidae and Uranoscopidae is supported only by AC 61, provided that the latter and PZ 9 are ordered (if unordered, no characters unambiguously support the monophyly of the four families).   Therefore, the hypothesis of Pietsch and Zabetian (1990) cannot be strongly supported.

The detailed examination of Leptoscopidae resulted in 61 apomorphies being recognized in the family.   Of them, five characters (AC 1, 3, 6, 13 and 49) were autapomorphic for Leptoscopidae, thereby supporting its monophyly, which has
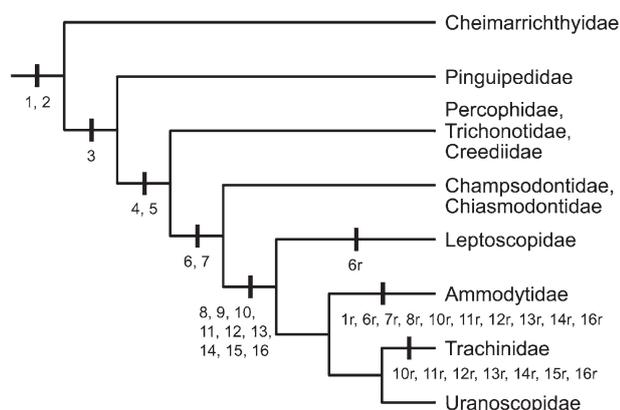

Fig. 9.   Phylogenetic relationships of trachinoid families proposed by Pietsch and Zabetian (1990).   Numbers of apomorphic characters correspond to those in text labeled "PZ".   Character optimization follows Pietsch and Zabetian (1990).   Only apomorphic characters associated with this study are shown.   "r" indicates reversal.

not been clearly demonstrated in previous reports. In addition, a further leptoscopid apomorphy, AC 52 (presence of the rectus dorsalis 3), was not found in other trachinoids. The last-mentioned character is comparatively rare, having been recognized in only a few perciforms, such as Callionymidae. Accordingly, we consider that AC 52 also supports leptoscopid monophyly.

Among the trachinoid families, Creediidae possessed the greatest number of leptoscopid apomorphies (43 in total; AC 2, 5, 7, 8, 9, 10, 11, 12, 14, 16, 17, 18, 21, 23, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 47, 48, 50, 51, 56, 57, 58 and 60) (Table 1). Of these, AC 8 (absence of pterosphenoid) and 51 (presence of rectus dorsalis 2) are considered to be extremely rare characters, recognizable in only a few taxa (see also discussion under AC 8 and 51). No other taxa sharing such a high apomorphic similarity with Leptoscopidae were recognized in the other perciform suborders. Accordingly, we concluded that Leptoscopidae has a sister relationship with Creediidae.

Several authors (e.g., Nelson, 1986; Johnson, 1993; Odani et al., 2006; Smith and Johnson, 2007) have suggested a close relationship between Creediidae, Trichonotidae and the percophid subfamily Hemerocoetinae, due to the following two common apomorphies: (1) a rod-like ectopterygoid, largely free from the endopterygoid and articulating directly with the palatine only at its anterior tip and the quadrate (movable) at its posterior tip; and (2) posterior part of the endopterygoid upwardly curved. In this study, a rod-like ectopterygoid was also found in Leptoscopidae (recognized as AC 14 here), although the bone was connected with the palatine anteriorly and the quadrate posteriorly through cartilage (Fig. 3A). The posterior part of the endopterygoid was not upwardly curved in the leptoscopid *Leptoscopus* and the element entirely absent in *Lesueurina* (Fig. 3A). However, in addition to AC 14, Leptoscopidae, Creediidae, Hemerocoetinae and Trichonotidae commonly possessed an additional 16 apomorphies (AC 10, 11, 12, 16, 21, 23, 25, 27, 29, 30, 34, 40, 42, 45, 56 and 57). Of these 17 characters (including AC 14), the following four were extremely rare and not detected in other perciforms: AC 11 (lower jaw and hyoid arch connected by ligament); AC 14 (ectopterygoid rod like); AC 27 (presence of ligament connecting posttemporal and epiotic); and AC 29 (anterior cartilages of pelvic bones fused). Accordingly, the following new relationship is proposed, *viz.* Leptoscopidae, Creediidae, Hemerocoetinae and Trichonotidae represent a monophyletic group, supported by 17 apomorphies. This hypothesis partially supports the close relationships of Creediidae, Hemerocoetinae and Trichonotidae, previously suggested. Acceptance of the hypothesis leads to recognition of the polyphyly of the family Percophidae, as suggested by Odani et al. (2006).

Among the apomorphies commonly recognized in the Leptoscopidae and Creediidae, two and seven, respectively (AC

18 and 60, and AC 9, 26, 31, 32, 33, 35 and 47), were also recognized in the Trichonotidae and Hemerocoetinae. However, because the relationships of Leptoscopidae plus Creediidae, Hemerocoetinae and Trichonotidae remain unresolved, it is unclear what clades these characters support. In addition, five apomorphies commonly found in Leptoscopidae and Creediidae (AC 2, 36, 39, 50 and 58) were also recognized in Trichonotidae and part of Hemerocoetinae (Table 1). These are likely to be additional synapomorphies supporting the monophyly of Leptoscopidae plus Creediidae, Hemerocoetinae and Trichonotidae, but including reversals. This inference can be evaluated following a reconstruction of the relationships of the three groups, which shows the monophyly of Leptoscopidae and Creediidae to be directly supported by 12 reliable synapomorphies.

Further consideration of AC 4 (opening of dermosphenotic (continuous with sensory canal of adjacent infraorbital) directed anteriorly) and AC 55 (transversus dorsalis anterior comprising only transversus epibranchialis 2) is also necessary. AC4 occurs in Hemerocoetinae and part of Creediidae, and AC 55 in Hemerocoetinae, Trichonotidae and part of Creediidae. Therefore, although initially excluded from the 43 common apomorphies of Leptoscopidae and Creediidae, several genera of creediids lacking those characters, they may yet be considered as supporting the monophyly of Leptoscopidae, Creediidae, Hemerocoetinae and Trichonotidae, on the basis of reversals having occurred in the above several genera.

It is probable that the remaining 10 leptoscopid apomorphies (AC 15, 19, 20, 22, 24, 46, 53, 54, 59 and 61) have been acquired independently in both Leptoscopidae and other trachinoid taxa, including Ammodytidae, Chiasmodontidae and Pinguipedidae, because there is no evidence of a close relationship of Leptoscopidae with the latter three families. If this is true, the 10 apomorphies become additional synapomorphies of Leptoscopidae.

The relationships of Leptoscopidae and related taxa, and the apomorphies reliably supporting them, are summarized in Figure 10.

Uranoscopidae also possesses many leptoscopid apomorphies (24 in total; AC 5, 9, 10, 12, 18, 20, 21, 23, 24, 30, 32, 33, 34, 35, 42, 43, 44, 53, 55, 56, 57, 58, 59 and 60). However, Imamura and Matsuura (2003) inferred Uranoscopidae as having a close relationship with Trachinidae, sharing the following 16 apomorphies: (1) parasphenoid and pterosphenoid attached; (2) cranium with many tubercles and/or lumps; (3) supratemporal sensory canal on both sides continuous with each other; (4) presence of a developed hyomandibular process; (5) six branchiostegal rays (= AC 19 of this study); (6) cleithrum with a strong spine posteriorly; (7) lateral and medial surfaces of the lower two actinosts expanded anteriorly to sandwich the coracoid; (8) pelvic girdle strongly anteriorly extended from pectoral girdle; (9) three or more proximal-middle pterygiophores of anal fin anterior to first

Table 1. Comparison of apomorphic characters recognized in Leptoscopidae, other trachinoids and typical percoids

Taxon	Apomorphic Characters (AC)																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Leptoscoidae	+*	+	++*	+	2	+*	+	+	+	+	+	+	+*	+	+	+	+	1	6	+	+
Ammodytidae	−	+	+	−	0	−	−	−	−	−	−	+	−	−	+	+	−	2	7	−	−
Trachinidae	−	−	+	−	1	−	−	−	−	+	−	+	−	−	−	+	−	2	6	−	−
Uranoscopidae	−	−	+	−	2	−	+	−	+	+	−	+	−	−	−	−	−	1	6/7	+	+
Creediidae	−	+	+/−	+/?	2	−	+	+	+	+	+	+	−	+	−	+	+	1	7	−	+
Trichonotidae	−	+	+	−	1	−	−	−	−	+	+	+	−	+	−	+	−	1	7	−	+
Bembropinae[1]	−	+	+	−	1/2	−	+/−	−	+/−	+	−	+	−	−	−	+	−	1	7	−	−
Hemerocoetinae[1]	−	+/−	+	+	0/2	−	+/−	−	+	+	+	+	−	+	−	+	+/−	2	7	+/−	+
Percophinae[1]	−	−	+	−	1	−	+	−	−	+	−	+	−	−	−	+	−	2	7	−	−
Champsodontidae	−	+	−	?	2	−	−	−	−	+	−	−	−	−	+	+	−	2	7	−	−
Chiasmodontidae	−	+	+	−	0	−	−	−	−	−	−	+	−	−	+	+	−	2	7	+	+
Pinguipedidae	−	+	+	−	2	−	−	−	−	+	−	+	−	−	−	+	+	1	6	−	−
Typical percoids	−	−	+	−	1	−	−	−	−	−	−	−	−	−	−	−	−	2	7	−	−

Table 1. Continued

Taxon	Apomorphic Characters (AC)																				
	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Leptoscoidae	+	+	+	+	++	+	0	+	+	+	0	R	+	+	+	+	+	+	+	+	+
Ammodytidae	−	+	+	−	++	−	2	?	+	−	0	−	+	+	+	+	+	−	+	+	−
Trachinidae	−	+	−	−	−	−	2	−	−	−	0	SR	+	+	−	−	−	−	+	−	+
Uranoscopidae	+/−	+	+	+/−	−	−	2	−	+	−	0	R	+	+	+/−	−	−	−	−	+/−	+
Creediidae	−	+	−	+	++	+	0	+	+	+	0	R	+	+	+	+	+	+	+	+	+
Trichonotidae	−	+	−	+	+	+	1	+	+	−	1	S	+	−	+	+/−	−	+	−	−	+
Bembropinae¹	−	+	−	−	−	−	2	−	−	−	0	−	+	−	−	−	−	−	−	−	−
Hemerocoetinae¹	−	+	−	+	++	+	2	+	+	+	0	R	+	+	+/−	+/−	−	+/−	+	+/−	+
Percophinae¹	−	+	−	−	−	−	2	−	+	−	5	−	+	−	−	−	−	−	−	−	−
Champsodontidae	−	+	−	+	++	−	2	−	+	−	0	R	+	−	−	−	−	+	+	+	+
Chiasmodontidae	−	+	−	+	−	−	2	−	+	−	0	SS	+	−	−	−	−	−	+	−	+
Pinguipedidae	−	+	+	−	−	−	2	−	−	−	0	S	+	+	−	−	−	−	−	−	−
Typical percoids	−	−	−	−	−	−	2	−	−	−	3	SS	−	−	−	−	−	−	−	−	−

Table 1. Continued

Taxon	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	N
Leptoscopidae	+	+	0	2	4	4	+*	+	+	+	+	+	++	+	+	++	+	+	++	–
Ammodytidae	+	+	1	2	7	6	–	–	–	–	–	–	++	–	+	–	–	–	+	21
Trachinidae	–	+	1	1	7	6	–	–	–	–	–	–	–	+	+	++	+	+	+	16
Uranoscopidae	+	+	1	3	5	5	–	–	–	–	+	–	++	+	+	++	+	+	+	24
Creediidae	+	+	0	1/2	4	4	–	+	+	–	+/–	–	++/+	+	+	++	–	+	–	42
Trichonotidae	+/–	+/–	0	1	6	5	–	+	–	–	–	–	++	+	+	++	–	+	–	25
Bembropinae¹	–	–	1	3	6	5	–	–	–	–	–	–	–	–	–	++	–	–	–	9
Hemerocoetinae¹	+/–	+/–	0	3	4	3/4	–	+/–	–	–	–	+/–	++	+	+	++/–	–	–	–	26
Percophinae¹	–	–	1	3	7	6	–	–	–	–	–	–	++	+	+	++	–	–	–	10
Champsodontidae	+	+	0	3	7	6	–	–	–	–	+	–	–	–	+	++	–	–	–	21
Chiasmodontidae	–	+	1	3	8	7	–	–	–	–	–	–	–	–	–	+	–	–	–	15
Pinguipedidae	–	+	1	3	8	7	–	–	–	–	–	–	++	+	+	++	–	–	–	17
Typical percoids	–	–	2	3	8	7	–	–	–	–	–	–	–	–	–	+	–	–	–	–

Numbers of apomorphic characters correspond to those in text labeled "AC"

¹Percophid subfamilies

Asterisk and slash indicate an autapomorphy of Leptoscopidae and polymorphism, respectively

N indicates number of apomorphic characters in common with Leptoscopidae

Apomorphic Characters: 1, arrangement of circumorbital bones, U-shaped (+) or semicircular (–); 2, presence (–) or absence (+) of suborbital shelf; 3, dermosphenotic, fused with sphenotic (++), attached to sphenotic (+), or absent (–); 4, direction of opening of dermosphenotic continuous with sensory canal of adjacent infraorbital, anterior (+), lateral (–) or dermosphenotic absent (?); 5, number of tooth plates on vomer; 6, presence (+) or absence (–) of laminar process on dorsal surface of ethmoid; 7, presence (+) or absence (–) of frontal and parasphenoid connection; 8, presence (+) or absence (+) of pterosphenoid; 9, presence (+) or absence (+) of basisphenoid; 10, exoccipital condyles on both sides, separated (+) or connected (–); 11, presence (+) or absence (–) of ligament connecting lower jaw and hyoid arch; 12, presence (+) or absence (+) of supramaxilla; 13, presence (+) or absence (–) of medially–directed process on palatine; 14, shape of ectopterygoid, rod–like (+) or triangular (–); 15, presence (–) or absence (+) of metapterygoid lamina; 16, presence (–) or absence (+) of beryciform foramen; 17, presence (+) or absence (–) of small laminar process on ceratohyal; 18, number of branchiostegal rays on epihyal; 19, number of branchiostegal rays; 20, presence (–) or absence (+) of gill rakers and/or tooth plates on hypobranchial; 21, presence (–) or absence (+) of interarcual cartilage; 22, third basibranchial, cartilaginous (+) or ossified (–); 23, presence (–) or absence (+) of first pharyngobranchial; 24, presence (–) or absence (+) of tooth plate on third epibranchial; 25, presence (–) or absence (+) of autogenous tooth plate on ventromedial part of second epibranchial; 26, presence (–) or absence (+) of medial supratemporal; 27, presence (+) or absence (–) of ligament connecting posttemporal and epiotic; 28, number of postcleithra; 29, anterior cartilages of contralateral pelvic bones, fused (+), separated (+), or pelvic bones absent (?); 30, neural spine and centrum of first abdominal vertebrae, fused (+) or separated (–); 31, presence (–) or absence (+) of pleural ribs; 32, number of supraneurals; 33, ventral margin of first proximal–middle pterygiophoreof anal fin, with one soft ray (R), with one spine (S), with spine and soft ray (SR), with two spines (SS), or without rays (–); 34, ventral margin of second proximal–middle pterygiophoreof anal fin, with soft ray (+) or with spine (–); 35, presence (–) or absence (+) of middle pterygiophores of dorsal and anal fins; 36, presence (–) or absence (+) of stays of dorsal and anal fins; 37, last dorsal fin soft ray, comprised of two ray elements (+) or single element (–); 38, last anal fin soft ray, comprised of two ray elements (+) or single element (–); 39, hemal spine and second preural centrum, fused (+) or separated (–); 40, hemal spine and third preural centrum, fused (+) or separated (–); 41, urostyle and hypurals, fused (+) or separated (–); 42, first and second hypurals, fused (+) or separated (–); 43, third and fourth hypurals, fused (+) or separated (–); 44, presence (–) or absence (+) of hypurapophysis; 45, number of uroneurals; 46, number of epurals; 47, number of branched rays on upper caudal lobe; 48, number of branched rays on lower caudal lobe; 49, adductor mandibulae section A1, with two tendons inserted onto maxilla laterally and medially (+), or with single tendon inserted onto maxilla medially (–); 50, presence (+) or absence (–) of posterodorsal part of adductor mandibulae section A1 and lateral portion of cranium connection; 51, presence (+) or absence (–) of rectus dorsalis 2; 52, presence (+) or absence (–) of rectus dorsalis 3; 53, presence (–) or absence (+) of levator externus 3; 54, posterior element of levator internus, penetrating middle portion of obliquus dorsalis (+) or passing through lateral margin of latter (–); 55, transversus dorsalis anterior, comprised of only transversus epibranchialis 2 (++), comprised of transversus dorsales 1 and 2 (+) or comprised of transversus epibranchialis 2 and transversus pharyngobranchialis 2 (–); 56, presence (+) or absence (–) of adductores 1–3; 57, presence (–) or absence (+) of adductor radialis; 58, extensor proprius, connected with cleithrum (++), connected with pelvic bone (+), or absent (–); 59, presence (+) or absence (–) of cirri on upper lip; 60, presence (+) or absence (–) of cirri on lower lip; 61, body scales, completely covered with skin and not forming discrete oblique rows (++), completely covered with skin and forming discrete oblique rows (+), or partially covered with skin and not forming discrete oblique rows (–)
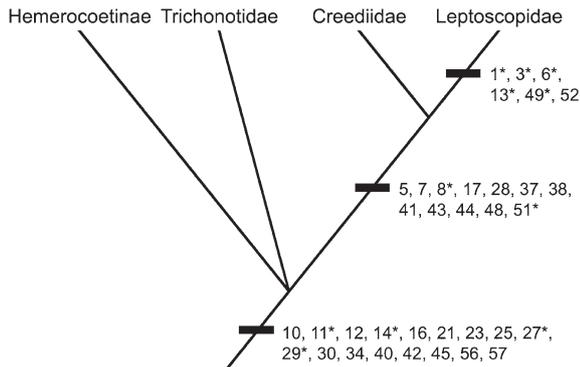
Fig. 10. Proposed phylogenetic relationships of Leptoscopidae and related taxa. Numbers of apomorphic characters correspond to those in text labeled "AC". Only apomorphic characters which reliably support clades are shown. Asterisk indicates autapomorphy or rare apomorphy.

hemal spine; (10) soft ray present on posterior portion of first proximal-middle pterygiophore of anal fin (=AC 34); (11) relationship between neural spines and dorsal fin proximal-middle pterygiophores 1 : 1; (12) supraneurals absent (=AC 32); (13) lower two hypurals fused (=AC 42); (14) branched caudal fin rays fewer than 15 (=AC 47 and 48); (15) body scales completely covered with skin, forming discrete oblique rows (=AC 61); and (16) presence of cutaneous axillary appendage associated with pectoral fin. In addition, the present study revealed an additional 12 apomorphies (AC 3, 10, 12, 23, 34, 35, 44, 56, 57, 58, 59 and 60) shared by the Uranoscopidae and Trachinidae (Table 1), resulting in a total of 28 shared characters. Acceptance of a close relationship between Uranoscopidae and Leptoscopidae, based on 24 apomorphies (above), requires the acceptance of a much less parsimonious hypothesis that all 12 leptoscopid apomorphies shared in common with creediids (and 17 in common with the Hemerocoetinae and Trichonotidae) were acquired independently in Leptoscopidae and Creediidae. In addition, Leptoscopidae and Uranoscopidae lack common apomorphies recognized only in those families. In contrast, character 7 (lateral and medial surfaces of the lower two actinosts expanded anteriorly to sandwich the coracoid) was found among the perciforms examined, only in Uranoscopidae and Trachinidae. Therefore, it is reasonable to consider Uranoscopidae as having a much closer relationship with Trachinidae than with Leptoscopidae.

Although the present study has resulted in a new hypotheses that Leptoscopidae and Creediidae have a sister relationship and together with Hemerocoetinae and Trichonotidae are monophyletic (Fig. 10), closely-related taxa to this monophyletic group are still not determined. The resolution of this question would require a comprehensive phylogenetic analysis of a large range of perciforms, as would that pertaining to the trichotomy of Leptoscopidae plus Creediidae, Hemero-

coetinae and Trichonotidae.

We consider that Percophidae is polyphyletic, but leave that issue for a future comprehensive phylogenetic analysis of the family and other trachinoids.

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