

Oligocene killifishes (Teleostei: Cyprinodontiformes) from southern France: relationships, taxonomic position, and evidence of internal fertilization

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> Abstract

Phylogenetic relationships of five species of *Prolebias* from the Oligocene of southern France (*P. aymardi*, *P. cephalotes*, *P. delphinensis*, *P. meridionalis*, and *P. stenoura*) were examined under an analysis comprising 36 terminal taxa, representing all the main lineages of the order Cyprinodontiformes. It indicated *Prolebias* as a polyphyletic group, supporting *Prolebias stenoura*, the type species of the genus, as a valenciid monotypic lineage. *Prolebias aymardi* and *P. delphinensis* comprise a new valenciid genus, *Francolebias*, gen. nov., diagnosed by a unique morphology of pelvic bone, anterior proximal radials of the dorsal fin and anal fins, and hemal spines in putative males. The apomorphic specialized morphology of the anal fin and adjacent vertebrae is interpreted as evidence of an internal fertilization reproductive mode. *Prolebias meridionalis* is designated as the type species of a new monotypic cyprinodontid genus, *Eurolebias*, gen. nov., hypothesized to be the sister group to a clade comprising all other cyprinodontids, which is diagnosed by the apomorphic morphology of jaws, parhypural, and absence of parietals. Close relationships between *P. cephalotes*, *P. egeranus* from the lower Miocene of Czech Republic, and recent species of the poeciliid genus *Pantanodon* are corroborated on the basis of the apomorphic morphology of the dentary, pharyngobranchials, pelvic bone, and pelvic-fin rays, justifying the transference of those two species to the latter genus. The present study indicates that the European Oligocene fauna of cyprinodontiform fishes was greatly diversified when compared to its present poor fauna, comprising lineages now extinct or restricted to other continents.

> Key words

Eurolebias, *Francolebias*, Osteology, Palaeontology, *Pantanodon*, *Prolebias*.

Introduction

Contrasting with the great diversity of living cyprinodontiform species (about 1,120 species in 125 genera and ten families), the fossil record of the order Cyprinodontiformes is poor, mainly concentrated in Europe (COSTA, 2012). The oldest records are from the Lower Oligocene, all belonging to the European genus *Prolebias* SAUVAGE, 1874, known until the middle Miocene (e.g., GAUDANT, 2003).

SAUVAGE (1874) first considered *Prolebias* as a member of the Fundulina sensu GÜNTHER (1866), which then included species presently distributed among all cyprinodontiform families excluding the Cyprinodontidae. WOODWARD (1901) restricted *Prolebias* relationships to the North American fundulid

genera *Lucania* and *Fundulus*, the latter at that time also including species today placed in the European valenciid genus *Valencia*. However, PARENTI (1981) included *Prolebias* in the Cyprinodontidae without justification, a placement followed by subsequent authors without criticisms (e.g., OBRHELOVÁ, 1985; REICHENBACHER & GAUDANT, 2003; GAUDANT, 2009). GAUDANT (1988) considered *Prolebias* possibly related to the Andean cyprinodontid genus *Orestias*, but several new species have been described without checking characters supporting its inclusion in that family and objective comparisons to recent cyprinodontiforms were never made. However, THÉOBALD & PITON (1937) had formerly noted that species placed in *Prolebias* had

uncertain relationships among the several distinct recent cyprinodontiform genera, additionally suggesting that *Prolebias goreti* SAUVAGE, 1880 is closely related to *Fundulus gardneri* (= *Fundulopanchax gardneri*) and *Fundulus guentheri* (= *Nothobranchius guentheri*), two species today placed in the African family Nothobranchiidae. More recently, COSTA (2012) recorded a great morphological diversity among some species of *Prolebias*, suggesting that the genus is polyphyletic, probably comprising species related to different cyprinodontiform families.

GAUDANT (2003) listed 15 valid species in *Prolebias*, of which six are only known from the Oligocene of southern France. The southern France species assemblage, besides exhibiting a great morphological variability, contrasts with other taxa by being richly represented in fossil collections deposited in easily accessible European museums. In addition, among these species is *Prolebias stenoura* SAUVAGE, 1874, the type species of the genus, providing unique possibility of testing monophyly and the taxonomic position of the genus. Thus, the present paper primarily focuses on five species of *Prolebias* from the Oligocene of southern France (the type species of the genus and *P. aymardi* (SAUVAGE, 1869), *P. cephalotes* (AGASSIZ, 1839), *P. delphinensis* GAUDANT, 1989, and *P. meridionalis* GAUDANT, 1978), for which there are available representative collections adequate for searching characters currently employed in phylogenetic studies on cyprinodontiforms (PARENTI, 1981; COSTA, 1997, 1998), with the objective of elucidating their phylogenetic position among cyprinodontiform lineages.

Material and methods

The phylogenetic analysis was based on a data matrix including five species of *Prolebias* from the Oligocene of southern France (*P. aymardi*, *P. cephalotes*, *P. delphinensis*, *P. meridionalis*, and *P. stenoura*) as terminal taxa. To test the phylogenetic position of those species among cyprinodontiforms, the data matrix also included 27 recent species representing all the main lineages of the order Cyprinodontiformes. Due to previous evidence supporting *Prolebias* in the Cyprinodontoidei clade (COSTA, 2012), taxon sample was more concentrated in the seven families of the latter clade and proportional to the diversity found in each family (two anablepids, eight cyprinodontids, two fundulids, four goodeids, five poeciliids, one profundulid, and two valenciids). The taxon sample also particularly focused on species endemic to Europe, thus including the only two species belonging to the European family Valenciidae, and two species of *Aphanius*, the

only recent cyprinodontid genus occurring in Europe. In order to test the proposed close relationships between *Prolebias* and the South American cyprinodontid *Orestias* (GAUDANT, 1988), between *P. cephalotes* and *Prolebias egeranus* from the upper Miocene of the Cheb basin (GAUDANT, 2009), and between those species and the recent African poeciliid genus *Pantanodon* MYERS, 1955 suggested by COSTA (2012), two species of *Orestias*, *P. egeranus*, and *Pantanodon stuhlmanni* (AHL, 1924), the type species of *Pantanodon*, were included in the analysis. Additional outgroup taxa were *Oryzias matanensis* and *Oryzias sarasinorum* representing the Adrianichthyidae, the most basal family of the Beloniformes, the sister group of the Cyprinodontiformes; and, *Melanotaenia affinis*, a representative of the Atheriniformes, the sister group of Beloniformes plus Cyprinodontiformes. Comparative material, including that used in the phylogenetic analysis, is listed in COSTA (2012). Osteological data from extant species was obtained from material prepared according to the clearing and staining techniques described by TAYLOR & VAN DYKE (1985). Characters, mainly extracted from COSTA (1998) and listed in Appendix 1, focused on bone structure, excluding characters involving cartilages and superficial ossifications, which show high levels of subjectivity in character state delimitation among the present taxon sample. Character statements were formulated following SERENO (2007). Distribution of character states among taxa appears in the data matrix of Appendix 2. All characters were treated as unordered. The search for most parsimonious trees (using 'traditional' search and setting random taxon-addition replicates to 1,000, tree bisection-reconnection branch swapping, multitrees in effect, collapsing branches of zero-length, characters equally weighted, and a maximum of 1,000 trees saved in each replicate), bootstrap analysis (1,000 replicates) and Bremer-support indices were performed with TNT 1.1 (GOLOBOFF *et al.*, 2008).

Institutional abbreviations

MB.f	Museum für Naturkunde, Berlin;
MNHN.P	Muséum national d'Histoire naturelle, Paleontology, Paris;
NHMUK(P)	Natural History Museum, Palaentology, London;
NHMUK(Z)	Natural History Museum, Zoology, London;
NMP	Národní Muzeum, Prague.

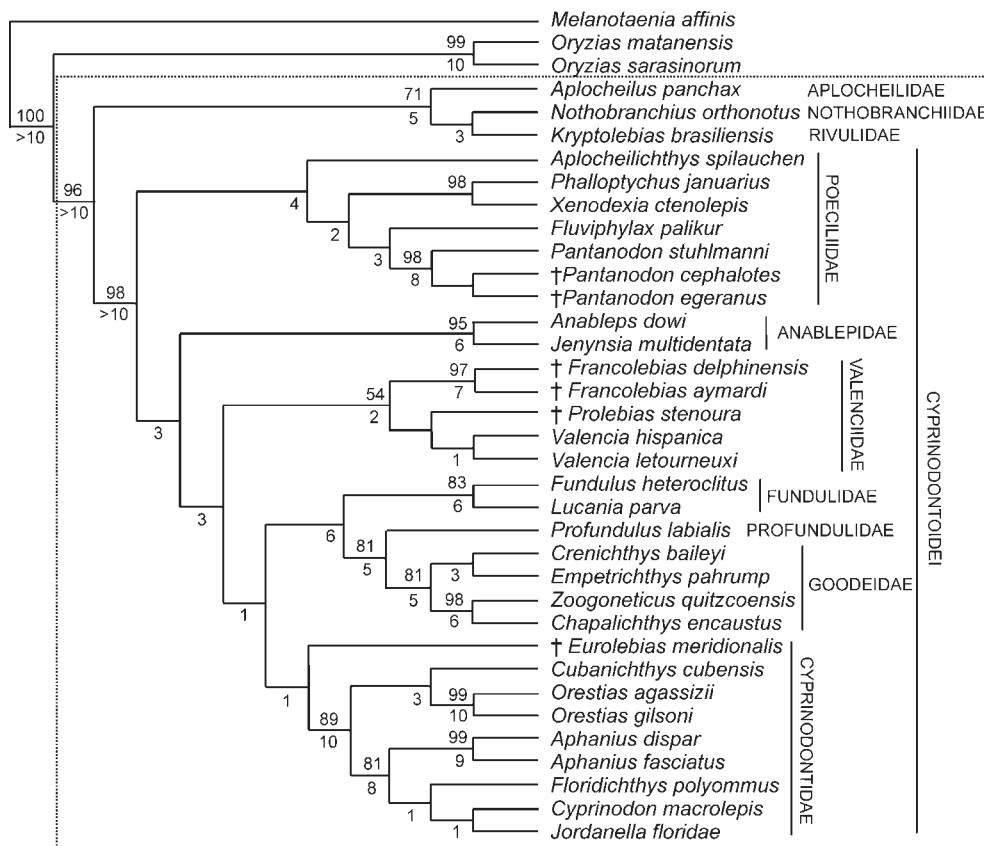


Fig. 1. Most parsimonious cladogram of phylogenetic relationships among six Cenozoic European cyprinodontiforms (indicated by a †-symbol), 27 recent cyprinodontiforms and three outgroups (tree length: 190; consistency index: 0.5105; retention index: 0.7896). Numbers above branches are bootstrap values, below Bremer-support indices. Dotted rectangle delimits the order Cyprinodontiformes.

Results

Phylogenetic relationships

The single most parsimonious phylogenetic tree for 33 cyprinodontiform taxa (six fossil and 27 recent) and three outgroups is illustrated in Fig. 1. The analysis supports the inclusion of all European fossil cyprinodontiforms in the suborder Cyprinodontoidei, but indicates that they do not form a monophyletic group. *Prolebias stenoura* and an independent lineage comprising *P. aymardi* and *P. delphinensis* are closely related to the two living valenciids, whereas *P. cephalotes* and *P. egeranus* are closely related to the African poeciliid *Pantanodon stuhlmanni*, and *Prolebias meridionalis* is the sister group of a clade comprising recent cyprinodontids. Consequently, only the type species of *Prolebias*, *P. stenoura*, is retained in the genus, whereas the remaining four species analysed are removed to other genera, including two new genera named below.

Systematic Accounts

Family Valenciidae PARENTI, 1981

Genus *Prolebias* SAUVAGE, 1874

Type species. *Prolebias stenoura* SAUVAGE, 1874, by original designation.

Emended diagnosis. Similar to other valenciids by having: long premaxillary ascending process; jaw teeth conical and arranged in multiple rows; dorsal fin posteriorly positioned on body, dorsal-fin origin behind anal-fin origin; neural spine of preural vertebra 2 greatly widened, its width about three to four times the width of neural spine of preural vertebra 4; and, anal-fin rays distinctively thicker than dorsal-fin rays. Distinguished from *Valencia* and *Francolebias* nov. gen. by having dorsal and ventral hypural plates separated (vs. fused); distinguished from *Valencia* by having ossified ventral process of post-temporal (vs. unossified).

sified); distinguished from *Francolebias* nov. gen. by having slender pelvic bone, greatest width about 50 % of length (vs. widened, about 70 %); hemal spines of caudal vertebrae above anal fin unmodified, similar to subsequent hemal spines (vs. distinctively widened in putative males); anterior proximal radials of dorsal fin separated (vs. coalesced); and, anterior proximal radials of anal fin short, reaching vertical through distal portion of adjacent hemal spines (vs. long, close to basal portion of adjacent hemal spines).

Included Species, age and range. Only the type species, *P. stenoura*, from the lower Oligocene of Corent, Puy-de-Dôme, southern France (see Discussion below).

Remarks. *Lebias cephalotes* AGASSIZ, 1839 sometimes appears as the type species of *Prolebias* (e.g., PARENTI, 1981; OBRHELOVÁ, 1985), whereas old catalogues of fish genera indicated *Prolebias gregatus* (AYMARD, 1856) (= *Lebias aymardi* SAUVAGE, 1869) as the logotype of *Prolebias* (e.g., JORDAN, 1963). However, these equivocal taxonomical accounts are unfounded, since SAUVAGE (1874:189) had already designated *P. stenoura* as the type species of his genus.

Material examined. †*Prolebias stenoura*: NHMUK(P) P1832 (4), P28491 (30), 57050 (1), 57052–57074 (25), 57078 (1); MNHN.P PTF-126–144, 304, 307, 313, 321 (about 20 exemplars completely and partially articulated, and numerous isolated bones); France: Puy-de-Dôme, Corent (Lower Oligocene).

Francolebias gen. nov.

Type species. *Prolebias delphinensis* GAUDANT, 1989.

Diagnosis. Similar to other valenciids in having: long premaxillary ascending process; jaw teeth conical and arranged in multiple rows; dorsal fin posteriorly positioned in body, dorsal-fin origin behind anal-fin origin; neural spine of preural vertebra 2 greatly widened, its width about three to four times the width of neural spine of preural vertebra 4; and, anal-fin rays distinctively thicker than dorsal-fin rays. Distinguished from all other valenciid genera by possessing broad pelvic bone, greatest width about 70 % of length (vs. slender, about 45–50 %); hemal spines of caudal vertebrae above anal fin in putative males distinctively widened (vs. not widened); anterior proximal radials of dorsal fin coalesced (vs. not coalesced); and, anterior proximal radials of anal fin long, reaching vertical through basal portion of adjacent hemal spines (vs. at level of distal portion of adjacent hemal spines). Also distinguished from *Valencia* by possessing ossified ventral process of post-temporal (vs. unossified) and from

Prolebias by having the dorsal and ventral hypural plates fused (vs. separated).

Etymology. Franco, a combining form representing French or France, and the Greek word lebias, meaning a small fish, a name often used to compose generic names of cyprinodontiform fishes, referring to the known geographic distribution of this cyprinodontiform taxon restricted to France. Gender masculine.

Included Species, age and range. *Francolebias delphinensis* (GAUDANT, 1989) from the lower Oligocene of Montbrun-les-Bains, Drôme, southern France, and *Francolebias aymardi* (SAUVAGE, 1869) from the lower Oligocene of Ronzon, Haute-Loire, southern France.

Remarks. The name *Pachylebias gregatus* was published by AYMARD (1856) without illustrations or mention to any character, thus it was considered as an invalid name (nomen nudum) by SAUVAGE (1869), who described that species as *Lebias aymardi* (see GAUDANT, 1988 for a historic review and species redescription). Thus *Pachylebias*, nomen nudum, should be placed in the synonymy of *Francolebias*.

Material examined. †*Francolebias aymardi*: MNHN.P PTF-164–175 (about 25 completely and partially articulated, and numerous isolated bones); NHMUK(P) P.8984 (3), P.9218 (1), P.10678 (1); MB.f.16450 (1); France: Haute-Loire, Ronzon (Lower Oligocene). †*Francolebias delphinensis*: MNHN.P MBR-1–18, 21, 48–49, 52–53, 62–63 (about 25 completely and partially articulated, and numerous isolated bones); France: Drôme, Montbrun-les-Bains (Lower Oligocene).

Family Cyprinodontidae GILL, 1865

Eurolebias gen. nov.

Type species. *Prolebias meridionalis* GAUDANT, 1978a.

Diagnosis. Similar to other cyprinodontids by having: jaw dentition comprising single outer tooth row followed or not by few smaller teeth near symphyses; anterior and posterior portions of jaw suspensorium nearly parallel. Also similar to cyprinodontids by largest specimens being deep-bodied (body depth about 28–30 % standard length, vs. about 21–26 % standard length in other Oligocene killifish taxa). It differs from all other cyprinodontids by having long, almost rectangular premaxillary ascending process, (vs. short, sharp, almost triangular), long proximal part of parhypural overlapping preural centrum 1 (vs. not overlap-

ping), well-developed parietals (vs. absent), dentary not expanded ventrally (vs. expanded) and absence of distinctive groove on dorsal maxillary process (vs. presence).

Etymology. Euro, from the Greek word Europa, and the Greek word lebias, meaning a small fish, a name commonly used to compose generic names of cyprinodontiform fishes, and an allusion to the unique occurrence of this basal cyprinodontid lineage in Europe. Gender masculine.

Included species, age and range. Only *Eurolebias meridionalis* (GAUDANT, 1978) from the upper Oligocene of Manosque, Alpes de Haute-Provence, southern France (see Discussion below).

Material examined. †*Eurolebias meridionalis*: MNHN.P MSQ1–16, 26–48, 50, 52–59, 86–94, 96–100 (about 40 completely and partially articulated exemplars, and numerous isolate bones); France: Haute-Provence, Manosque (Upper Oligocene).

Family Poeciliidae GARMAN, 1895

Genus *Pantanodon* MYERS, 1955

Type species. *Pantanodon podoxys* MYERS, 1955 [= *Pantanodon stuhlmanni* (AHL, 1924)], by monotypy.

Emended diagnosis. Similar to other poeciliids and distinguished from all other cyprinodontoids in having pectoral-fin base laterally inserted in body; also similar to poeciliids by possessing pelvic-fin base closer to pectoral-fin base than to anal-fin base, short ascending process of premaxilla, and anterior proximal radials of anal fin inserted between pleural ribs. Distinguished from all other poeciliid genera by having postero-dorsal border of the dentary expanded (vs. not expanded), third and fourth pharyngobranchial toothplates coalesced (vs. not coalesced), pelvic bone long and narrow, its greatest width about 30 % of length (vs. short, about 50 %), and extremity of pelvic-fin rays in males thickened, often with curved tips (vs. distal portion unmodified). Also distinguished from all other poeciliids, except New World poeciliines, by having fifth ceratobranchial broad, drop-shaped (vs. narrow, boomerang-shaped) and teeth of third pharyngobranchial and fifth ceratobranchial regularly arranged in transverse rows (vs. irregularly arranged).

Included species, age and range. *Pantanodon cephalotes* (AGASSIZ, 1839) from the upper Oligocene of

d'Aix-en-Provence, southern France; *Pantanodon egeranus* (LAUBE, 1901) from the Karpatian, lower Miocene of the Cheb basin, Czech Republic; *Pantanodon madagascariensis* (ARNOULT, 1963), Recent taxon, from Madagascar; *Pantanodon malzi* (REICHENBACHER & GAUDANT, 2003) from the upper Oligocene-lower Miocene of Germany; and, *Pantanodon stuhlmanni* (AHL, 1924), Recent, from Tanzania and Kenya.

Remarks. The inclusion of *Prolebias malzi* REICHENBACHER & GAUDANT, 2003 in *Pantanodon*, as indicated above, is tentative based on the original description of REICHENBACHER & GAUDANT (2003), which indicated the presence of pelvic fin close to pectoral fin, often with thickened and curved tips, anterior proximal radials of the anal fin inserted between pleural ribs, and dorsal and ventral hypural plates separated by anterior gap, since material of this species was not available for study.

Material examined. †*Pantanodon cephalotes*: NHMUK(P) 20071, 21390, 21396, 36131, 21397, 43438, P1831, P4266 (over 200 articulated specimens and fragments); MNHN.P AIX-67, 80–81, 90, 92, 95–97, 98, 102, 107–108, 129–131; (about 40 exemplars completely and partially articulated); MB.f.16454–59 (about 30 exemplars completely and partially articulated); France: Aix-en-Provence. †*Pantanodon egeranus*: NMP Pc16, 550–677, 883–885, 893, 927–960, 1720, 1775, 1813 (over 200 partially and completely articulated specimens, and numerous isolated fragments and bones); MB.f.16460–64 (13 partially and completely articulated specimens); Czech Republic: Cheb basin (lower Miocene). *Pantanodon stuhlmanni*: NHMUK(Z) 1968.10.7 (2); Kenya: Gongoni.

Discussion

Relationships of *Prolebias stenoura*

The analysis supports *Prolebias stenoura* (Fig. 2A) as a member of the Valenciidae. This family is endemic to Europe and presently comprises only two extant species in a single genus, *Valencia*. PARENTI (1981) diagnosed the Valenciidae on the basis of the unique presence of an elongate and attenuate dorsal process of the maxilla, but COSTA (1998) noted that a similar process is also found in non cyprinodontiform atheriniforms, making polarization ambiguous. However, independently from the character state polarization assumed, that process morphology distinguishes Valenciidae from all other cyprinodontiforms, since it is short, roughly triangular in aplocheilids, notho-

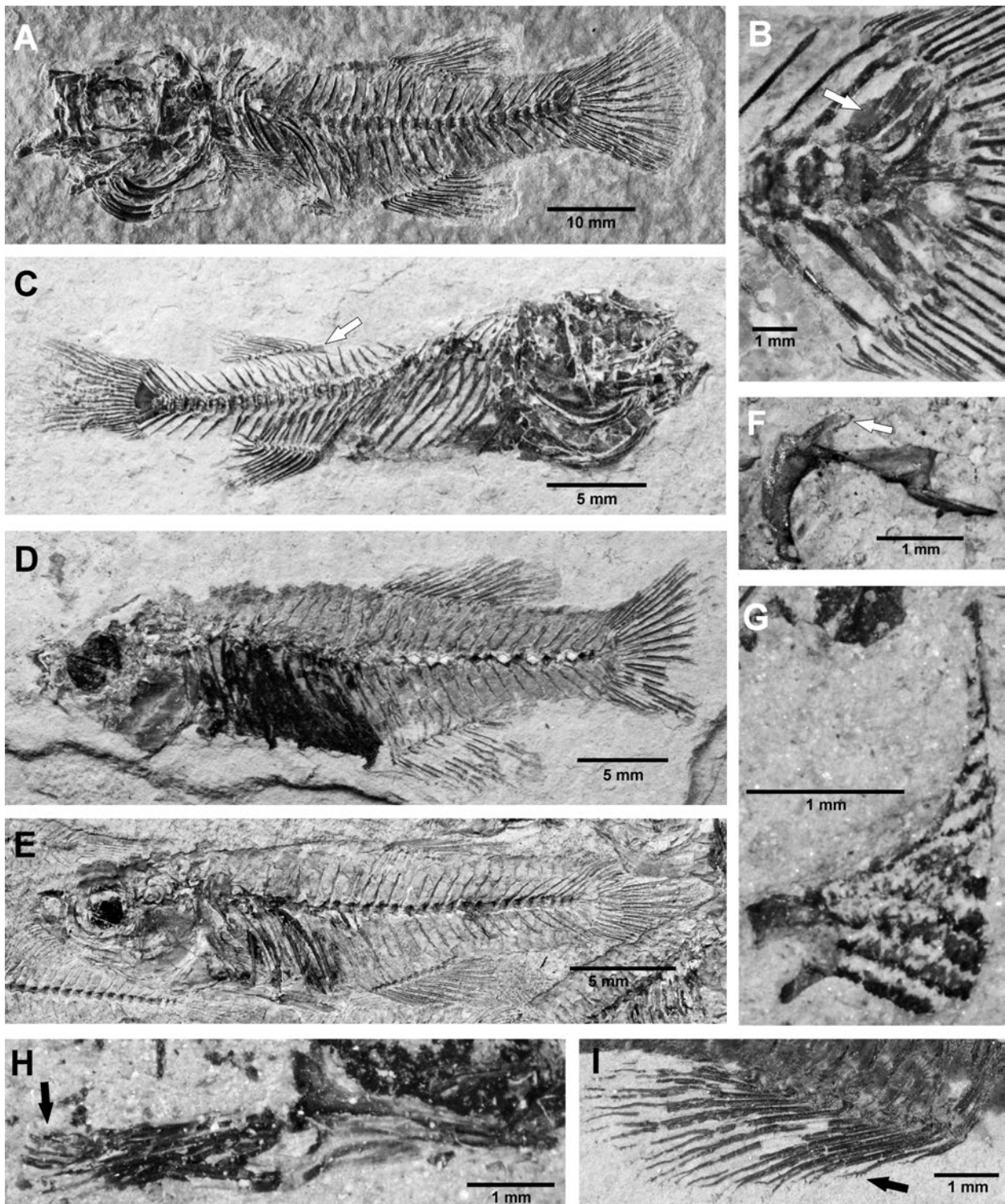


Fig. 2. Representatives of the four cyprinodontiform lineages from the Oligocene of southern France (A, C–E) and some anatomical structures (B, F–I). **A:** *Prolebias stenoura*, NHMUK 28491; **B:** caudal skeleton of *P. stenoura*, left lateral view, NHMUK 28491 (arrow indicates the greatly widened neural spine of preural vertebra 2); **C:** *Francolebias delphinensis*, holotype, MNHN.P MBR-49 (arrow indicates the coalesced anterior proximal radials of the dorsal fin); **D:** *Eurolebias meridionalis*, paratype, MNHN.P MSQ-1D; **E:** *Pantanodon cephalotes*, NHMUK 20071; **F:** left dentary, lateroventral view, of *P. egeranus*, NMP Pc606 (arrow indicates the expansion on the postero-dorsal border); **G:** left fifth ceratobranchial, dorsal view, of *P. egeranus*, NMP Pc562; **H:** pelvic girdles and fins, ventral view, of *P. egeranus*, NMP Pc651 (arrow indicates thickened extremity of pelvic-fin rays); **I:** anal fin, right view, of *P. cephalotes*, NHMUK P.1831a (arrow indicates spine-like contact organs on the second fin ray).

branchiids, and rivulids, rudimentary in fundulids, goodeids, profundulids, and some poeciliids, and well-developed but widened in anablepids, cyprinodontids, and most poeciliids. The present analysis supports the last condition as plesiomorphic for cyprinodontoids. A long and narrow dorsal process of the maxilla is visible in some specimens of *P. stenoura* (Fig. 3A), as well as in species of *Francolebias* (see below).

Unique derived conditions supporting monophyly of the Valenciidae, herein first reported, are the greatly widened neural spine of preural vertebra 2, its width about three to four times the width of neural spine of preural vertebra 4 (Fig. 2B), and anal-fin rays distinctively thicker than dorsal-fin rays (Fig. 2A), which are not found elsewhere among cyprinodontiforms. The analysis also indicates that no other examined species of *Prolebias* is closely related to *P. stenoura*. Since *P. stenoura* is the type species of the genus, *Prolebias* is herein considered as a monotypic genus.

Relationships of *Francolebias*, evidence of sexual dimorphism and putative internal fertilization

The presence of a greatly widened neural spine of preural vertebra 2 and anal-fin rays distinctively thicker than dorsal-fin rays supports inclusion of *Francolebias* among valenciids, as well as the presence of a broad pelvic bone, coalesced anterior proximal radials of the dorsal fin, and long anterior proximal radials of the anal fin with tip at the level of the basal portion of the adjacent hemal spines unambiguously distinguish *Francolebias* from all other fossil killifish taxa. GAUDANT (1988, 1989) already noted the peculiar morphology of the pelvic bone in *F. delphinensis* and *F. aymardi*, suggesting that the species are closely related. In those two species, the greatest width of the pelvic bone is about 70 % of the bone length (Fig. 3B), in contrast to never more than 50 % in other cyprinodontiforms, besides the anterior portion being rounded, instead of pointed as in other cyprinodontiform taxa. The coalesced anterior proximal radials of the dorsal fin (Fig. 2C) and the long anterior proximal radials of the anal fin (Fig. 3D, E), although not previously reported, are conspicuous in all specimens studied. Among cyprinodontiforms, similar conditions to those were, respectively, only found in the Goodeinae clade of Goodeidae and in the anablepid clade comprising *Anableps* and *Jenynsia*, parsimoniously supported as homoplastic.

As already reported by GAUDANT (1989), in some specimens of *F. delphinensis*, the distal portion of the hemal spines adjacent to the anal fin are strongly wid-

ened (Fig. 3D), whereas in other specimens with similar size and sharing all other morphological characters that widening is not present (Fig. 3E). This putative sexual dimorphism character is easily observable in specimens about 30–35 mm SL, whereas in smaller specimens of about 20–25 mm SL, this condition is present but much less conspicuous, as occurring in *F. aymardi*, a smaller species, with examined specimens not surpassing 22 mm SL. Interestingly, only in those individuals with widened hemal spines, the first anal-fin rays are robust, distinctively broader than subsequent rays and the proximal radials are proportionally wider (Fig. 3D, E).

Internal fertilization is relatively common among living cyprinodontoids, occurring in numerous species of three families, which corresponds to three independent evolutionary events - in the clade comprising the American genera *Anableps* and *Jenynsia* of the Anablepidae, in the Mexican subfamily Goodeinae of the Goodeidae, and in the American subfamily Poeciliinae of the Poeciliidae (PARENTI, 1981; MEYER & LYDEARD, 1993). Even with internal fertilization being independently acquired in those three cyprinodontoid families, all evolutionary acquisitions involve striking modifications in the anal fin structure (ROSEN & GORDON, 1953; ROSEN & BAILEY, 1963; PARENTI, 1981; GHEDOTTI, 1998). These bone modifications, which are much more pronounced in males, are always associated with anal fin mobility during sperm transference (e.g., ROSEN & GORDON, 1953). On the other hand, no modification is found in externally fertilizing species of anablepid, goodeid and poeciliid lineages, thus indicating a high level of dependence between internal fertilization and modified anal fin structure.

Strong sexually dimorphic modifications in the structure of the hemal arches above the anal fin associated with robust anal-fin rays and corresponding proximal radials, analogous to that occurring in *Francolebias*, are only present in internal inseminating taxa of the Anablepidae and Poeciliidae (e.g., ROSEN & BAILEY, 1963; PARENTI, 1981; GHEDOTTI, 1998), as well as in species of the internal inseminating rivulid genus *Campellolebias* VAZ-FERREIRA & SIERRA, 1974 (COSTA, 1995). Since sexually dimorphic modifications of the anal-fin structure in living cyprinodontiforms are always related to morphological specializations associated to internal fertilization, the presence of such modifications in Oligocene valenciid cyprinodontiforms highly supports an internal fertilization mode.

Eurolebias and other cyprinodontid fossils

The placement of the taxon *Eurolebias meridionalis* (Fig. 2D) among cyprinodontids is supported by the presence of a reduced jaw dentition, consisting of an

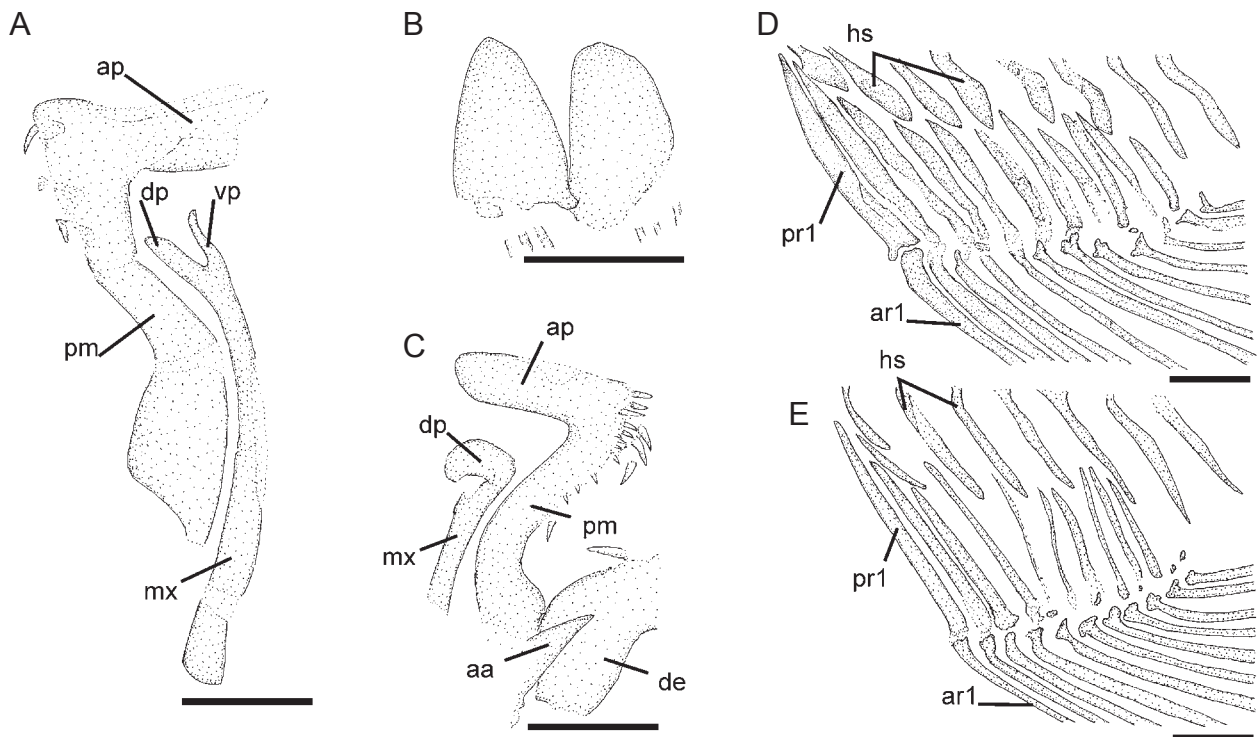


Fig. 3. Anatomical structures of the some cyprinodontiforms from the Oligocene of southern France. **A:** right upper jaw, dorsolateral view, of *Prolebias stenoura*, MNHN.P PTF-321; **B:** pelvic bones, ventral view, of *Francolebias delphinensis*, MNHN.P MBR-48D; **C:** right jaws, medial view (maxilla distorted), of *Eurolebias meridionalis*, MNHN.P MSQ-56; **D** and **E:** anal fin and support, left lateral view, two individuals of *F. delphinensis* from the same slab, MNHN.P MBR-53. Abbreviations: aa – angulo-articular; ap – ascending process of premaxilla; ar1 – anal-fin ray 1; de – dentary; dp – dorsal process of maxilla; hs – hemal spines; mx – maxilla; pm – premaxilla; pr1 – anal-fin proximal radial 1; vp – ventral process of maxilla. Scales bar = 1 mm.

outer tooth row followed by a few smaller teeth near the symphysis of the premaxilla and dentary (Fig. 3C). In other cyprinodontiforms, there are multiple series of small teeth adjacent to a single outer row of larger teeth, except in the Recent North American fundulid genus *Lucania*, in which a similar reduction is convergently found. In addition, although head bones are highly fragmented in the material of *E. meridionalis*, it is possible to note that the anterior axis of the jaw suspensorium, comprising the autopalatine, and the posterior portion, comprising the hyomandibula, have their main vertical axes nearly parallel (not illustrated), a condition only recorded in cyprinodontids among cyprinodontiforms. Also supporting inclusion of *E. meridionalis* in the Cyprinodontidae is the broad dorsal process of the maxilla (Fig. 2E), a condition occurring only in cyprinodontids, poeciliids and anablepids. However, some derived conditions shared by all the cyprinodontids do not occur in *E. meridionalis* - presence of a distinct groove on the dorsal process of the maxilla; a short, sharp, almost triangular ascending process of the premaxilla; dentary with a ventral expansion; proximal part of the parhypural short, not overlapping preural centrum 1; and, parietals absent (PARENTI, 1981; COSTA, 1998). The presence of a long

almost rectangular ascending process of the premaxilla, parietals and a long parhypural overlapping preural centrum 1, as well as the absence of a distinct groove on the dorsal process of the maxilla, and a ventral expansion on the dentary in *E. meridionalis*, which are plesiomorphic conditions among cyprinodontoids, indicates its basal position among the Cyprinodontidae.

COSTA (2012) suggested inclusion of *E. meridionalis* among cyprinodontids on the basis of characters of the caudal skeleton, such as the presence of a constriction on the basal portion of the hemal spine of the preural centrum 2 and a short proximal part of the parhypural. However, re-examination of the entire type series, including several specimens with well-preserved caudal fin skeletons, confirmed that constriction on the hemal spine of the preural centrum 2, but also revealed that the parhypural is not so short, but slightly overlaps the preural centrum 1.

Abundant fossil material from the Miocene of Europe and Middle East have been assigned to the cyprinodontid genus *Aphanius* (e.g., GAUDANT, 1979, 1993, 2009, 2011), which also comprises numerous recent species (e.g., HRBEK & MEYER, 2003). Both recent and fossil species of *Aphanius* share a pronounced hook-shaped process on the ventral portion

of the dentary (PARENTI, 1981; COSTA, 1997), which is not present in *E. meridionalis*. The fossil cyprinodontid record is also represented in South America by the Miocene Andean taxon *Carrionellus diumortuus*, which is closely related to the recent genus *Orestias*, and may be distinguished from *E. meridionalis* by the presence of large tricuspidate teeth on jaws (WHITE, 1927; COSTA, 2011).

Poeciliid fossils

COSTA (2012) recently recorded some morphological evidence supporting close relationships between *Prolebias cephalotes* and *P. egeranus*, and the Recent African poeciliid genus *Pantanodon*, which is confirmed in the present study. *Prolebias cephalotes* and *P. egeranus* have the general morphology typical among poeciliids, such as dorsal-fin origin posterior to anal-fin origin, pectoral-fin base high on flank, pelvic-fin girdle placed just posterior to shoulder girdle, besides a small size, barely surpassing 30 mm SL (COSTA, 2012) (Fig. 2E).

Pantanodon has been known from two small and rare species inhabiting brackish waters of East Africa and Madagascar (*P. stuhlmanni* and *P. madagascariensis*). Their peculiar morphology inspired two papers focusing on osteology (WHITEHEAD, 1962; ROSEN, 1965), the first one proposing inclusion in their own subfamily Pantonodontinae (WHITEHEAD, 1962), which has not been followed by recent authors (e.g., PARENTI, 1981). Some apomorphic features shared by *Prolebias cephalotes*, *P. egeranus* and recent species of *Pantanodon*, not occurring in other poeciliids and other cyprinodontiforms, support monophyly of a group comprising all these taxa: presence of an expansion on the postero-dorsal border of the dentary, which terminates posteriorly as a long narrow prolongation (Fig. 2F); third and fourth pharyngobranchial toothplates coalesced; pelvic bone long and narrow, and extremity of pelvic-fin rays thickened in males, often with curved tips (Fig. 2H).

The presence of transverse rows of minute teeth on the fifth ceratobranchial and pharyngobranchials, as well as the wide, drop-shaped fifth ceratobranchial, with two lateral processes (Fig. 2G), are particularly remarkable, being identical in *P. cephalotes*, *P. egeranus* and in both recent species of *Pantanodon*. This morphology strongly contrasts with the slender, boomerang-shaped fifth ceratobranchial, with a single terminal process and large teeth irregularly arranged, which is present in all other cyprinodontiforms except in some New World poeciliids.

Pantanodon stuhlmanni and *P. madagascariensis* are clearly more closely related to one another than to congeneric fossil species by the two former sharing a

greatly enlarged second pharyngobranchial toothplate, a condition unique among cyprinodontiforms (ROSEN, 1965; PARENTI, 1981). In addition, the presence of spine-like contact organs on the extremities of the anterior rays of the dorsal and anal fins rays is herein first recorded for some specimens of *P. cephalotes* (Fig. 3I). Contact organs on fin rays and body scales are common in males of several cyprinodontiform lineages, particularly in aplocheiloids, which is usually related to elaborate courtship behaviour (e.g., COSTA, 2006).

Incertae sedis species of *Prolebias*

The material of *Prolebias goreti* from the lower Oligocene of Céreste, France available for study did not provide useful evidence about its phylogenetic position. Details on jaw and caudal skeleton morphology were not clearly visible, and no data about other structures were seen. Although the premaxilla morphology and tooth arrangement of *P. goreti* are similar to those in *Prolebias stenoura*, the thin anal-fin rays and the dorsal-fin origin anteriorly positioned relative to the anal-fin origin indicate that the taxa are not congeneric. Thus, *P. goreti* is herein considered as an incertae sedis taxon.

Other well established nominal species of *Prolebias*, including *P. catalaunicus* GAUDANT, 1982 from the lower Oligocene of Sarreal, Spain, *P. euskadiensis* GAUDANT, 2003 from the upper Oligocene–lower Miocene of Izarra, Spain, *P. hungaricus* GAUDANT, 1991 from the middle Miocene of Szurdokpüspöki, Hungary, and *P. rhenanus* GAUDANT, 1981 from the lower Oligocene of Kleinkems, Germany, which were not available for the present study and are still known only from a limited set of characters provided in the literature (GAUDANT, 1981, 1982, 1991, 2003), are presently considered as incertae sedis taxa.

Other European killifish fossil genera

The monotypic genus *Cryptolebias* GAUDANT, 1978, was based on a single specimen of *Cryptolebias senogalliensis* (COCCHI, 1859) from the Messinian marls of Senigallia, Italy (GAUDANT, 1978b). The genus was then placed in the Cyprinodontiformes on the basis of the typical structure of the caudal skeleton, but the poorly preserved specimen does not provide evidence supporting its inclusion in any cyprinodontiform family. *Cryptolebias senogalliensis* differs from all other Cenozoic killifish taxa by the anal-fin origin positioned through a vertical through the posterior half of the dorsal-fin base and a very slender body, depth about 12 % standard length.

The genus *Aphanolebias* REICHENBACHER & GAUDANT, 2003 was erected to include *Lebias meyeri* AGASSIZ, 1939 from the Miocene of Frankfurt, Germany (REICHENBACHER & GAUDANT, 2003), which had been previously placed in *Prolebias* since SAUVAGE (1874). Material of this taxon was not available for the present study and the few characters presented in the description do not permit an accurate character analysis. However, *Aphanolebias meyeri* does not present the derived character states of the two new genera herein described, as well it does not present the diagnostic conditions of *Pantanodon*. Some character states of *A. meyeri*, including the dorsal-fin origin posterior to anal-fin origin, pelvic-fin base slightly closer to anal-fin origin than to pectoral-fin base, jaw teeth conical and arranged in multiple series and hypural plates partially separated, suggest a basal position among cyprinodontoids, but an analysis based on examination of material is necessary to establish hypotheses of relationships. Several other species of *Aphanolebias* have been uniquely proposed on the basis of otolith morphology (e.g., REICHENBACHER & KOWALKE, 2009), which does not provide evidence of relationships among cyprinodontoids.

Conclusion

The present study indicates that the European Oligocene fauna of cyprinodontiform fishes was diversified, including at least four distinct lineages, thus highly contrasting with the present day European fauna of cyprinodontiforms, comprising only four species belonging to two genera and two families. In addition, the Oligocene cyprinodontiform taxa exhibited a great morphological complexity, including characters related to sexual dimorphism and probably to internal fertilization, today only paralleled by cyprinodontiform taxa inhabiting subtropical and tropical zones of New World with high species diversity.

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Appendix 1

List of characters used in the phylogenetic analysis. Characters were taken from ROSEN & BAILEY (1963), ROSEN (1964), PARENTI (1981, 1984, 2008), COSTA (1991, 1997, 1998, 2012), and GHEDOTTI (1998), often modified to follow Sereno's (2007) proposal for character statement formulation.

Jaws

- (1) Maxilla, dorsal process, development: well-developed (0); rudimentary (1) (modified from COSTA, 1998: ch. 1).
- (2) Maxilla, dorsal process, width relative to ventral process: about equal in width or slightly wider (0); three or more times wider (1); species with rudimentary dorsal process (?) (modified from COSTA, 1998: ch.2).
- (3) Maxilla, dorsal process, distinct groove: absent (0); present (1) (PARENTI, 1981; COSTA, 1998: ch. 3).
- (4) Maxilla, ventral process, development: well-developed (0); rudimentary (1) (modified from PARENTI, 1981).
- (5) Maxilla, ventral process, orientation: medial (0); antero-ventral (1); taxa with rudimentary process (?) (PARENTI, 1981; COSTA, 1998: ch. 5).
- (6) Maxilla, ventral process, shape: straight to slightly curved (0); bent, assuming triangular shape (1); taxa with rudimentary process (?) (modified from PARENTI, 1981; COSTA, 1998: ch. 4).
- (7) Maxilla, ventral process, distal tip, hook-like end: absent (0); present (1); taxa with rudimentary process (?) (modified from PARENTI, 1981; COSTA, 1998: ch. 7).
- (8) Maxilla, distal portion, shape: continuously narrow or gradually widening (0); abrupt widening (1) (modified from PARENTI, 1981; COSTA, 1998: ch. 6).
- (9) Premaxilla, alveolar arm, prominent anterior process: absent (0); present (1) (modified from PARENTI, 1981; COSTA, 1998: ch. 13).
- (10) Premaxilla, alveolar arm, posterior projection: absent (0); present (1) (modified from PARENTI, 1981; COSTA, 1998: ch. 14).
- (11) Premaxilla, ascending process, development: well-developed (0); rudimentary (1) (modified from PARENTI, 1981).
- (12) Premaxilla, ascending process, length relative to premaxilla main axis length: long, about half (0); short, one third or less (1) (modified from COSTA, 1998: ch. 16).
- (13) Premaxilla, ascending process, shape: posterior portion truncate or rounded, process about rectangular (0); posterior portion sharply narrowing, process triangular (1) (modified from PARENTI, 1981).
- (14) Dentary, shape: thin (0); robust (1) (PARENTI, 1981).
- (15) Dentary, ventro-posterior process, development: well-developed (0); rudimentary (1) (modified from PARENTI, 1981; COSTA, 1998: ch. 20).

- (16) Dentary, ventral portion, expansion: absent (0); present (1) (modified from COSTA, 1997: ch. 26).
- (17) Dentary, ventral portion, pronounced hook-shaped process: absent (0); present (1) (modified from PARENTI, 1981).
- (18) Dentary, postero-dorsal border, expansion: absent (0); present (1) (new character).
- (19) Angulo-articular, ventral process, development relative to retro-articular: well-developed, retro-articular restricted to posteroventral corner (0); minute, retro-articular along most of ventral surface (1) (modified from PARENTI, 1981; COSTA, 1998: ch. 21).
- (20) Premaxilla and dentary, teeth, arrangement: outer row with larger teeth and multiple inner rows of smaller teeth (0); single row (outer position) (1); outer row with larger teeth and few smaller internal teeth near symphysis (2) (modified from COSTA, 1997: ch. 28).
- (21) Premaxilla and dentary, teeth of outer row, shape: conical (0); bicuspidate (1); tricuspidate (2); spatulate (3) (modified from COSTA, 1997: ch. 27).
- (22) Premaxilla and dentary, teeth of inner rows, shape: conical (0); flattened with pointed tip or spatulate (1); tricuspidate (2) (modified from COSTA, 1997: ch. 27). [Remark: since tooth morphology may vary independently in outer and inner rows, the teeth morphology of each row is analysed as distinct characters].
- (23) Autopalatine, head, shape and articulation with upper jaw: relatively narrow, without strong connection to maxilla (0); expanded and articulating with maxilla via dense ligament (1) (PARENTI, 2008: ch.5).
- (24) Autopalatine, dorsal extremity, shape and orientation relative to main longitudinal axis: slightly curved anteriorly, continuous with main longitudinal axis (0); bent anteriorly, slightly displaced laterally (1); taxa with dorsal extremity rudimentary (?) (modified from PARENTI, 1981; COSTA, 1998: ch. 27).
- (25) Autopalatine, dorsal extremity, prominent antero-medial process: absent (0); present (1); taxa with dorsal extremity rudimentary (?) (modified from COSTA, 1998: ch. 29).
- (26) Autopalatine, dorsal extremity, development: well-developed (0); rudimentary (1).
- (27) Endopterygoid, dorsal extent: projecting below infra-orbital region (0); restricted to jaw suspensorium region (1) (modified from COSTA, 1998: ch. 32).
- (28) Quadrate, dorso-posterior margin, deep concavity: absent (0); present (1) (COSTA, 1998: ch. 33).
- (29) Metapterygoid: present (0); absent (1) (PARENTI, 1981).
- (30) Symplectic, dorsal flap: present (0); absent (1) (new character).
- (31) Jaw suspensorium, general shape focusing on orientation of anterior and posterior portions: not vertically elongated, divergent axes (0); vertically elongated, parallel or slightly convergent axes (1) (new character).

Hyoid arch

- (32) Urohyal, dorsal process, development: well-developed (0); rudimentary (1) (COSTA, 1998: ch. 38).
- (33) Dorsal hypohyal: present (0); absent (1) (PARENTI, 1981).
- (34) Anterior ceratohyal, condyles: double (0); single (1) (PARENTI, 1981).
- (35) Basihyal, shape: slender, sub-rectangular (0); anterior portion wide, sub-triangular (1) (PARENTI, 1981).
- (36) Basihyal, cartilaginous portion extent relative to bony portion: longer (0); shorter (1) (COSTA, 1998: ch. 44).
- (37) Anterior and posterior ceratohyals, relative position: in close proximity, separated by narrow cartilaginous interspace (0); separated by broad cartilaginous interspace (1) (modified from PARENTI, 1984).

Jaw suspensorium and opercular series

- (23) Autopalatine, head, shape and articulation with upper jaw: relatively narrow, without strong connection to maxilla (0); expanded and articulating with maxilla via dense ligament (1) (PARENTI, 2008: ch.5).
- (24) Autopalatine, dorsal extremity, shape and orientation relative to main longitudinal axis: slightly curved anteriorly, continuous with main longitudinal axis (0); bent anteriorly, slightly displaced laterally (1); taxa with dorsal extremity rudimentary (?) (modified from PARENTI, 1981; COSTA, 1998: ch. 27).
- (25) Autopalatine, dorsal extremity, prominent antero-medial process: absent (0); present (1); taxa with dorsal extremity rudimentary (?) (modified from COSTA, 1998: ch. 29).
- (26) Autopalatine, dorsal extremity, development: well-developed (0); rudimentary (1).
- (27) Endopterygoid, dorsal extent: projecting below infra-orbital region (0); restricted to jaw suspensorium region (1) (modified from COSTA, 1998: ch. 32).

Branchial arches

- (38) First basibranchial: present (0); absent (1) (PARENTI, 1981).
- (39) First hypobranchial, anterior projection: absent (0); present (1) (new character).
- (40) Third ceratobranchial, teeth: absent (0); present (1) (COSTA, 1998: ch. 50).
- (41) Fourth ceratobranchial, teeth: present (0); absent (1) (COSTA, 1998: ch. 50).
- (42) Fourth ceratobranchial, ventral flange projecting below anterior portion of fifth ceratobranchial: absent (0); present (1) (modified from COSTA, 1997: ch. 11).
- (43) Fourth ceratobranchial, proximal portion, anteriorly directed process: absent (0); present (1) (COSTA, 1997: ch. 12).
- (44) First epibranchial, medial end, shape and cartilage zone: narrow to moderately wide, with single terminal cartilage zone (0); broad, with two lateral cartilage zones (1) (COSTA, 1998: ch. 54).

- (45) Second epibranchial, process, development: well-developed (0); rudimentary or absent (1) (modified from COSTA, 1998: ch. 55).
- (46) Second pharyngobranchial, teeth, shape: conical or spatulate (0); tricuspidate (1) (COSTA, 1997).
- (47) Third pharyngobranchial and fifth ceratobranchial, teeth, arrangement: irregular (0); regular (1) (COSTA, 1997: ch. 2).
- (48) Third pharyngobranchial and fifth ceratobranchial, teeth, expanded lobe adjacent to tooth tip: absent (0); present (1) (COSTA, 1997: ch. 10).
- (49) Third and fourth pharyngobranchial toothplates, coalescence: absent (0); present (1) (COSTA, 1997: ch. 1).
- (50) Fifth ceratobranchial, shape: narrow, boomerang-shaped (0); broad, drop-shaped (1) (modified from COSTA, 1991).

Neurocranium

- (51) Vomer: present (0); absent (1) (PARENTI, 1981, 1984).
- (52) Vomer, teeth: absent (0); present (1) (COSTA, 1998: ch. 60).
- (53) Mesethmoid, ossification as independent structure, development: well-developed (0); rudimentary or absent (0) (COSTA, 1997: ch. 56).

Paired fins and girdles

- (54) Pectoral fin, insertion position: lateral (0); ventro-lateral (1) (COSTA, 1998: ch. 74).
- (55) Post-temporal, ventral process: present (0); absent (1) (PARENTI, 1981).
- (56) Supracleithrum, shape: narrow, width about continuous with ventral posttemporal width (0); broad, occupying most width of dorsal portion of cleithrum (1) (modified from COSTA, 1998: ch. 75).
- (57) First post-cleithrum: present (0); absent (1) (PARENTI, 1981).
- (58) First post-cleithrum, shape: slender (0); scale-like (1) (PARENTI, 1981).
- (59) Cleithrum, dorsal portion, posterior margin, notch: absent (0); present (1) (COSTA, 1998: ch. 79).
- (60) Cleithrum, dorsal portion, posterior margin shape: slight convexity (0); pronounced posterior projection (1) (modified from COSTA, 1998: ch. 82).
- (61) Pelvic fin and girdle: present (0); absent (1) (PARENTI, 1981).
- (62) Pelvic bone, shape and width, expressed by percentage of greatest width in length: triangular, slender, about 50 % (0); subtriangular, anterior

extremity rounded, broad, about 70 % (1); triangular, long and narrow, about 30 % (2) (new character).

- (63) Pelvic fin, placement relative to pectoral-fin base and anal-fin origin: midway or closer to anal-fin origin (0); closer to pectoral-fin base (1) (modified from COSTA, 1998: 85).
- (64) Pelvic bone, medial process, development: well-developed (0); rudimentary (1) (modified from PARENTI, 1981).
- (65) Pelvic-fin rays in putative males, extremity, shape: distal portion similar to basal portion (0); distal portion conspicuously thickened, often curved (1) (new character).

Vertebrae and unpaired fins

- (66) Caudal vertebrae, prezygapophysis hemal, development: rudimentary (0); well-developed (1) (new character).
- (67) Caudal vertebrae above anal fin in putative males, hemal spines, distal widening: absent (0); present (1) (new character).
- (68) Posterior precaudal vertebrae in males, hemal arch, shape and function: unmodified, like anterior ones (0); modified as lygastyle and gonapophyses, acting in gonopodium movement (1) (ROSEN & BAILEY, 1963).
- (69) Anterior vertebrae, first pleural rib, position: third vertebra (0); second vertebra (1) (PARENTI, 1981).
- (70) Stegural, development: well-developed (0); minute (1) (COSTA, 2012).
- (71) Stegural, ventral portion, lateral process: absent (0); present (1) (COSTA, 2012).
- (72) Upper hypurals and compound caudal centrum, degree of fusion: attached, limited by cartilage edge (0); complete ankylosis (1) (COSTA, 2012).
- (73) Upper and lower hypural plates, degree of fusion: completely separated (0); partially fused (1); completely fused (2) (modified from COSTA, 1998: ch. 88).
- (74) Caudal fin, ventral accessory bone: absent (0); present (1) (PARENTI, 2008: ch.16).
- (75) Caudal-fin rays, zone between upper and lower hypural plates, arrangement: separated by broad interspace (0); continuously arranged (1) (COSTA, 2012).
- (76) Epurals, number: three or two (0); one (1) (ROSEN, 1964).
- (77) Epural, shape: rod-like (0); blade-like (1) (ROSEN, 1964).
- (78) Preural vertebra 2, neural spine, development: absent (0); well-developed, distal tip acting in support of caudal-fin rays (1) (COSTA, 2012).

- (79) Preural vertebra 2, neural spine, width relative to neural spine of preural vertebrae 4: equal or slightly wider (0); much wider, at least three or four times wider (1) (new character).
- (80) Preural vertebra 2, hemal spine, sub-basal region, deep constriction: absent (0); present (1) (modified from COSTA, 1998: ch. 92).
- (81) Preural vertebra 3, neural and hemal spines, width relative to neural and hemal spines of preural vertebrae anterior to preural vertebra 4: about equal (0); distinctively wider (1) (COSTA, 2012).
- (82) Parhypural, proximal part, relative position to preural centrum 1: overlapped (0); not overlapped (2) (modified from COSTA, 1998: ch. 91).
- (83) Dorsal fin, anterior proximal radials, coalescence: absent (0); present (1) (new character).
- (84) Anal fin in males: unmodified, like females (0); anterior rays shortened and unbranched (1); rays thickened and elongated, covered by fleshy tube (2); transformed into a gonopodium formed by rays 3–5 (3) (PARENTI, 1981).
- (85) Anal fin, rays, thickness relative to dorsal-fin rays: equally thickened (0); distinctively thicker (1) (new character).
- (86) Anal fin, anterior proximal radials, extent relative to adjacent hemal spines: distal (0); proximal (1) (new character).
- (87) Anal fin, anterior proximal radial, position relative to vertebrae: at level of precaudal vertebrae, between pleural ribs (0); close to limit between precaudal and caudal vertebrae, between posterior pleural ribs and anterior hemal spines (1) (new character).
- (88) Anal fin in males, anterior proximal radial, fusion to subsequent proximal radials: absent (0); present (1) (modified from GHEDOTTI, 1998: ch. 53).
- (89) Anal fin in males, anterior rays, contact organs: absent (0); present (1) (new character).

