Anatomy, systematics and phylogeny of both Recent and fossil latid fishes (Teleostei, Perciformes, Latidae)

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The anatomical investigation of the osteology of both fossil and Recent species of the so-called Centropomidae was conducted with three aims: of improving the taxa definition, providing anatomical descriptions suitable for palaeontological studies and establishing a hypothesis for the phylogenetic relationships of the family. The family interrelationships are reviewed according to phylogenetic principles and reconstructed based on a cladistic analysis using 29 characters (28 osteological, and one myological). The family Centropomidae as previously defined is paraphyletic. The new family Latidae is monophyletic and includes *Lates*, *Psammoperca* and †*Eolates*. The two former genera are monophyletic whereas the latter genus is polyphyletic. Three fossil species are attributed to †*Eolates*. The family Centropomidae is monogeneric with *Centropomus*. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, **141**, 81–133.

ADDITIONAL KEYWORDS: Centropomidae – *Centropomus* – cladistics – *Eolates* – *Lates* – *Psammoperca* – Tertiary.

INTRODUCTION

Previously, there was a consensus regarding the classification and relationships of the Recent genera *Centropomus*, *Lates* and *Psammoperca*, which were grouped in the Centropomidae Poey, 1868, a family of Recent tropical, marine and freshwater percoid fish and fossils from the Tertiary through prehistoric times. However, according to other authors, more genera were added to the family: *Ambassis* and *Glaucosoma* (Regan, 1913), *Ambassis* (Greenwood *et al.*, 1966; Nelson, 1976) and *Niphon spinosus* (Rivas & Cook, 1968). Greenwood (1976) later restricted the family to the four genera *Centropomus*, *Lates*, *Psammoperca* and †*Eolates*, and established a hypothesis of their interrelationships (Fig. 1A). This definition of the family Centropomidae was contested by Waldman (1986), who suggested that *Lateolabrax* and *Siniperca* also belong to the family. Recently, Mooi & Gill (1995) questioned the relationship of Recent Latinae (*Lates + Psammoperca*) with the Centropominae (*Cen-tropomus*) as proposed by Greenwood (1976), based on the observed distribution of the dorsal epaxial musculature pattern among percoid fish and more generally acanthomorphs. Consequently, they proposed to replace the two subfamilies by the families Latidae and Centropomidae. The anatomical investigation of the osteology of the species reported in *Lates* (Recent and fossil), †*Eolates* (fossil) and *Psammoperca* (Recent) was conducted with the three aims of improving the taxa definition, proposing a hypothesis of the phylogenetic relationships of the family Latidae, including both Recent and fossil species, and providing anatomical descriptions suitable for palaeontological studies.

THE LATID FOSSIL RECORD

The anatomical re-investigation of †*Eolates* species, i.e. †*E. gracilis* (Lower Eocene, Monte Bolca), †*E. aquensis* (Lower Oligocene, Provence) and †*E. macrurus* (Lower Eocene, Paris Basin), allows them to be distinguished based on the skeleton of several specimens of both the former species. The preservation of the specimens of †*E. macrurus* is too poor to

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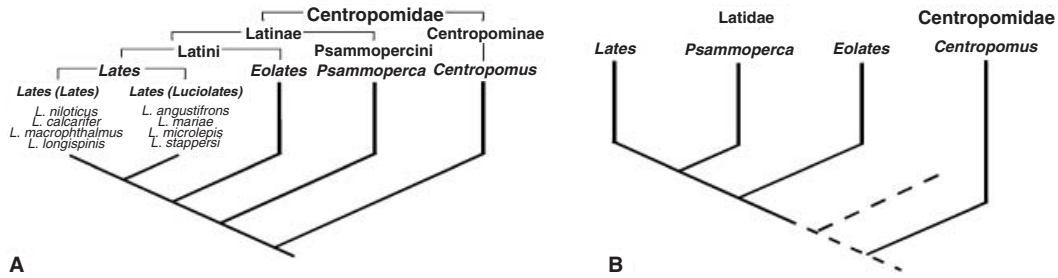
Figure 1. Phylogenetic relationships of the fish family Latidae: A, according to Greenwood (1976); B, new proposal.

allow new results. For the same reason, notes on *Lates* fossil species mainly concern †*Lates bispinosus* (Neogene, Turkey), †*Lates karungae* – of which only vertebrae are known (Miocene, Kenya), and a few †*L. partshii* (Miocene, Austria), †*L. gregarius* (Miocene, Moldavia), †*L. croaticus* (Miocene, Croatia) and †*L. macropterus* (Oligocene, Italy). Apart from fossil latid species, many fossils from the Mio-Pliocene of the Afro-Arabian plate were described and/or referred to *Lates* (*Lates*) sp. or to *Lates* sp. cf. *niloticus* from the Lower Miocene of Saudi Arabia, Sultanate of Oman (Greenwood, 1987; Otero & Gayet, 2001), Israel (Goldsmith *et al.*, 1982), Egypt (Priem, 1920) and Congo (Greenwood & Howes, 1975); from the Upper Miocene of Egypt (Priem, 1914), Tunisia (Greenwood, 1973) and Kenya (Greenwood, 1951; Stewart, 1994); from the Upper Miocene and Pliocene of Chad (Brunet *et al.*, 2000; Vignaud *et al.*, 2002); and from the Pliocene of Egypt (Greenwood, 1972), Libya (Gaudant, 1987), Congo (Greenwood, 1959; Greenwood & Howes, 1975; Van Neer, 1992) and Uganda (White, 1934; Van Neer, 1994). Part of this material was re-examined (see Appendix). In addition, the study of the fossil specimen from the Messinian of Monte Castellaro (Italy) led Otero & Sorbini (1999) to attribute it to the species *Lates niloticus*. †*L. maliensis* (Holocene, Mali), described by Gayet (1983), is also *L. niloticus* (Van Neer & Gayet, 1988).

Another species of *Lates* has just been described in the Lower Oligocene of Egypt (Murray & Attia, 2004).

Finally, the material of a proposed latid fish from the Maastrichtian and Early Late Palaeocene of Bolivia was described by Gayet & Meunier (1998). No apomorphies at the familial or generic level are described for this perciform fish, and therefore I tentatively propose that it be placed as *incertae sedis* in the order. †*Lates rhachirhynchus* (Greenwood & Howes, 1975) and †*Lates fajumensis* (Weiler, 1929) are now removed from the family Latidae. They belong to two new genera: †*Semlikiichthys rhachirhynchus* (Otero & Gayet, 1999a) and †*Weilerichthys fajumensis* (Otero & Gayet, 1999b), and as they could not be

assigned to any family they remain in Percoidei *incertae sedis* and are thus not included in the analysis.

NEW PROPOSAL FOR THE PHYLOGENETIC RELATIONSHIPS OF THE FAMILY LATIDAE (FIG. 1B)

This results from a cladistic analysis (following Hennig, 1966) based on 29 characters (28 osteological and one myological): *Lates*, *Psammoperca* and †*Eolates* form a paraphyletic group with *Centropomus*; the monophyletic subfamily Latinae Jordan, 1923 is established as a family (Fig. 1B), and the family Centropomidae is monogeneric (*Centropomus*), in agreement with Mooi & Gill's (1995) proposal. Three genera belong to the family Latidae:

– *Lates* includes the Recent species *L. niloticus, L. calcarifer, L. macrophthalmus, L. longispinis, L. angustifrons, L. microlepis, L. mariae* and *L. stappersi* (the last four are endemic to Lake Tanganyika), and the fossil species †*L. bispinosus,* †*L. partshii,* †*L. gregarius, L. croaticus, L. karungae* and †*L. macropterus*. Many African fossils from Miocene and Pliocene sites are assigned either to *Lates*, or to *L. niloticus*. The genus *Lates* is established on apomorphic characters.

– *Psammoperca* is a monotypic genus.

– the fossil genus †*Eolates* has three species: †*E. gracilis*, †*E. aquensis* and †*E. macrurus*. The validity of this genus, established by Sorbini (1970), was discussed by Gaudant (1977) and Gaudant & Sen (1979), who argued to keep only the genus *Lates*, because †*Eolates* characters (all of the caudal skeleton) are not observable in every fossil. I adopt another point of view. Whether or not †*Eolates* is monophyletic, *Lates* is a monophyletic genus based on three synapomorphies, and they form a paraphyletic group with the †*Eolates* species. So, †*Eolates* is kept as a separate genus containing the 'basal' latids, i.e. the non-*Lates* and non-*Psammoperca* latids.

Psammoperca and *Lates* appear to form a monophyletic group, based on at least two apomorphies.

TERMINOLOGY AND MATERIAL

ABBREVIATIONS

DS: dry skeleton; FSL: Faculté des Sciences de Lyon (Lyon, France); JFM: François Meunier personal collection (Paris, France); MCSNV: Museo Civico di Storia Naturale di Verona (Verona, Italy); MG: Mireille Gayet personal collection (Lyon, France); MNHN: Muséum national d'Histoire naturelle (Paris, France); MRAC: Musée royal d'Afrique centrale (Tervuren, Belgium); NHM: The Natural History Museum (London, UK), formerly the British Museum of Natural History; NKM: Naturkunde Museum (Stuttgart, Germany); SI: Senckenberg Institut (Frankfurt, Germany); *: individuals prepared following the transfer method of Toombs & Rixon (1950); †: fossil taxa.

FORMULAE

The *vertebral formula* gives the number of abdominal vertebrae, the number of postabdominal vertebrae (the pseudurostylar complex is counted as one element); and the number of postabdominal vertebrae supporting the caudal skeleton is given in parentheses. For example, VC = 10 + 14/15 (4): ten abdominal and 14 or 15 postabdominal vertebrae, among which are four caudal.

The *predorsal formula*, defined by Ahlstrom, Butler & Sumida (1976) and Johnson (1984), and modified following Patterson's (1992) definition of the supernumerary spines, gives the count and the position of predorsal bones (0) and of the first dorsal pterygiophores; the pterygiophores are represented by the number of the supernumerary spine(s) they support, in bold Roman numerals, and/or by the number of spine(s) serially associated with it, in normal Roman numerals. Predorsal = 0/0/0+II/I+I/: front to back, first predorsal, first neural spine, second predorsal, second neural spine, third predorsal, first dorsal pterygiophore supporting one supernumerary spine and one serial spine, third neural spine, second and third dorsal pterygiophores, each supporting one serial spine, fourth neural spine.

The *dorsal and anal formulae* give the number of spines (Roman numeral) and rays (Arabic number). When the dorsal fin is double, the formulae are separated by a –. D = VIII/IX – I+10/12: eight or nine spines (first dorsal fin), one spine and 10–12 rays (second dorsal fin).

The *caudal formula* gives, from top to bottom, the number of dorsal procurrent rays (Arabic number in parentheses), the dorsal unbranched principal ray (I), the number of dorsal branched principal rays (Arabic number), the number of ventral branched principal rays (Arabic number), the ventral unbranched principal ray (I) and the number of ventral procurrent rays (Arabic number in parentheses). C = (6/11)+I+7 – 6+I+(6/9): 6–11 dorsal procurrent rays, unbranched dorsal principal ray, seven branched dorsal principal rays, six branched ventral principal rays unbranched ventral principal ray, 6–9 ventral procurrent rays.

The *paired fin formulae* give the ray count (Arabic number), and the spine presence (I). Pect = 14: 14 rays in the pectoral fin; Pelv = I+5: one spine and five rays in the pelvic fin.

MATERIAL AND TAXA DEFINITION

A list of the studied material of Latidae, Centropomidae and comparative species is given in the Appendix.

Bibliographical data are mainly from Patterson (1964) and Gaudant (1978) for ctenothrissiforms, Gaudant (1978) for pattersonichthyiforms, Otero & Gayet (1996) for aipichthyoids and Zehren (1979) for Beryciformes. The definitions for percomorph taxa derive from Johnson & Patterson (1993) for percomorphs, this study for centropomids and latids, and Kendall (1984) for serranids.

SYSTEMATIC PALAEONTOLOGY

ORDER PERCIFORMES BLEEKER, 1859
SUBORDER PERCOIDEI BLEEKER, 1859
FAMILY LATIDAE JORDAN, 1923

Emended diagnosis: Percoid family characterized by: mesethmoid projections present; supraoccipital crest extending far forward between the frontals; reduction of the metapterygoid lamina to a relictual ridge and a notch; single supramaxilla with or without an anterior process; sensory canal on the ascending branch of the preoperculum in a bony tube; first haemal spine trifid; a single dorsal supernumerary spine; spines developed on the caudal border of the cleithral plate (lost by *Psammoperca*); ventral expansion of the cleithral plate; and a sharp pointed process of the pelvic girdle.

In addition, they have: laterally compressed body; maxillae extending posteriorly beyond the midpoint of the eyes (sometimes to the level of the posterior margin of the eyes); prognathus jaw; supraoccipital crest and continuous fronto-parietal crests; posterior process of the epiotic present; teeth on the vomer, palatine, ectopterygoid, premaxilla and dentary; posterior process of the premaxilla with a concave posterior border (unknown in †*Eolates*); ventral border of the first infraorbital and posterior border of the posttemporal serrated; cephalic sensory canals running in bony tubes; large triangular spine at the posterior angle of the two preopercular limbs; 3–4 (rarely more) strong triangular spines developed on the ventral border of the preoperculum horizontal limb (lost by *Psammoperca* and *L. stappersi*); one well-developed

opercular spine; vertebral column with 24 or 25 (sometimes 26) vertebrae, of which usually 11 are abdominal (ten in a single species); VC = 10/11+13/15(4); an enlarged neural spine of the second vertebra; no parapophyses on the 5–7 anteriormost vertebrae; 4–8 pairs of epineurals; Predorsal = /0/0+0+II/I+I/or 0/0/0+II/I+I/ (most common latid formulae) or other equivalent predorsal formula; one dorsal supernumerary spine; D = VIII/IX+8/13, dorsal fins separated by a gap with one or two isolated spines; A = II/III+7/9; first anal pterygiophore slightly inclined backwards and not hypertrophied; two anal supernumerary spines; anal and dorsal anteriormost pterygiophores bipartite, posteriormost ones tripartite; stegural present; uroneural present or absent; two or three epurals; caudal spur of the first ventral marginal ray absent or present; caudal fin with posterior border rounded, truncated   or   forked;   C = (6/11)-I-8 : 7-I-(6/9); Pelv = I+5; Pect = 16/17; seven branchiostegal rays; pseudobranch covered; ctenoid scales small to moderate in size, dorsally not extending on to the head in front of the midpoint of the eye (usually beyond the posterior border of the orbit), present on cheek and operculum and scaly sheath at the base of the median fins; lateral line scales extending on to the caudal fin and usually reaching its posterior border in one or three rows.

Occurrence: About ten Recent species within two genera (*Lates* and *Psammoperca*), in fresh to brackish and estuarine waters of tropical Africa and in the marine waters of the Indo-Pacific coasts, and nine fossil species in the genera *Lates* and †*Eolates*, in freshwater to brackish habitats and marine waters of Afro-Arabia and Europe (see below).

Remark: The material of a proposed latid fish from the Maastrichtian and early Late Palaeocene of Bolivia was noted by Gayet (1991), and described by Gayet & Meunier (1998). None of the apomorphies at the familial or generic level is described for this perciform fish, and therefore I remain cautious of this determination and propose it be left in an *incertae sedis* position.

GENUS †*EOLATES* SORBINI, 1970

1828 – *Lates* Cuvier & Valenciennes, p. 88.
1970 – †*Eolates* Sorbini, p. 11.

Type species: †*Lates gracilis* (Agassiz, 1843).

Emended diagnosis: A polyphyletic genus and latid stem group, it unites latid species that are plesiomorphic when compared with *Lates* + *Psammoperca*: there are three epurals, no apophysis on the haemal spine of the preural vertebra 2 and five free and autogenous hypurals. Moreover, their predorsal formula (/0/0+0/II/I+I/; 0/0/0+II/I+I/) often varies from that of

Recent latids; they have more than three small spines on the posterior border of the cleithrum; one row of lateral line scales on the caudal fin (as in *Lates*); VC = 10/11+13/15(4); epineurals developed on the first six or seven vertebrae; D = VIII/IX+I-(9)10/12; gap between the dorsal fins reduced in size when compared with Recent species; A = II/III+7/8, C = I-8 : 7-I; stegural and uroneural present; caudal fin with posterior border rounded. A caudal spur is present on the first procurrent ventral ray of †*Eolates* (observed in †*E. gracilis*).

The three †*Eolates* species differ from each other in the combination of several characters. They all are Palaeogene Tethyan species.

†*EOLATES GRACILIS* (AGASSIZ, 1843)

1843 – †*Lates gracilis* Agassiz, p. 25, pl. 3.
1843 – †*Lates gibbus* Agassiz, p. 27, pl. 4.
1843 – †*Lates notaeus* Agassiz, p. 29, pl. 5.
1970 – †*Eolates gracilis* (Agassiz), Sorbini, p. 11.

Emended diagnosis: †*Eolates* smaller than 0.3 m standard length. A posterior pad develops on infraorbital 1; VC = 10+14(4) (both those characters are unique in the family); no parapophysis on the first five abdominal vertebrae; epineurals on the first seven vertebrae; D = VIII – I+10(9); A = III+8; maximal depth of the body about 35–45% of standard length; biggest dorsal spine about 18–25% of standard length; caudal peduncle deeper than long.

Occurrence: Monte Bolca (Italy), Lower Eocene (Ilerdian or Cuisian), marine habitat.

†*EOLATES MACRURUS* (AGASSIZ, 1843)

1843 – †*Lates macrurus* Agassiz, p. 29, pl. 6.
1975 – †*Eolates macrurus* (Agassiz), Sorbini, p. 33.

Emended diagnosis: †*Eolates* smaller than 0.3 m standard length, usually 11 dorsal rays; maximal depth of the body about 20–25% of standard length; caudal peduncle longer than deep (×1.5).

Occurrence: Paris Basin (France), Lower Eocene (Lutetian), marine habitat.

†*EOLATES AQUENSIS* (GAUDANT, 1977)

1977 – †*Lates aquensis* Gaudant, p. 206, pl. 1, fig. 2.

Emended diagnosis: †*Eolates* smaller than 0.15 m standard length; VC = 11+13/14(15); no parapophysis on the first seven abdominal vertebrae; D = VII – I+10/12; A = III+7/8; maximal depth of the body is about 28–34% of standard length; biggest dorsal spine about 26–30% of standard length; caudal peduncle as deep as long.

Occurrence: Aix-en-Provence (France), Upper Oligocene (Upper Stampian), lacustrine habitat.

Note on an unnamed taxon and on the characters not observable in fossils

Lates and *Psammoperca* species form a monophyletic group sharing two apomorphies: two epurals and the fusion of hypurals 3 and 4 to the centrum. Moreover, a modification of the posttemporal in relation to its connection with the swimbladder tunica externa exists in *Lates* and *Psammoperca* but cannot be observed in the genus †*Eolates*. This character is either a latid or a third *Lates* + *Psammoperca* apomorphy. Lastly, *Psammoperca* and *Lates* resemble each other and differ from †*Eolates* in having a well-developed apophysis on the haemal spine of preural vertebra 2.

GENUS *PSAMMOPERCA* RICHARDSON, 1844

1828 – *Labrax* Cuvier & Valenciennes.
1844 – *Psammoperca* Richardson.

Type species: Labrax waigiensis Cuvier & Valenciennes, 1828.

Emended diagnosis: Latid genus characterized by: a smooth horizontal limb of the preoperculum; single supramaxilla without any anterior process; dorsal and anal pterygiophores bipartite; no uroneural; and smooth posterior border of the cleithrum.

It differs from *Lates* but resembles †*Eolates* in having one row of lateral line scales on the caudal fin. It differs from *Lates* in having the nostrils widely separated on each side of the head and several supralamellar toothpatches only on the outer face of the first four gill arches and one tooth patch on the basihyal (both those characters are unknown in †*Eolates*). In addition, *Psammoperca* is the only latid showing the combination of the following characters: VC = 11+14(4); no parapophysis on the first 5–6 abdominal vertebrae; epineurals on the first 7–8 abdominal vertebrae; Predorsal = 0/0/0+II/I+I/ D = VII – I+12; A = III+8; C = (7/8)-I-8 : 7-I-8(7/8); caudal fin with posterior border rounded; caudal spur absent.

Occurrence: One Recent species in the coastal Indo-Pacific marine waters.

Situation of Hypopterus: This genus was put in synonymy with *Psammoperca* by Greenwood (1976), who considered the type species of the genus *Hypopterus* (*Psammoperca macroptera* Günther, 1859) as a synonym of *P. waigiensis.* Several authors (Allen & Swainston, 1988; Paxton *et al.*, 1989) consider this taxon to be a valid genus. The question is not discussed here, and no specimen attributed to *Hypopterus* has been examined.

GENUS *LATES* CUVIER & VALENCIENNES, 1828

1758 – *Perca* Linnaeus (*erratum*).
1828 – *Lates* Cuvier & Valenciennes, p. 88.

Type species: Perca nilotica (Linnaeus, 1758).

Emended diagnosis: The genus is monophyletic and characterized by the presence of a ridge on the articular process of the premaxilla; the bean-shaped exoccipital facets for the articulation with the first centrum. Moreover, *Lates* differs from both *Psammoperca* and †*Eolates* in having three rows of lateral line scales on the caudal fin.

It differs from *Psammoperca* in having the nostril of each side close together; no basihyal tooth patch and several supralamellar tooth patches on both the outer and the inner faces of the first four gill arches (these characters are unknown in †*Eolates*). It differs from *Psammoperca* and resembles †*Eolates* in having a supramaxilla with an anterior process; a horizontal limb of the preoperculum with three or four spines (sometimes more) large and flattened in most species, reduced in some others; the posterior border of the posttemporal serrated; normally three small spines on the cleithrum posterior border; and a uroneural present.

In addition, *Lates* is characterized by the following characters: VC = 11+14(4); no parapophysis on the first 5–7 abdominal vertebrae; epineurals present on the first 5–7 abdominal vertebrae; Predorsal = 0/0/0+II/I+I/ D = VII(VIII) – I+10/12(13); A = III+7/9; the first 4–5 dorsal pterygiophores, and the first 2–5 anal pterygiophores bear bipartite rays (the rest of the pterygiophores in both the dorsal and the anal fins are tripartite); C = (6/11)-8-I : I-7-(6/9); stegural and uroneural present; caudal fin with a posterior border either rounded, truncated or forked; caudal spur present.

Occurrence: Eight Recent species, of which seven live in freshwater to brackish habitat of tropical Africa and one is in the coastal marine and estuarine waters of the Indo-Pacific. Fossil *Lates* are numerous in African and European continental deposits and they belong either to one of the six fossil †*Lates* species (see below), or to *Lates niloticus*, or are left as *Lates* sp.

Remark: Two subgenera were defined; however, they are not shown to be monophyletic. *Lates* (*Lates*) with Recent and fossil species is probably a paraphyletic group. *Lates* (*Luciolates*) could be monophyletic (see Discussion).

SUBGENUS *LATES* (*LATES*) GREENWOOD, 1976

1758 – *Perca* Linnaeus (erratum).
1828 – *Lates* Cuvier & Valenciennes, p. 88.
1976 – *Lates* (*Lates*) Greenwood, p. 77.

Type species: Perca nilotica (Linnaeus, 1758).

Emended diagnosis: The monophyly of the subgenus is poorly supported. It may be the *Lates* stem group. *Lates* (*Lates*) species have a well-developed pleurosphenoid pedicle; the posterior border of the lateral ethmoid between the parasphenoid and the frontal is almost vertical; no noticeable elongation of the ethmovomerian region (about 20% or less of the neurocranial length).

Occurrence: Four Recent species: *L. niloticus* (Linnaeus (1758), in the northern and western regions of tropical Africa and in lakes Chad, Albert (= Mobutu) and Turkana (introduced in lakes Victoria and Kioga); *L. macrophthalmus*, endemic to lake Albert; *L. longispinis* endemic to lake Turkana; and *L. calcarifer* (Bloch, 1790), living in coastal marine Indo-Pacific and Eastern Pacific waters [sometimes in estuarine habitats (Weber & Beaufort, 1929)].

SUBGENUS *LATES* (*LUCIOLATES*) GREENWOOD, 1976

1914 – *Luciolates* Boulenger (erratum).
1976 – *Lates* (*Luciolates*) Greenwood, p. 78.

Type species: Luciolates stappersi (Boulenger, 1914).

Emended diagnosis: The monophyly of *Lates* (*Luciolates*) is probable. They present an elongated ethmovomerian region (more than 20% of the neurocranial length); the posterior border of the lateral ethmoid slopes backward from the parasphenoid to the frontal in a sharp angle; the parasphenoid is angled behind the level of the orbit; and the pleurosphenoid pedicle is little or not at all developed.

Occurrence: Four Recent species, all of which, and only these four species of the genus, are endemic to Lake Tanganyika: *L. angustifrons* Boulenger, 1906; *L. microlepis* Boulenger, 1898; *L. mariae* Steindachner, 1909; *L. stappersi* Boulenger, 1914.

Six fossil species are attributed to genus *Lates*. †*Lates bispinosus* [Gaudant & Sen, 1979; Neogene, Altinova (Turkey)] is known by a single specimen missing both its anteriormost and posteriormost parts. The specimen has a standard length of at least 0.5 m; formulae: VC = 11+?, D = VII – I+10, A = II+7(?); no parapophysis on the first seven abdominal vertebrae; epineurals on the first six vertebrae. †*L. partshii* [Heckel, 1856; Middle Miocene from Breitenbrun (Vienna Basin, Austria)] shows enough characteristics to be recognized as a *Lates* with two epurals and three small spines on the posterior border of the cleithrum. By contrast, the four other species do not show enough diagnostic characteristics to be referred to either *Lates*, or any other latid genus: †*L. macropterus* (Bassani, 1889; Oligocene of Chiavon, Italy) is very badly preserved (Sorbini, 1975); †*L. gregarius* (Bannikov, 1992; Upper Miocene of Northern Moldavia) has the latid common predorsal formula (0/0/0+II/I+I/); †*L. croaticus* (Kramberger, 1902; Miocene of Croatia); †*L. karungae* (Greenwood, 1951; Miocene, Palaeo-lake Victoria, Kenya) is only known by its vertebrae, similar to those of *L. niloticus* or *L. calcarifer*, except for a posterior concavity at the base of the anterior facet of the first vertebra, and the third vertebra, the centrum of which is as long as wide and the facet for the articulation of the rib as deep as long.

Remark: L. albertianus (Recent, Lake Albert) and †*L. maliensis* (Holocene, Mali) are synonyms of *L. niloticus*.

COMPARATIVE ANATOMY OF LATID FISHES

Among the latid species, the Recent species from Lake Tanganyika are elongate in shape compared with the others. The general elongation of the body is more or less apparent depending on the species. The elongation of the neurocranium in these species is correlated with that of the body, and the increased gracility of the bones and their ornamentation is less apparent.

NEUROCRANIUM

Greenwood (1976) noted there are two different types of latid fish according to the development of the neurocranium. *Psammoperca waigiensis*, *Lates niloticus*, *L. calcarifer*, *L. longispinis* and *L. macrophthalmus* have a wide, strongly ossified neurocranium, whereas the Tanganyikan species show a narrowing of the whole neurocranium in dorsal view along a gradient from *L. angustifrons* (the less modified species when compared with *L. niloticus*) – *L. microlepis* – *L. mariae* – *L. stappersi*. Among the former group, *L. macrophthalmus*, *L. longispinis* (Greenwood, 1976) and *Psammoperca waigiensis* have a narrower anterior part of the neurocranium (in dorsal view) compared with their large braincase. *L. longispinis* and *L. macrophthalmus* have a larger orbit. The narrowing of the neurocranium, the elongation of the ethmovomerian region (Table 1, ratio d/a), the reduction of the pleurosphenoid region (Table 1, ratio e/a), the increased expansion of the supraoccipital between the frontals (Table 1, ratio b/a compared with c/a), and the gracility of the bones (the lateral ethmoid projections and the crests, among others, are thinner) are correlated. There are merely slight differences between the dimensions of the neurocranium of *Lates niloticus* and *L. calcarifer*, when comparing specimens of equal sizes (Table 1). Greenwood (1976) noticed that a more forward position of the orbit in young *L. calcarifer* compared with equal-sized *L. niloticus* disappeared when comparing larger specimens of both species [see

Table 1. Variation in the dimensions of the neurocrania in Recent *Lates* species

Specimens/measures	a (mm)	b/a	c/a	(b + c)/a	d/a	e/a	f/a	g/a
L. niloticus MG 205	114	57	53	110	18	52	6	37
L. niloticus MG 206	96	50	60	110	18	51	5	41
L. niloticus MG 207	405	61	52	113	18	55	6	34
L. niloticus NHM 28.228 [4]	75.9	54	>54	110 (?)	19	36	4	48
L. niloticus NHM 28.228 [zoo]	122.9	48	60	108	19	38	5	53
L. calcarifer MG 26	38	55	53	108	19	47	5	20
L. calcarifer NHM 28.228 [1873-1-21:2]	102.7	56	53 (?)	109 (?)	15	36	4	50
L. calcarifer NHM 28.228 [1985-11-14:1]	129.4	54	54 (?)	108 (?)	14	37	4	55
L. angustifrons NHM 28.228 [1955-12-20:17222]	118.9	54	>54	109 (?)	23	33	5	42
L. stappersi NHM 28.228 [1975-4-23:1]	103.7	43	57	110	28	26	2	32

(a) Distance from the front of the vomer to the back of the basioccipital.

(b) Distance from the front of the vomer to the front of the supraoccipital.

(c) Length of the supraoccipital crest dorsal border.

(d) Distance from the vomer anteriormost level to the orbital anteriormost level.

(e) Distance from the posteriormost level of the otic commissure anterior border to the basioccipital posteriormost level.

(f) Minimal width of the otic commissure in front of the trigemino-facialis chamber.

(g) Distance from the anteriormost level of the orbital posterior border to the posteriormost level of the basioccipital.
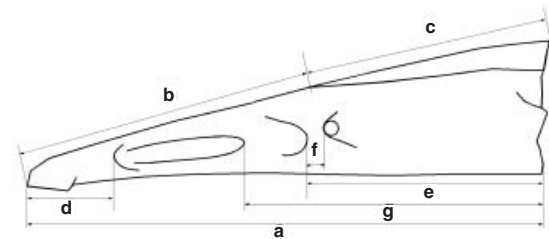

Rates are given in per cent.

also Table 1 (g/a)]. †*Eolates gracilis*, †*E. aquensis* (poorly preserved) and †*Lates bispinosus* (only the postorbital part of its neurocranium is known) show the same proportions as *L. niloticus*. Intraspecific variations in the neurocranium shape do exist: the skull of one *L. niloticus* from the London Zoo Aquarium shows a massive skeleton, particularly the crests and processes, which are much wider and higher than in any wild individual. More generally, in larger individuals the snout is bulkier, the neurocranium is shallower and the orbit is relatively smaller in diameter than in smaller individuals.

The ethmovomerine region is at least 20% of the neurocranial length (Table 1, ratio d/a). Greenwood (1976) considered this strong development of the ethmovomerine region one of the characteristics strengthening his concept of the family Centropomidae (i.e. Latidae + Centropomidae). Its development is similar in *Psammoperca*, *Lates niloticus*, *L. macrophthalmus* and *L. longispinis*; the snout of *L. calcarifer* is a little shorter. In comparison with the former species, the snout in the Tanganyikan species is elongated (Fig. 2A–F; Table 1, ratio d/a). Moreover the general narrowing of the skull described before, the lengthening of the ethmovomerine region in the Tanganyikan species is correlated with weakly demarcated articular facets. Greenwood (1976) considered

this to be a strong argument for the monophyly of the Tanganyikan group uniting *Lates* (*Luciolates*) species.

The lateral ethmoid (Fig. 2) shows three articular facets: the antero- and posteroventral facets, respectively, articulate with the anterior and posterior dorsal facets of the palatine; the lateral facet on the tip of the lateral projection articulates with the first infraorbital (Greenwood, 1976). This corresponds to the general pattern observed in perciforms. In Tanganyikan species, the posterior border of the lateral ethmoid slopes backward from the parasphenoid to the frontal in a sharp angle (Fig. 2D–F), whereas in other *Lates* species, *Psammoperca* (Greenwood, 1976) and †*Eolates*, the posterior border from the parasphenoid to the frontal is almost vertical (e.g. *Lates calcarifer*, Fig. 2B). The orbital part of the lateral ethmoid always inserts on the ventral face of the frontal, and thus those variations are correlated with the general elongation of the ethmovomerine region. Likewise, the narrowing of the lateral ethmoid (particularly of the lateral projections) and the poorly differentiated limits of the facet are correlated with the decreasing ossification of the neurocranium. Consequently, the lateral ethmoid is narrower and the lateral projections are more reduced in Tanganyikan species. Moreover, there are some variations in the lateral ethmoid among individuals: the foramen for nerve I opens more or less anterodorsally and lat-
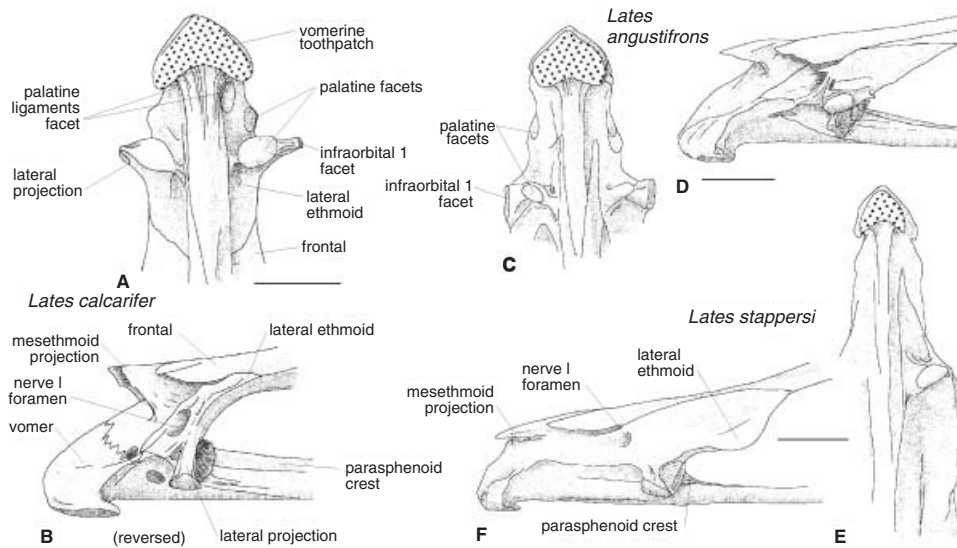
Figure 2. Ethmovomerine region in some Recent *Lates* species: A, B, *L. calcarifer*; C, D, *L. angustifrons*; E, F, *L. stappersi*; in, A, C, E, ventral, and, B, D, F, left lateral views. Scale bars = 10 mm.
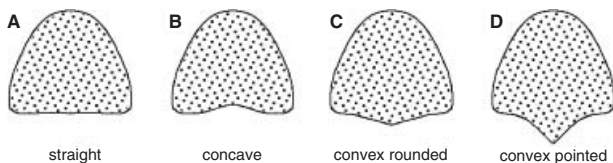
Figure 3. The different types of the vomerine tooth patch according to Van Neer (1987): A, type 1; B, type 2; C, type 3; D, type 4.

erally (as observed in *Lates niloticus* by Van Neer & Gayet, 1988); the shape, the size and the direction of the facets vary (the ventro-posterior facet, which shows the greatest variation, is dramatically reduced in larger individuals); the lateral ethmoid is more or less flattened (the whole orbital region is more flattened in large individuals); the lateral projection makes a slope or an angle with the body of the bone. In larger *L. niloticus*, the lateral ethmoid ventrally extends posteriorly on the parasphenoid.

The vomer (Figs 2, 3) of *Psammoperca* is smaller and its tooth patch projects ventrally below the level of the parasphenoid. It is narrow in Tanganyikan species. In other *Lates* species, the vomer is stockier and bulkier and the tooth patch barely projects below the level of the parasphenoid. In all latid fish, the tooth patch is perfectly fused with the body of the vomer. Van Neer (1987) defined four different types of tooth patch outlines in *Lates niloticus* (Fig. 3A–D). He noted that type 3 is rare in Recent *L. niloticus* (usually showing type 1) and common in the Quaternary Malian *L. niloticus*, probably due to interpopulation

variation but also correlated with the individual's growth. In *L. niloticus*, the tooth patch can be very reduced (Gayet, 1983). In the Tanganyikan species (Fig. 2C–F), *L. calcarifer* (Fig. 2A, B) and other species except *L. niloticus* the tooth patch belongs to type 2. The vomerian teeth are numerous, villiform and undifferentiated, except in *Lates stappersi*, the teeth of which are caniniform and variable in size according to their position on the patch.

The mesethmoid (Figs 2, 4) bears projections in both Recent and fossil latids. They project anteriorly, not parallel but with a sharp angle between them (Fig. 4A–G). However, they show some interspecific differences: less elongated in *Lates mariae* and *L. stappersi* (Fig. 4C, D); they can be horizontal as in *L. calcarifer* (Fig. 2B) and *L. niloticus*, or directed slightly downwards (Fig. 2D, F). In *Psammoperca* (Fig. 4G), they are very thin and directed more laterally than in other latids. There is an attachment surface for the upper jaw ligaments on the tip of each projection. According to the individuals, it varies in shape from concave and oval to flat and polygonal, and it can be directed ventrally or anteriorly, changing the outline of the projection tip from pointed to truncated.

The pleurosphenoid pedicle (Figs 5–9) is a bony structure formed by the parasphenoid, the pleurosphenoid and the prootic in place of the lateral ligament that joins the prootic and the pleurosphenoid and covers the internal jugular (Fig. 5A–D). It develops only in *Lates* (*Lates*) species and in *L. angustifrons* but not in other *L.* (*Luciolates*) and *Psammoperca*. In agreement with the observations of Greenwood (1976; he described the state of the pedicle in each species
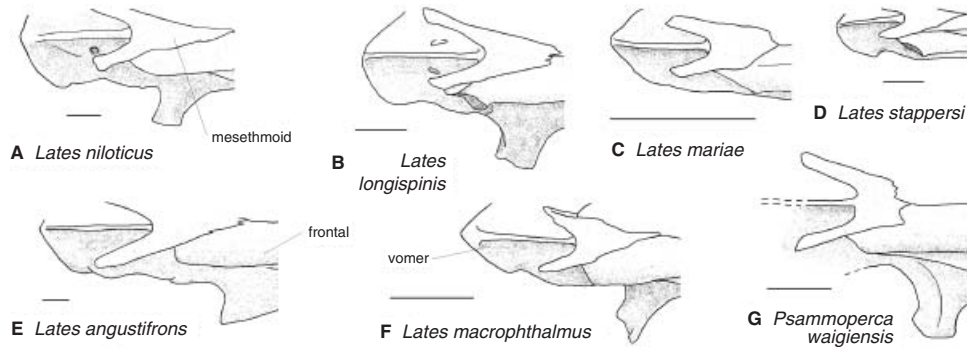
Figure 4. Variations in the outline of the mesethmoid projections in Recent latids, in dorsal view: A, *Lates niloticus* (NHM 28.228 [4]); B, *L. longispinis* (NHM 28.228); C, *L. mariae* (NHM [1936-6-15: 1672-86]); D, *L. stappersi* (NHM 28.228 [1936-6-15: 1705-6]); E, *L. angustifrons* (NHM 28.228 [1955-12-20: 1722]); F, *L. macrophthalmus* (NHM unnumbered); G, *Psammoperca waigiensis* (NHM 31.160 [1888-11-6-6]). Scale bars = 3 mm.
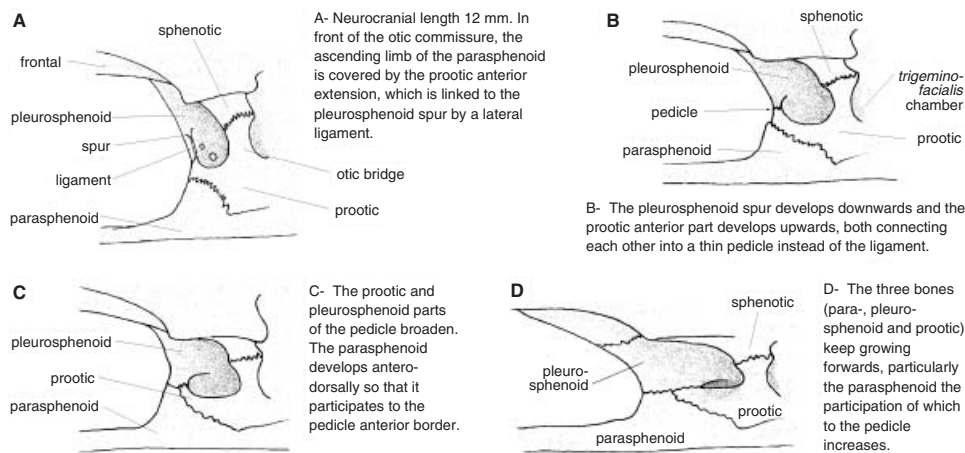

Figure 5. Diagram showing the pleurosphenoid pedicle development in *Lates niloticus*, after Greenwood's (1976) figures and remarks, and personal observations.
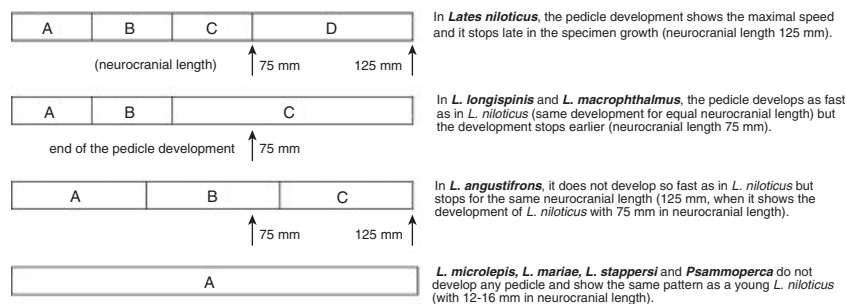

Figure 6. Schematic drawings of the pleurosphenoid pedicle development in Recent latids, after Greenwood's (1976) figures and remarks, and personal observations (see Fig. 5 for the definition of states A, B, C and D).

and the ontogenetic process of its development), the main developmental stages in *Lates niloticus* (Figs 5A–D, 6, 7, 8A) and those reached in the affected latid species are described and figured (Figs 6, 8B–H). However, he assumed that the low ridge observed in a

44-mm *L. microlepis* neurocranium, in a 104-mm *L. mariae* neurocranium, and its absence in *L. stappersi* corresponded to a very early phase of the pedicle developmental sequence. I found no argument to support this. The pedicle development appears to be
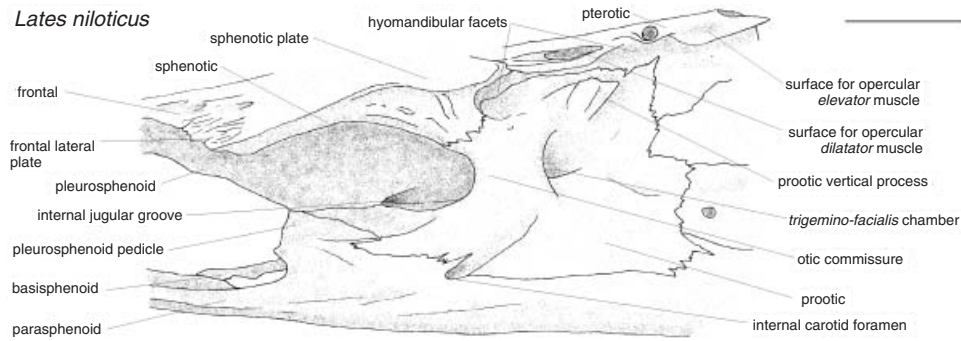
Figure 7. Pleurosphenoid region of *Lates niloticus* (MG 205), in left lateral view. Scale bar = 10 mm.
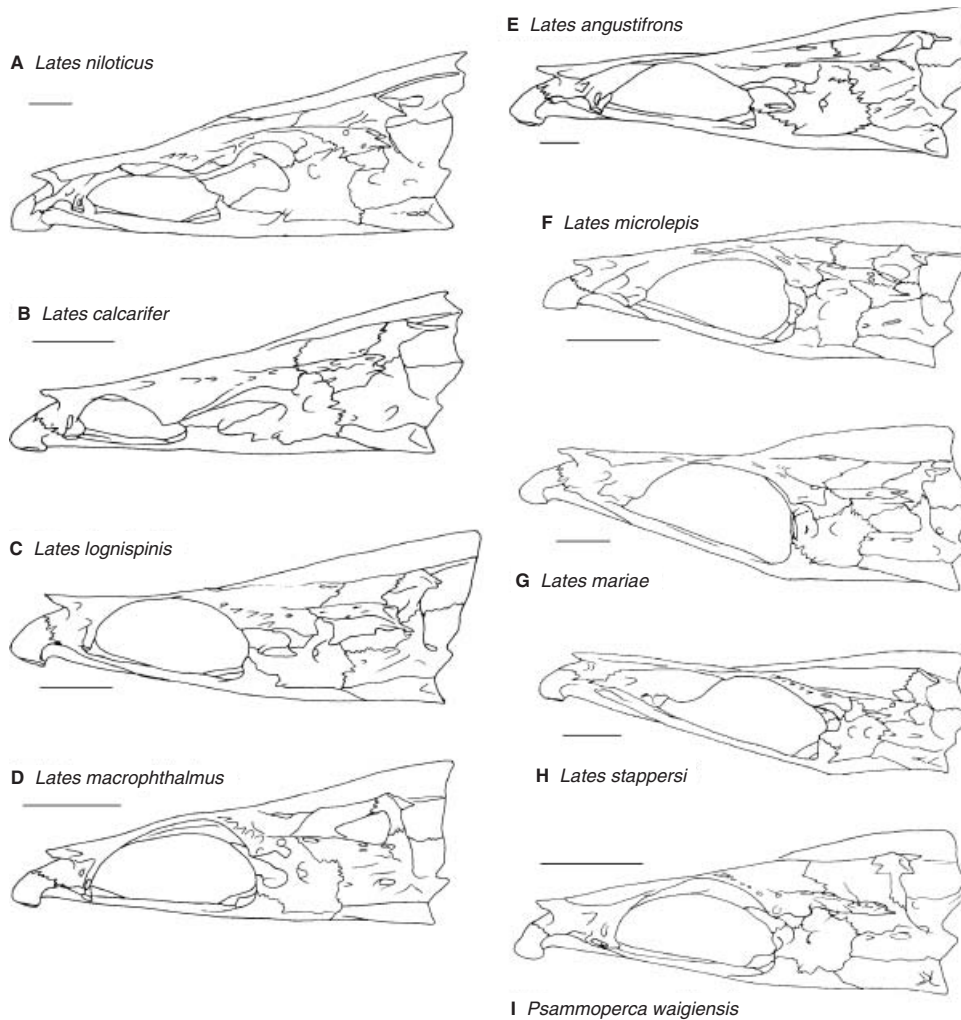
Figure 8. Outlines of the neurocrania of Recent latids, in left lateral view: A, *Lates niloticus*; B, *L. calcarifer*; C, *L. longispinis*; D, *L. macrophthalmus*; E, *L. angustifrons*; F, *L. microlepis*; G, *L. mariae*; H, *L. stappersi*; I, *Psammoperca waigiensis*; modified from Greenwood (1976). Scale bars = 10 mm.

correlated with the broadening of the otic commissure and the lateral extension of the frontal plate above the posterior part of the orbit. This is observed in †*Lates bispinosus* (Fig. 9), but the bones are crushed or cov-

ered in this area, so that the probable presence of the pedicle cannot be ascertained. †*Eolates gracilis* specimens do not show any bone in the area; the pedicle is absent.
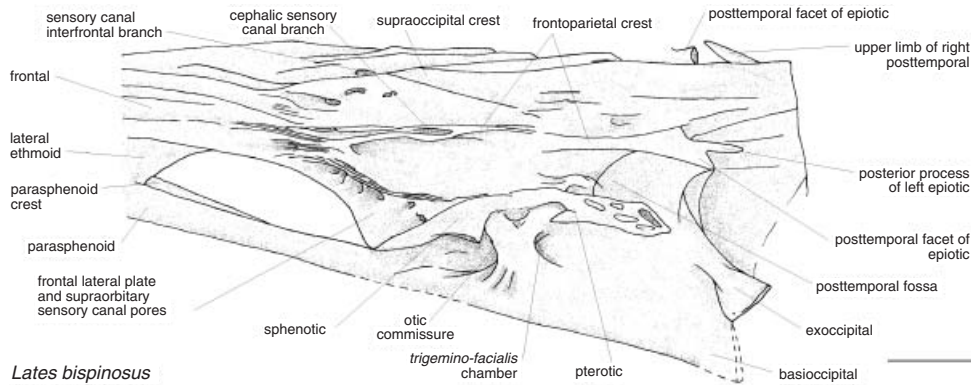
**Figure 9.** Dorsicranium of †*Lates bispinosus* (holotype), in dorso-lateral view. Scale bar = 5 mm.

The sphenotic and the prootic share the anterior facet of the articulation of the hyomandibula; the sphenotic and the pterotic share a longitudinal surface for the opercular dilatator muscle, followed by the pterotic oval surface for the opercular levator muscle (Fig. 7). This pattern is common to perciform fish. However, in some the facets are fused whereas they are always separate in latid fish. The sphenotic lateral plate develops from the anterior facet to the otic commissure level, at which point it is narrower in Tanganyikan species than in other latids (as is the whole neurocranium). The prootic part of the otic commissure anteriorly borders the trigemino-facialis chamber. The chamber is wider in larger individuals, particularly in species with a pleurosphenoid pedicle. A vertical process of the prootic is present, posterior to the hyomandibular anterior facet. On the sphenotic, the otic commissure is ornamented with small pores aligned parallel to the sphenotic anterior border, whereas it is smooth on the prootic.

The pleurosphenoid and the basisphenoid (Figs 7–9) do not show clear differences among Recent latid species and they are not preserved in the examined fossils.

The parasphenoid (Figs 8, 9) ventral border is either straight [*Lates niloticus*, *L. calcarifer*, *L. macrophthalmus*, †*Eolates gracilis*, †*E. aquensis*, †*Lates bispinosus* (Figs 8A, B, D, 9)] or slightly curved [*Lates angustifrons*, *L. longispinis*, *Psammoperca waigiensis* (Fig. 8C, E, I)], to strongly bent behind the level of the orbit [*Lates microlepis*, *L. stappersi*, *L. mariae* (Fig. 8F–H)]. The 'different stages' of angling recognized by Greenwood (1976) are doubtful and probably a result of the method of drawing (the horizontal level is given by the parasphenoid either in its orbital part or in its braincase part). In transverse section, the parasphenoid ventral face is either flat or slightly concave in the orbital region and convex in the braincase region. A median crest develops on the parasphenoid between the orbits. It starts with a maximal height

between the lateral ethmoids and decreases posteriorly (Figs 2B, D, F, 8A–H, 9) and also depending on the size of the individuals. In larger *L. niloticus* and in *L. macrophthalmus*, the crest is a low pad. In *L. niloticus*, Van Neer & Gayet (1988) observed strong variations in the development of the parasphenoid interdigitating suture with the basioccipital and the vomer. The interdigitations are shorter in larger individuals.

Among fossil latids, the temporal region and the dorsicranium are well known in †*Lates bispinosus* (Fig. 9). The posttemporal fossa is opened as in Recent latids, in which, according to Greenwood (1976), the fossa is deep (except *Lates stappersi*) and closed off by a tough membrane. The supraoccipital (Figs 8–10) separates the parietals and inserts between the frontals, reaching far anteriorly to the level of the median sensory opening (Greenwood, 1976). More precisely, it borders from one-quarter to half the frontal length: around one-quarter in *Lates calcarifer*, *L. macrophthalmus* and *L. mariae* (Figs 8B, D, G, 10B, D, G), one-third in *L. longispinis* and *L. microlepis* (Figs 8C, F, 10C, F), between one-third and a half in *L. angustifrons* (Figs 8E, 10E), and a half in *L. stappersi* and *Psammoperca* (Fig. 8H, I). These observations, made on few individuals (sometimes a single one), have to be interpreted according to the observations made in *L. niloticus*. In this species, the larger the individual, the shorter is the extension of the supraoccipital between the frontals (from one-third of the frontal length in small individuals to one-quarter in larger ones). Thus I do not follow Greenwood's (1976) assumption that in *Lates angustifrons*, *L. mariae* and *L. microlepis* the weakness of the supraoccipital extension is correlated with the ethmoid lengthening. In fact, the development of the pleurosphenoid pedicle may imply that it is the development of the frontal which limits the supraoccipital to the posterior region. Additionally, the elongation of the ethmovomerine region may involve the anterior development of the
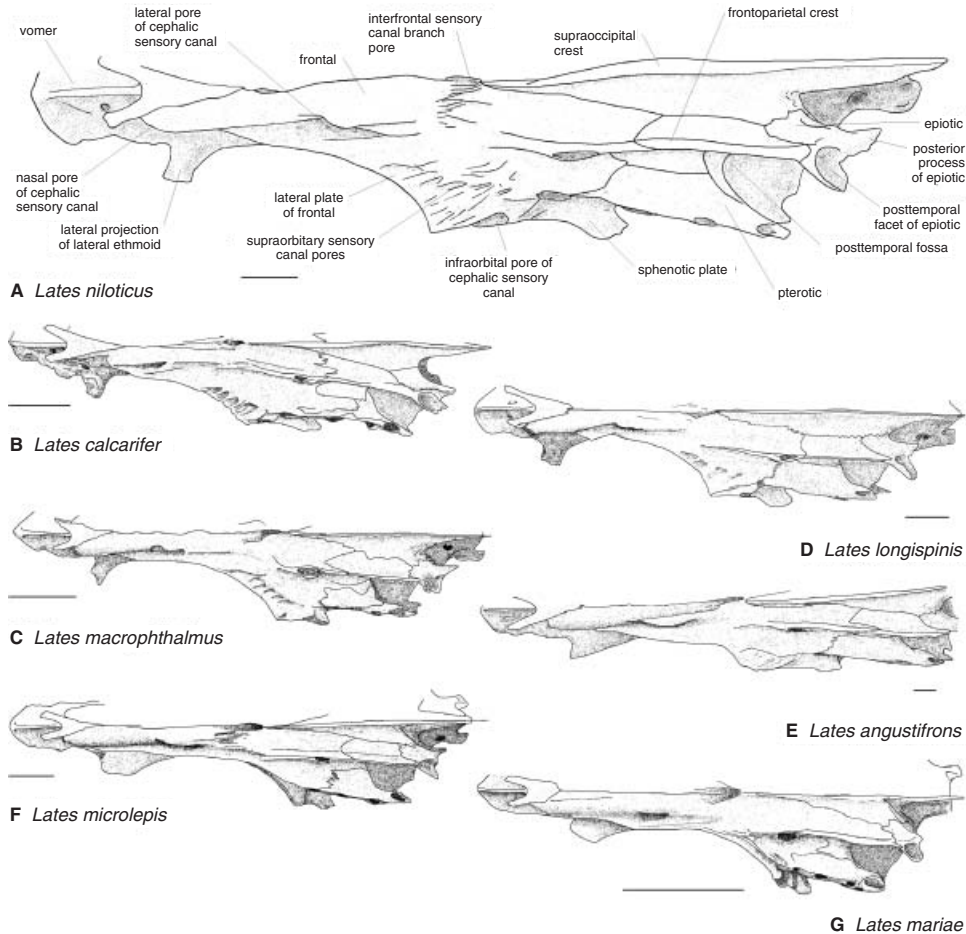
Figure 10. Dorsicranium of Recent latids, in dorsal view: A, *Lates niloticus* (NHM 28.228 [4]); B, *L. calcarifer* (MG 26); C, *L. longispinis* (NHM 28.228); D, *L. macrophthalmus* (NHM unnumbered); E, *L. angustifrons* (NHM 28.228 [1955-12-20: 1722]); F, *L. microlepis* (NHM 28.228 [1900-12-1]); G, *L. mariae* (NHM [1936-6-15: 1672–86]); H, *L. stappersi* (NHM 28.228 [1936-6-15: 1705–6]). Scale bars = 5 mm.

frontals and possibly of the supraoccipital. The supraoccipital limit observed in †*L. bispinosus* is similar to *L. niloticus*; that indicates the presence of a pleurosphenoid pedicle in the fossil species. A saggital crest develops along the whole supraoccipital length (see below). In *L. stappersi*, the supraoccipital lateral flanges are confined anteriorly whereas they develop all along the crest in other latids.

The frontal lateral plate lies in front of the sphenotic (Figs 7–11). Its development beyond the orbit seems to be correlated with that of the pleurosphenoid pedicle: it is absent in *Psammoperca* (Fig. 11D), reduced in *L. mariae* (Figs 8G, 10G) and *L. stappersi* (Fig. 8H), little developed in *L. macrophthalmus* (Figs 8D, 10D) and *L. longispinis* (Figs 8C, 10C, 11C), and well developed in *L. niloticus* (Figs 7, 8A, 10A, 11B), *L. calcarifer* (Figs 8B, 10B) and *L. angustifrons* (Figs 8E, 10E, 11A), particularly in larger individuals. Concerning the other latid species, it is well developed

in †*L. bispinosus* (Fig. 9) and reduced in †*E. gracilis*; these indicate, respectively, the presence and the absence of a pleurosphenoid bridge. The supraorbital sensory canal openings lie on the dorsal face of the plate (Fig. 11A–C), or in the edge of the bone when the plate is reduced or absent (Fig. 11D).

The latid epiotic (Figs 9, 10) has a well-developed facet for the articulation of the upper limb of the posttemporal that projects latero-posteriorly, a strong horizontal posterior process that projects medial to the articular facet, and the anterior border inserts between the supraoccipital and the parietal. The posterior process varies in length and shape within a single species and sometimes between both left and right epiotics of a single individual (bifurcated in some individuals). In addition, the observation of several specimens of *Lates niloticus* and *L. calcarifer* supports a probable size-correlated variation, and species with a narrow
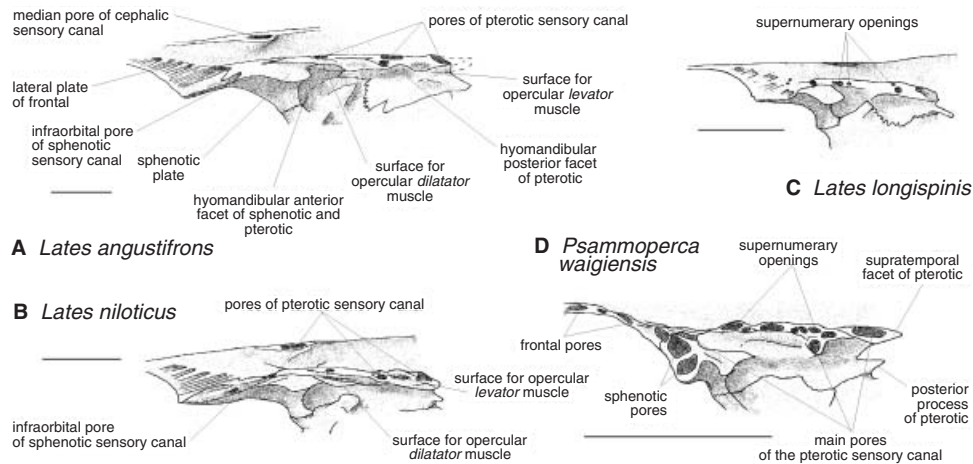
Figure 11. Variations in the cephalic lateral line openings in the pterotic region in some Recent latids, in left lateral view: A, *Lates angustifrons* (NHM 28.228 [1955-12-20: 1722]); B, *L. niloticus* (NHM 28.228 [4]); C, *L. longispinis* (NHM 28.228); D, *Psammoperca waigiensis* (NHM 31.160 [1888-11-6: 6]). Scale bars = 10 mm.
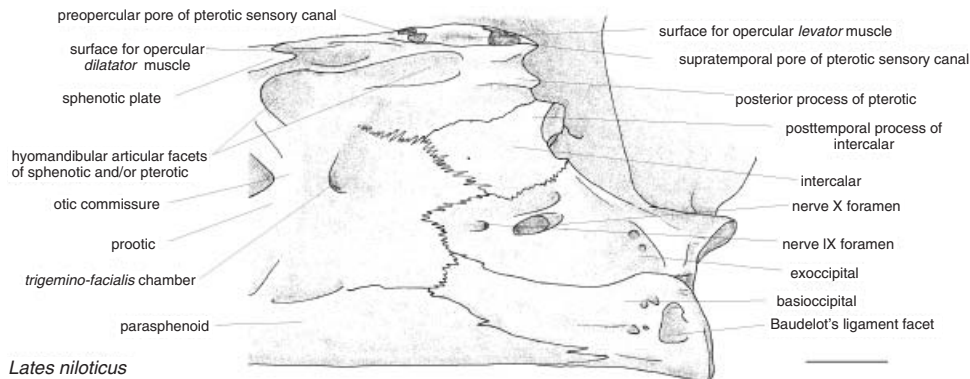
Figure 12. Posterior part of the neurocranium of *Lates niloticus* (MG 205), in left lateral view. Scale bar = 5 mm.

neurocranium have a thinner posterior process and a smaller articular facet.

Both Recent and fossil latids bear fronto-parietal crests lateral to the supraoccipital crest (Figs 8–10; in †*Eolates aquensis* specimens only the saggital zone is suitable for observations). The height of the crests is inversely correlated with the neurocranial width. Van Neer & Gayet (1988) and Greenwood (1976), respectively, observed this correlation within a species (*Lates niloticus*) and among the Tanganyikan species. The crests seem to develop more in smaller individuals.

On the pterotic (Figs 9, 12), the oval-shaped surface for the opercular levator muscle is placed between the level of the two posterior openings of the cephalic sensory canal. The pointed posterior process develops under the supratemporal posterior facet of the pterotic. In some specimens, it develops back toward the posttemporal facet of the intercalar but in other specimens it does not even reach the anterior part of

the intercalar. This is also the case for the posttemporal facet of the pterotic. The dimensions and directions of the processes and facets are variable and do not correlate with the neurocranial dimensions.

The cephalic sensory canal (Figs 9–11) runs in a bony tube with several openings. The main openings are constant in latid fish. On the nasal, the canal runs in a tube with an anterior opening for the sensory branch to the first infraorbital, and a posterior one toward the frontal. On the frontal, the lateral opening is placed at the level of the posterior tip of the lateral ethmoid [unknown in †*Eolates*]; posteriorly, the interfrontal branch opens between the frontals in front of the anterior tip of the supraoccipital (e.g. in †*Lates bispinosus*, Fig. 9), and on the lateral side of the frontal, the pore for the sensory branch to both the sphenotic and the pterotic is placed at the intersection of the sphenotic, pterotic and frontal. On the dermosphenotic, the canal runs in a tube with an opening for the

branch to the infraorbital series. On the pterotic itself, two main pores allow the canal to reach the preoperculum (posterolateral opening) and the supratemporal (posterodorsal opening). The pores are smaller relative to the size of the skull in larger individuals. There are supernumerary openings on the pterotic; their count varies depending on the species and the individuals and is largest in *Psammoperca* (Fig. 11D).

The occipital region is poorly known in fossils. The walls of the braincase are flat in Recent latids other than *Psammoperca* (Fig. 13A), *Lates macrophthalmus*, *L. microlepis*, and larger *L. mariae* (which had the walls inflated in a specimen with a 25-mm-long neurocranium). In posterior view, the braincase of these species shows a basal inflation. Therefore, the inflation is observed in species with a curved parasphenoid, except in the case of small *L. stappersi* and large *L. mariae* (which have a curved parasphenoid but flat braincase walls).

The intercalar (Figs 9, 12) has the posttemporal articular facet placed on a bulky knob.

The exoccipitals (Figs 12, 13) articulate with the first centrum by facets that join above the basioccipital facet. In *Lates* (Fig. 13B), the facets are bean-shaped and participate in forming the base and part of the walls of the foramen magnum, whereas in *Psammoperca* (Fig. 13A), they are teardrop-shaped and only form the base of the foramen magnum. Moreover, as in all the other percoids examined, the large foramen for nerve X (vagus) and the small and anteriormost foramen for nerve IX (glossopharyngial) are broadly separated.

The basioccipital (Fig. 12) usually bears relatively smaller surfaces for the Baudelot's ligament in larger individuals. They are pointed or rounded in shape, and
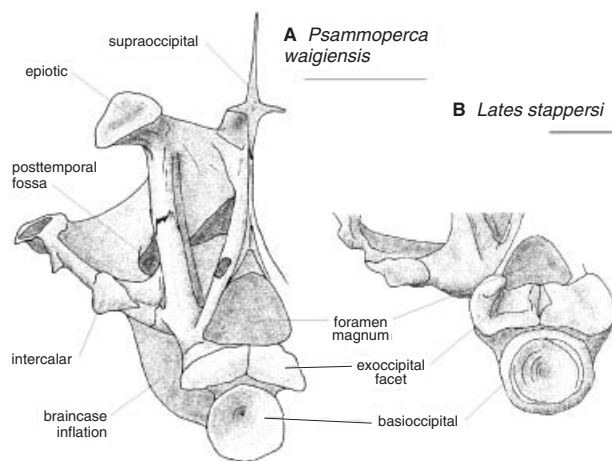

Figure 13. Posterior view of the neurocranium, A, *Psammoperca waigiensis* (NHM 31.160 [1888-11-6: 6]); B, *Lates stappersi* (NHM 28.228 [1936-6-15: 1706]). Scale bars = 5 mm.

flatter in Tanganyikan species. Anterior to these are one or two depressions of variable size and more or less ornamented with small pores. As for the vomer, the suture of the basioccipital with the parasphenoid has interdigitations that seem shorter in larger individuals, as described by Van Neer & Gayet (1988), in *L. niloticus*. The median ventral groove on the basioccipital never reaches the parasphenoid, in *L. niloticus* (Van Neer & Gayet, 1988), nor in any other Recent latid (unknown in fossil species).

SPLANCHNOCRANIUM

The general outline of the splanchnocranium is elongated depending on the species. As for the neurocranium, it is more or less elongated in *Lates* (*Luciolates*). In *Psammoperca*, the bones are particularly shallow when compared with *Lates* (e.g. *L. niloticus*); this characteristic is most apparent in the lower jaw. The splanchnocranium of †*Eolates gracilis* and †*E. aquensis* shows the same shape as *Lates niloticus*, and that of the single-known specimen of †*L. bispinosus* is largely crushed.

The depth of the bones of the infraorbital series decreases posteriorly (Fig. 14). In Recent latid species, the infraorbital sensory canal runs in a bony tube with five openings on infraorbital 1 (Greenwood, 1976), i.e. one anterior, one posterior shared with the second infraorbital bone, and three placed ventrally at the tip of short canals. On infraorbitals 2–5, the canal runs in a bony tube with pores located only between the infraorbitals in *Psammoperca*, and between the infraorbitals, plus one on infraorbital 3 in *Lates*. In †*Eolates gracilis*, there are three pores on infraorbital 1, one between infraorbitals 2 and 5, and two on infraorbitals 2 and 3. In *Lates niloticus*, *L. angustifrons*, *L. calcarifer*, *Psammoperca waigiensis* and †*Eolates gracilis*, the anterior part of infraorbital 3 is broad, and the following infraorbitals are reduced to the sensory canal bony tube. In †*E. gracilis*, a posterior pad develops on infraorbital 1, above infraorbital 2. In Recent latids (unknown in fossils), a subocular shelf develops from the dorsal border of infraorbital 3. It extends medially, anteriorly (along infraorbital 2) and posteriorly (along infraorbital 4). As in the whole cranium, the infraorbitals of the Tanganyikan species are antero-posteriorly elongated and narrower, and the subocular shelf reaches the maximum 'antero-posterior length/width' rate (see Greenwood, 1976, for details). Moreover, the dorsal border of infraorbital 1 extends posteriorly, correlated with the mesethmoid extension (these two bones are in contact along a great part of their length). The infraorbital ventral border is smooth in *L. stappersi* and *Psammoperca waigiensis*, whereas posteriorly directed serrations develop along the ventral border of certain infraorbit-
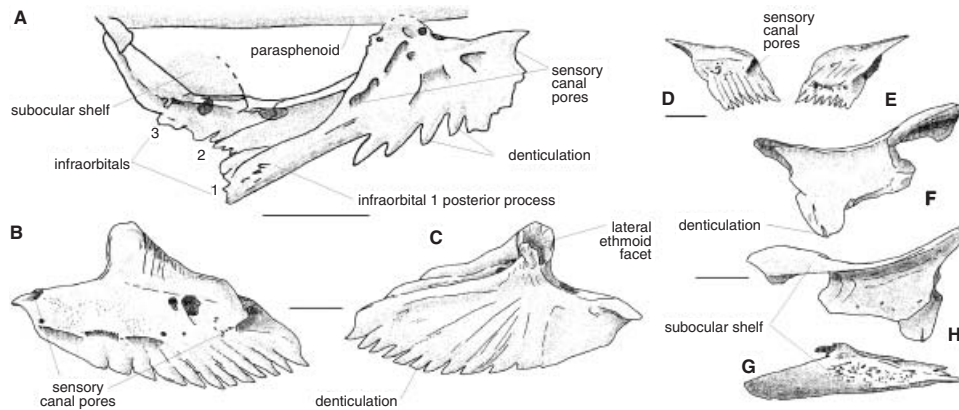
Figure 14. Infraorbital bones of †*Eolates* and *Lates*: A, †*Eolates gracilis* (from MNHN Bol 0267 and MCSNV IG 23.151), in lateral view; B–H, *Lates niloticus* (MG 205): B, C, first, and, D, E, second infraorbitals, in, respectively, lateral and medial views; F–H, third infraorbital in lateral, dorsal and medial views. Scale bars = 5 mm.
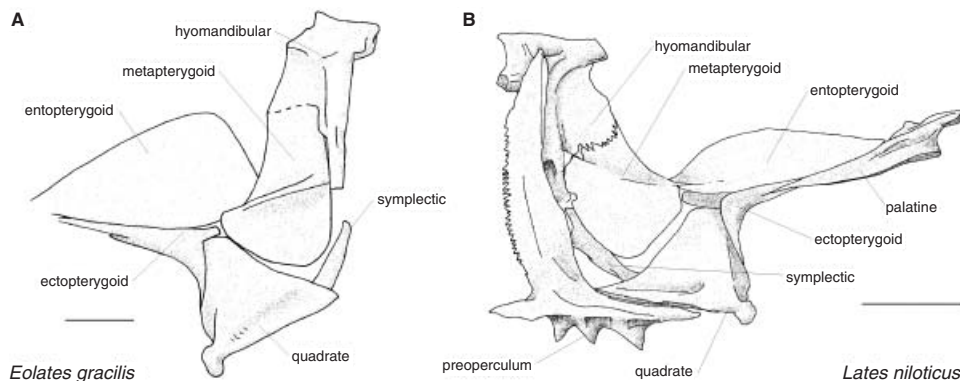
Figure 15. Hyopalatine arch of †*Eolates* and *Lates*, in lateral view: A, left hyopalatine arch of †*Eolates gracilis* (from MCSNV VI.N.62 and VI.N.65); B, right hyopalatine arch and preopercular bone of *Lates niloticus* (NHM 28.228 [4]). Scale bars: A = 5 mm, and B = 40 mm.

als in other latid species: infraorbitals 1 and 2 in *Lates calcarifer*; infraorbitals 1, 2 and the anterior part of 3 in *L. niloticus*, *L. angustifrons* and †*Eolates gracilis*. The number of small spines varies from eight to 11 in *L. niloticus* and †*Eolates gracilis* (Sorbini, 1975).

Among fossil latids, the only known hyopalatine arch is that of †*Eolates gracilis* (Fig. 15A); it is similar to *Lates niloticus* (Fig. 15B). Greenwood (1976) noted the similarities between the arch of his latines and his centropomines and stressed variations in their dimensions. The ectopterygoid, entopterygoid and palatine are thinner and the articular facets are smaller in the Tanganyikan species (particularly in *L. stappersi*) than in other latids. The hyopalatine arch shows the same lengthening and narrowing as the whole skull.

The symplectic groove is not demarcated by any notch on the quadrate dorsal border (Fig. 15). The shape of the antero-ventral border of the quadrate varies from straight to curved, and the articular

condyle is more or less flattened. Van Neer (1987) and Van Neer & Gayet (1988) noted such variations in both Recent and fossil *L. niloticus* (which usually shows a straight antero-ventral border). Moreover, they noted that the estimation of the variation in this characteristic is strongly related to the angle of observation.

The articulations of the bones of the pterygoid series are common to all latids (Figs 15–17A). Variations in the shape of the bones, caused by the elongation of the skull in certain species, are observed (Fig. 15A, B; Greenwood, 1976: figs 11, 12, 30). As described by Greenwood (1976), some pterygoid bones bear a villiform dentition developed on a surface which is more or less wide depending on the species. In fossil species, the presence of very small tooth sockets allows us to infer that a villiform dentition was present.

The entopterygoid (Fig. 15) is a wide oval toothless thin bone. Its articulation with the palatine is large and that with the metapterygoid is made through its posterior pointed tip.
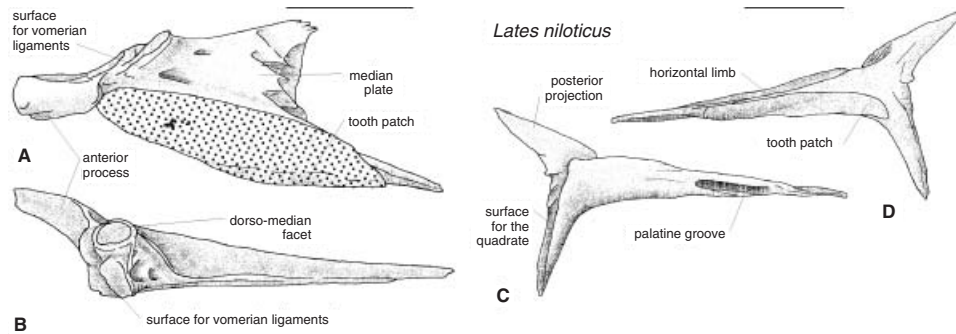
Figure 16. Right palatine and ectopterygoid of *Lates niloticus* (MG 205): A, B, palatine; C, D, ectopterygoid; in A, medioventral, B, D, medial, and, C, lateral views. Scale bars = 10 mm.
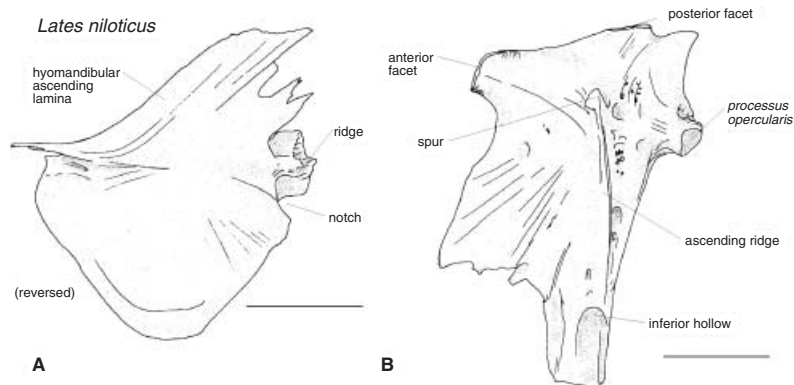
Figure 17. Left metapterygoid and hyomandibula of *Lates niloticus* (MG 206), in lateral view: A, metapterygoid; B, hyomandibula. Scale bars = 10 mm.

The palatine (Figs 15, 16A, B) has a median triangular plate along the anterior half of the alveolar process that articulates with the entopterygoid; an anterior strongly rectangular-shaped process [according to Greenwood (1976) there is a cartilaginous projection on its upper face in Recent species]; a ventral maxillary facet; a dorso-medial infraorbital 1 facet; an antero-dorsal lateral ethmoid facet; and a medioventral surface for vomerine ligaments. The posterior lateral ethmoid facet is weakly delimited and lies medial to the palatine plate where there is a generally wide and large oval tooth patch (narrower or absent in Tanganyikan species).

The ectopterygoid is trifid (Figs 15, 16C, D). The short vertical limb runs along the anterior edge of the quadrate. The long horizontal limb supports the entopterygoid and its anterior pointed tip articulates with the palatine. Those two limbs form a single unit, angled at almost 90°. The third, postero-dorsal, limb develops posteriorly from the angle of this unit; it separates the entopterygoid and the quadrate and extends ventrally on to the dorsal part of the quadrate medial face. As described by Greenwood (1976) in Recent species, an ovoid tooth plate (variable in size,

sometimes on both sides in a single individual) develops on the medial face of the horizontal limb and/or the upper part of the vertical limb.

The metapterygoid (Figs 15, 17A) articulates with the antero-ventral plate of the hyomandibula through an ascending lamina, which is wide in *Lates* (*Lates*), and narrow in Tanganyikan species (following the narrowing gradient of the whole cranium). The posterior pointed tip of the entopterygoid inserts in a thin latero-ventral groove of the metapterygoid. In most perciforms, an additional metapterygoid lamina exists. It develops dorsally, lateral to the ascending lamina, creating an interosseous space where the lateral part of the levator arcus palatini inserts (Johnson, 1980); it contacts the hyomandibula vertical ridge tightly. In latid fish, the metapterygoid lamina is absent. There is a thickening of the metapterygoid where the base of the lamina would be, and a strong notch just above on the metapterygoid posterior border (this notch is present in percoid fish with a lamina but not in other examined fish). In agreement with Greenwood (1976), the thickening and the notch are interpreted as relics of a metapterygoid lamina. None of the examined specimens shows a foramen instead of the notch

(Greenwood noted the presence of a notch or a foramen). Among fossil latids, the ridge is observable in †*L. bispinosus*, whereas the preservation is too poor in other fossils.

The latid hyomandibula (Figs 15, 17B) shows perciform characteristics: two well-separated facets for the articulation with the neurocranium (Greenwood, 1976); one opercular facet at the tip of the processus opercularis; on the lateral face of the bone one prominent spur on the upper tip of the vertical ridge along which the preoperculum lies; and an anterior flange connected with the ascending lamina of the metapterygoid through a zigzag suture. Among latid fish, the dimensions of the hyomandibula (particularly the anterior flange) vary according to the general proportions of the skull. The position of the hollow on the lower tip of the vertical ridge shows individual variation.

The fossil latid preoperculum (Figs 15B, 18) (known in †*Eolates aquensis*, †*E. gracilis*, †*Lates bispinosus* and *Lates* sp. from As-Sarrar and Negev) shows the latid characteristics described by Greenwood (1976): serration on the posterior border of the vertical limb (except its extremities); large flat triangular posterior spine at the angle of the two limbs; preopercular horizontal limb with three or four strong spines (Fig. 18A, B). The ventral border of the posterior spine is horizontal and sometimes the spine is bifurcated. The spines of the horizontal limb are directed ventrally, the two anterior spines anteroventrally and the posterior one(s) posteroventrally (Fig. 18A, B). The preopercular sensory canal runs in a tube on the vertical limb and in a gutter covered by several bridges on the horizontal one. There are intra- and interspecific variations in the preopercular ornamentation. In *Psammoperca*, the horizontal limb has a smooth ventral border (Greenwood, 1976: fig. 30). In *Lates stappersi*,

the serration of the vertical limb and the spines of the horizontal limb are reduced (Greenwood, 1976). In larger *L. niloticus*, the serration is limited to the central part of the posterior edge (Sorbini, 1973; Greenwood, 1976). Variations in the count of the horizontal limb spines were studied by Greenwood (1976). The ratio of 'number of individuals with four spines compared to number of individuals with three spines' varies among *Lates* species: 0/18 in *L. calcarifer* and *L. angustifrons*; 24/31 in *L. niloticus*; 16/20 in *L. mariae*; 25/27 in *L. microlepis*; 3/6 in *L. longispinis*; 4/11 in *L. macrophthalmus*. I do not agree with Greenwood (1976) who considered a close ratio value in the two latter species to be an argument for their phylogenetically close origin. Van Neer (1987) described the variation in the bridge count on the horizontal limb between *L. niloticus* from the Nile (two) and those from Niger (one or two), the posterior bridge always being present; and Van Neer & Gayet (1988) observed, in the fossil *L. niloticus* from the Holocene Malian sites, variation from two to no bridges. They interpreted the variation to be partly due to intraspecific variation and preservation.

The latid species show the typical complete opercular series (Fig. 19) of percoid fish, with an operculum, subopeculum and interoperculum. As in half the percoids they have one opercular spine (at least; McAllister, 1968). The preservation of the opercular series is poor in †*L. bispinosus* and †*Eolates aquensis*, and somewhat better in †*E. gracilis* (Fig. 19); they resemble that of *L. niloticus*.

The interoperculum is thinner than usual in perciform fish (Greenwood, 1976). In Tanganyikan species, there is an elongation of the bone and a smoothing of the angles.
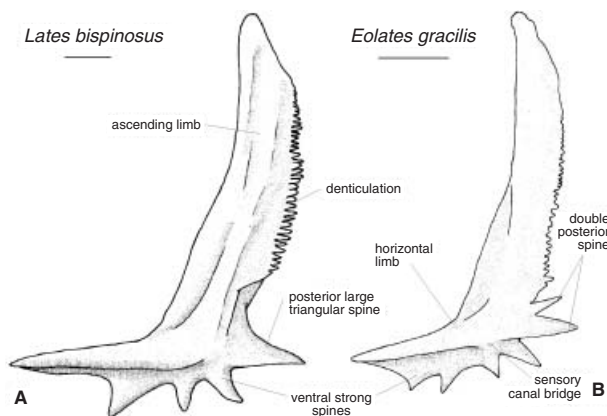
Figure 18. Preoperculi of fossil latids, in lateral view: A, †*Lates bispinosus* (holotype); B, †*Eolates gracilis* (MNHN Bol 267). Scale bars = 10 mm.
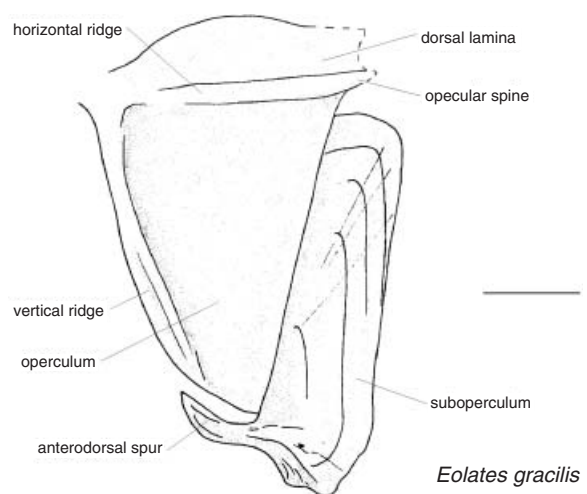
Figure 19. Left operculum and subopeculum of †*Eolates gracilis* (MCSNV VI.N.62), in lateral view. Scale bar = 5 mm.
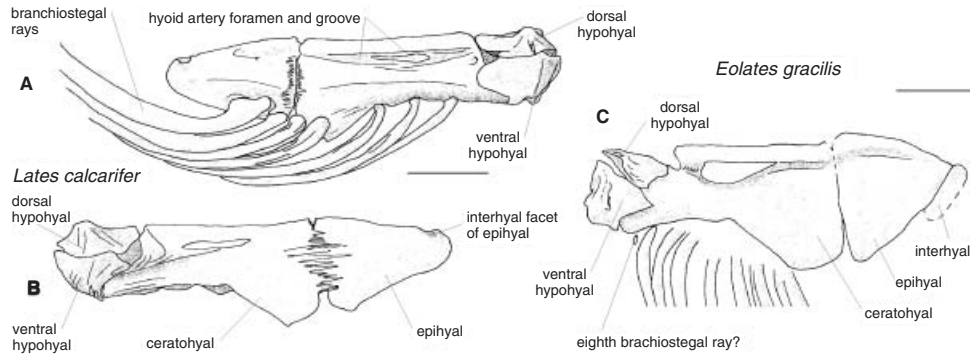
Figure 20. Right hyoid arch of *Lates* and †*Eolates*: A, B, *Lates calcarifer* (MG 26), in lateral and medial views; C, †*Eolates gracilis* (MCSNV VI.N.62), in lateral view. Scale bars = 5 mm.

The operculum (Fig. 19) has a horizontal ridge that develops from the articular facet to the posterior angle of the bone where it ends with a spine (Greenwood, 1976). The upper lamina develops along the whole ridge, except its posterior border which is sometimes notched. In Tanganyikan species, the ridge and spine development is weaker (the spine is even absent in *Lates stappersi*). The spine is also reduced in *Psammoperca waigiensis*.

The suboperculum spur is more robust than the rest of the bone, which is very thin (Fig. 19). The hook is the more variable part of the bone in *Lates* (*Luciolates*) (very weak and reduced in *L. stappersi*). By contrast, it is similar in *Lates* (*Lates*) species and in †*Eolates*.

As noted by Greenwood (1976), the hyoid arch (Fig. 20) is typical for basal percoids. That means the ceratohyal foramen is open and the hyoid artery gutter is present (on both the epihyal and the ceratohyal); the posteriormost branchiostegal rays are wider, and have a strongly notched articular head (Fig. 20A–C). In Recent species (Fig. 20A, B), the three anterior branchiostegal rays articulate with the ventral edge of the ceratohyal, the fourth lies on the ventral border of the lateral side of the ceratohyal, the fifth on the ceratohyal–epihyal suture or close to the suture on the ceratohyal, and the posterior branchiostegal rays lie on the ventral border of the lateral side of the epihyal. In †*E. gracilis* (the only known fossil latid hyoid arch skeleton) all the branchiostegal rays lie ventrally on the ceratohyal lateral surface. In addition, the general shape of the †*E. gracilis* hyoid arch is shorter and deeper than in any other latid, particularly when compared with *Lates* (*Luciolates*) species. The branchiostegal ray count is supposed to be seven in all the latid species (Greenwood, 1976), but Sorbini (1975) described eight rays in †*E. gracilis*. The single specimen with a preserved hyoid arch shows a small bone in place and orientation of a branchiostegal ray (Fig. 20C), but nothing else allows us to determine if it is an eighth reduced ray or not. If it is, the hypothesis

of a secondary 'teratological' development cannot be excluded.

The branchial skeleton is only known in Recent latid species and described by Greenwood (1976). In particular, the basibranchial series is toothless in *Lates* and toothed in *Psammoperca*. The glossohyal is an elongate trapezoidal bone, the base of which forms the anterior edge of the branchial apparatus; in larger individuals it is less elongated than in smaller individuals.

The upper jaw shows familiar, generic and specific differences.

The latid premaxilla (Fig. 21) is characterized by a pointed ascending process higher than the globular articular process; both processes are bracketed; the foramen for venous vessels and the maxillary nerve branch opens at the base of the articular process; the deep posterior process has an anterior convex curve and a posterior concave curve with the alveolar process; the low longitudinal groove develops along the alveolar process; the tooth plate develops along the ventro-medial surface of the alveolar process (Fig. 21A); the teeth are villiform and undifferentiated except in *Lates stappersi*, which has enlarged median teeth (Fig. 21B; Greenwood, 1976). In *Lates* and in *Psammoperca*, the intraspecific variations concern the distance between the articular and posterior processes of the premaxilla; sometimes both the premaxillae of a single individual are different (Van Neer, 1987; in *L. niloticus*). Van Neer & Gayet (1988) noted that part of the variation is correlated with the size of the individuals (the distance is shorter in larger individuals). By contrast, the ratio 'height of the ascending process/ height of articular process' is constant within a species (Van Neer, 1989; in *L. niloticus*), but varies between species: from 1 in *L. stappersi*, to 1.3–1.6 in 3 *Lates* (*Lates*) species, around 1.5 in †*Eolates* and 1.1 in *Psammoperca*. In †*Eolates* the premaxilla differs from *Lates* in the straightness of the posterior edge of the posterior process, in the space between the alveolar
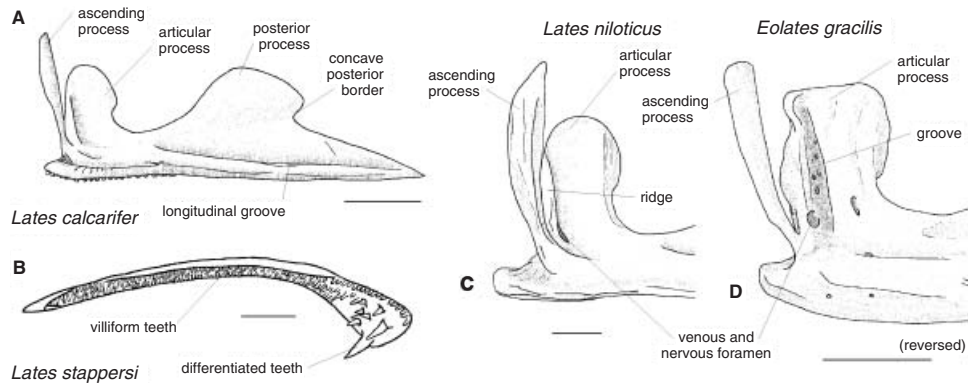
Figure 21. Premaxillae of some Recent and fossil latids: A, left premaxilla of *Lates calcarifer* (MG 26), in lateral view; B, right premaxilla of *L. stappersi*, in occlusal view, modified from Greenwood (1976); C, articular head of the left premaxilla of *L. niloticus* (MG 206), in lateral view; D, articular head of the right premaxilla of †*Eolates gracilis* (MCSNV IG.23.200), reversed, in lateral view. Scale bars = 3 mm.
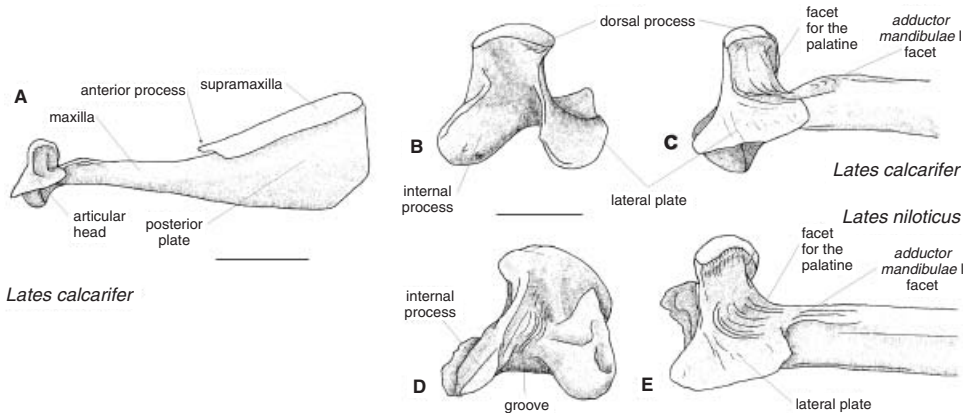
Figure 22. Upper jaw and articular heads of the maxilla of *Lates calcarifer* and *L. niloticus*: A, left upper jaw of *L. calcarifer* (MG 26), in lateral view; B–E, articular heads of the left maxilla of, B, C, *L. calcarifer* (MG 25), and, D, E, *L. niloticus* (MG 206), in, B, D, anterior, and, C, E, lateral views. Scale bars: A = 5 mm, and B–E = 2 mm.

and the articular processes, and in the strong vertical ridge that develops along the anterior border of the articular process in *Psammoperca* and *Lates* (Fig. 21C). This ridge does not exist in †*Eolates*, in which a vertical groove extends upwards from the venous and nervous foramen (Fig. 21D).

The maxilla (Fig. 22) of latid fish has an enlarged posterior dorsal plate with a straight ventral border (Fig. 22A). The shape of the articular head strongly varies among individuals of the same species, in the height, direction and extension of the dorsal process where the vomer articulates. The premaxillary internal process is medio-ventrally directed and surrounded by a groove. The lateral plate, on which the palatine ligaments insert, is more or less extended (Fig. 22B–E). Posterior to this plate, the adductor mandibulae I surface is anteriorly limited by a spur or a low ridge depending on the individual (Fig. 22C, E).

In *Lates* species and †*Eolates gracilis*, the single rectangular elongated supramaxilla has an antero-dorsal process (Fig. 22A), which is absent in *Psammoperca*.

According to Greenwood (1976) the lower jaw varies little, with the exception of the elongation in Tanganyikan species and the shallowness of the splanchnocranium bones in *Psammoperca*.

A plate develops ventrally on the dentary (Figs 23, 24), with an angle little greater than 90°. A large lateral groove for the jaw ligaments is anteriorly well defined, and extends posteriorly on to the supero-lateral face of the bone. The upper foramen of the dentary (both venous and arterial according to Gayet, 1983) is situated anterior to the groove. The nerve VII foramen opens near middle of the symphysial edge on the outer surface of the bone. The mandibular sensory canal runs in a bony tube on the medio-ventral plate; it
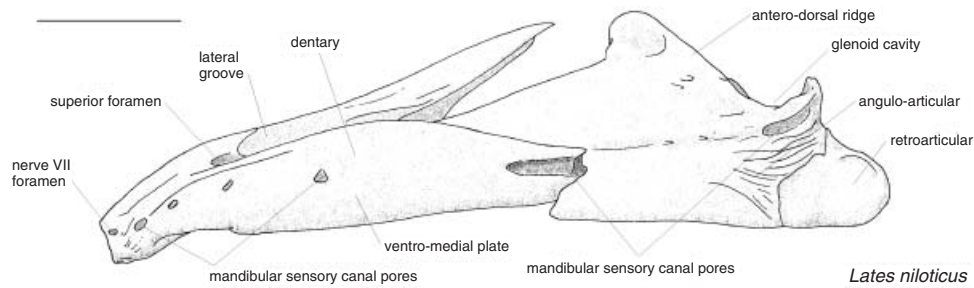
Figure 23. Right (reversed) lower jaw of *Lates niloticus* (NHM 28.228 [4]), in latero-ventral view. Scale bar = 10 mm.
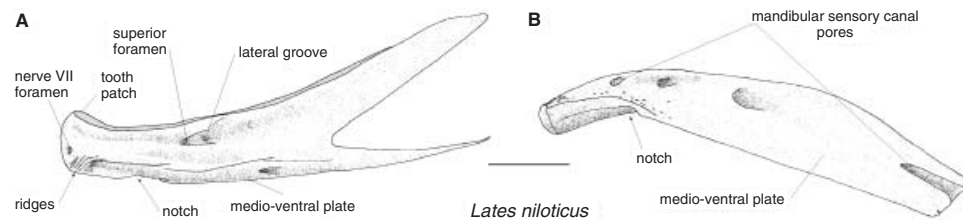
Figure 24. Left dentary of *Lates niloticus* (MG.206), in, A, lateral and, B, ventral views. Scale bar = 10 mm.
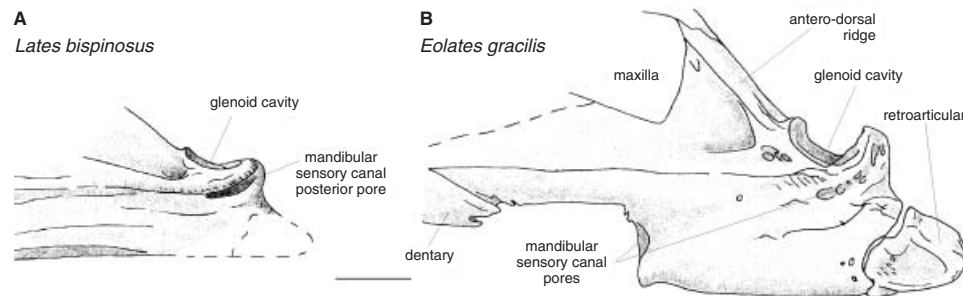
Figure 25. Left posterior part of the lower jaw in latid fossil species, in lateral view: A, †*Lates bispinosus* (holotype); B, †*Eolates gracilis* (MNHN, Bol 0267). Scale bar = 5 mm.

opens anteriorly at the edge between the plate and the lateral face of the bone, slightly posterior to the nerve VII foramen level; posteriorly, the opening is a notch on the ventral plate posterior border. The interspecific variations concern the teeth, the ventral openings of the sensory canal and the medio-ventral plate. The teeth are undifferentiated and villiform, except in *Lates stappersi*. According to Greenwood (1976), its dentary teeth are enlarged and caniniform on the external row, except at the symphysis, resembling a negative image of the premaxilla dentition. There are five openings of the mandibular sensory canal in *L. calcarifer*, whereas there are usually four in the other latid species, in which the third opening is close to the upper foramen level, as described by Van Neer (1987) in *L. niloticus*. He noticed that a few individuals of this species (3/30) have five openings (e.g. Fig. 23). In *L. stappersi*, the medio-ventral plate starts straight backward the symphysis, whereas there is a notch in other latid species (Fig. 24A, B). In *L. calcarifer* and *L. niloticus* striae develop at the symphysis (Fig. 24A).

The angulo-articular (Figs 23, 25) has an antero-dorsal ridge that develops from the glenoid cavity. It is straight, whereas there is a small posterior expansion in some perciform species. The angulo-articular sensory canal runs in a bony tube with an anterior notched opening (anterior to the dentary posterior one), and a posterior opening in a groove below the glenoid cavity. The groove length varies depending on the individual and sometimes between sides of a single individual [also described by Van Neer (1987) in *L. niloticus*]. The †*Eolates gracilis* angulo-articular (Fig. 25B) is higher and shorter than in any *Lates* species or in *Psammoperca*. The glenoid cavity is generally deep so that the articula-

tion with the quadrate might be quite restricted, particularly in some *L. calcarifer* and in †*Eolates gracilis*. This characteristic is less apparent in Tanganyikan species, *Psammoperca* and †*Lates bispinosus* (Fig. 25A), the glenoid cavity of which is somewhat flattened.

The shape of the retroarticular (Figs 23, 25B) matches the variations in the whole skull elongation. The only other difference within the family is the proportionally smaller retroarticular of †*Eolates gracilis* (Fig. 25B).

AXIAL SKELETON AND UNPAIRED FINS

Meristic counts of the axial, anal and dorsal fin skeleton in Recent and fossil latid species are given in Table 2.

In living and fossil *Lates* and in *Psammoperca*, the vertebral column (Figs 26–28; Table 2) contains 25 centra, 11 abdominal and 14 caudal including the fused preural and ural centra, e.g. †*Lates gregarius* (Fig. 26A). Epineurals are present on the fifth to seventh anteriormost vertebrae (and not only on the two anteriormost vertebrae, as stated by Greenwood, 1976). Parapophyses develop on the four to five posteriormost abdominal vertebrae (Sorbini, 1975) depending on the species and/or the individual. There are 11 abdominal vertebrae in †*E. aquensis* (Fig. 26A) and in †*L. bispinosus* (Fig. 27B) but ten in †*Eolates gracilis* (with a total count of 24). In this latter species only, epineurals are well preserved and observed on the seven anteriormost vertebrae. The number of caudal vertebrae is 14 in †*Eolates gracilis*, but it is unknown in †*L. bispinosus* (Fig. 27B) and variable in †*E. aquensis* (from 13 to 15; Gaudant, 1977).

Ribs articulate either directly on the centra or on the distal part of the parapophyses (Figs 26, 27, 28A; Table 2). In perciforms generally, they are present on the abdominal vertebrae except the two anteriormost. Parapophyses develop usually on the five posteriormost abdominal vertebrae in *Lates mariae*, *L. microlepis*, *L. macrophtalmus*, *L. longispinis*, *L. niloticus*, *L. calcarifer* and †*E. gracilis* (Figs 27A, 28A); on the last four in some young specimens of those species and in *Lates angustifrons*, †*L. gregarius*, †*L. bispinosus* and †*Eolates aquensis* (Figs 26A, B, 27B); on the last six in *Lates stappersi*; and on the 5–6 posteriormost ones in *Psammoperca waigiensis*. Their size increases posteriorly and they are directed ventrally.

The anteriormost parapophyses are free (Fig. 29A) whereas a bony transversal bridge (Fig. 29B) frequently develops between parapophyses of the 2–3 posteriormost abdominal vertebrae in living latids except *L. stappersi*, where they develop on the last four. This bridge delimits a median space where

Table 2. Numerical characteristics of the axial skeleton and of anal and dorsal fins in latid species

	No. of abdominal vertebrae	No. of postabdominal vertebrae	No. of epineural pairs	Abdominal vertebrae without parapophyse	Predorsal formula	Dorsal fin formula	Bisegmented dorsal pterygiophores supporting rays	Anal formula	Bisegmented anal pterygiophores supporting rays
Eolates gracilis	10	14	7	5	0/0/0 + II/	VIII – I + 10(9)	?	III + 8	?
Eolates aquensis	11/12	13/14(15)	?	7	/0/0 + 0 + II/	VII-I + 10/12	?	III + 7/8	?
Lates bispinosus	11	?	6	7	0 + 0/0 + II/	VII-I + 10	?	II + 7(?)	?
Lates gregarius	11	14	6	7	0/0/0 + II/	VII-I + 11	?	III + 8	?
Lates niloticus	11	14	6/7	6/7	0/0/0 + II/	VII-I + 12(11)	(5)6 (7)	III + 8	2/4
Lates longispinis	11	14	5/7	6	0/0/0 + II/	VII-I + 11/12	5/7	III + 8(7)	3/5
Lates macrophtalmus	11	14	7	6/7	0/0/0 + II/	VII-I + 12(11)	6 (7)	III + 7/8	3
Lates calcarifer	11	14	?	6/7	0/0/0 + II/	VII-I + 11	4/5	III + 8	2/3
Lates angustifrons	11	14	6 (7)	7	0/0/0 + II/	VII-I + 12	6	III + 8	3
Lates microlepis	11	14	7	6/7	0/0/0 + II/	VII-I + 12(13)	7	III + 8	2/4
Lates mariae	11	14	7	6/7	0/0/0 + II/	VII(VIII) – I + 11	6	III + 8	3
Lates stappersi	11	14	5	5	0/0/0 + II/	VIII – I + 10	4/5	III + 9	2/4
Psammoperca waigiensis	11	14	7/8	5/6	0/0/0 + II/	VII-I + 12	all	III + 8	6
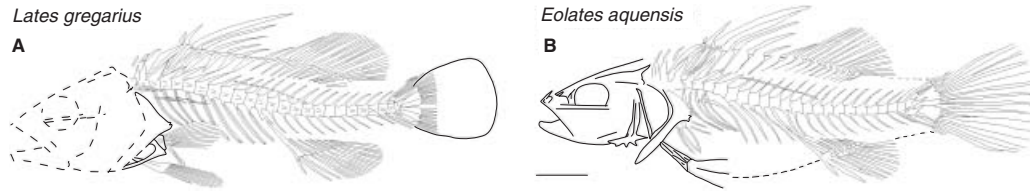
Figure 26. General view of the postcranial skeleton, in lateral view, of A, †*Lates gregarius* (from Bannikov, 1992; modified), and B, †*Eolates aquensis* (reconstruction mostly from NHM P3912). Scale bar = 10 mm.
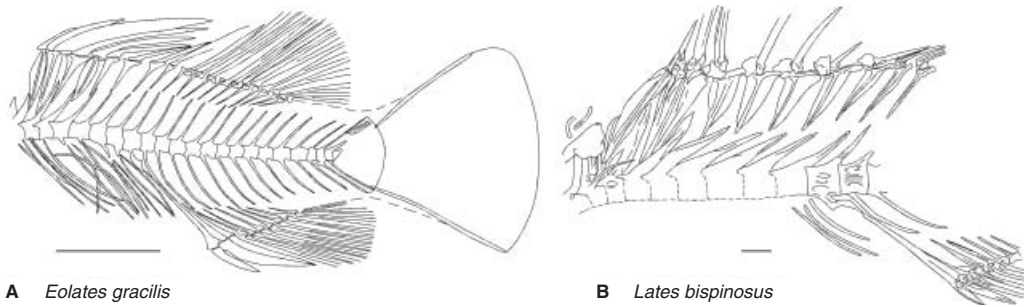
Figure 27. General view of the postcranial skeleton, in lateral view, of A, †*Eolates gracilis* (NHM P24C38), and B, †*Lates bispinosus* (holotype and only known specimen). Scale bars = 10 mm.
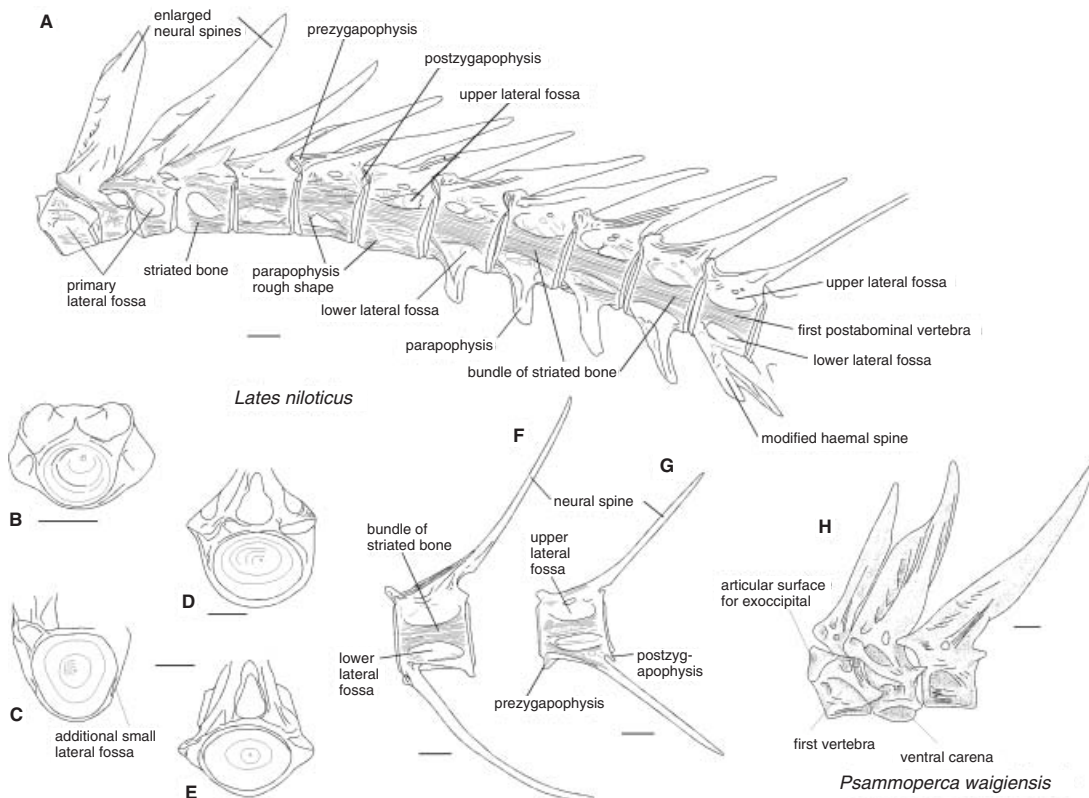
Figure 28. Vertebrae of *Lates* and *Psammoperca*: A–G, *Lates niloticus*; H, *Psammoperca waigiensis*. A, anterior part of the vertebral column (MG 206), in left lateral view; B, first (MG 206), C, second (MG 205) and, D, third (MG 205) centra, in cranial view; E, second centrum (MG 205), in posterior view; F, anteriormost, and, G, posteriormost postabdominal vertebrae (MG 206), in left lateral view; H, the three first vertebrae of *P. waigiensis*, in left lateral view, modified from Greenwood (1976). Scale bars = 5 mm.
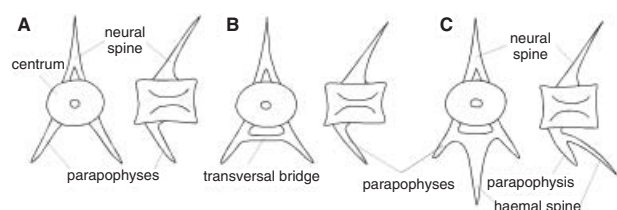
Figure 29. Schematic drawing of the different types of abdominal vertebrae, in anterior and left lateral views: A, vertebra with free parapophyses; B, vertebra with parapophyses linked by a bony horizontal bridge; C, vertebra with a modified haemal spine.

vessels run below the vertebral column. It cannot be observed in articulated fossil latids when the body is preserved in lateral view.

The first haemal spine partially fuses with the parapophyses and the bony transversal bridge (Figs 26, 27, 28A, 29C). In anterior or posterior views, they show a trifid pattern, and in lateral view, the haemal spine appears posterior to the parapophysis (Fig. 29C). Such a pattern is present in *Psammoperca*, *Lates* (e.g. †*L. bispinosus*) and †*E. gracilis* (Figs 26A, 27A, B, 28A). It cannot be observed in †*E. aquensis* specimens. This haemal spine carries the first anal pterygiophore.

The first neural spine is autogenous (Figs 26, 27, 28A) and is primitive for acanthomorphs (Johnson & Patterson, 1993). In latids, the neural spines of the three anteriormost abdominal vertebrae are antero-posteriorly enlarged, particularly the second one. The lateral surface of the spine is ornamented with arch-shaped striae. The following abdominal neural spines are rather massive at their bases whereas those of the caudal vertebrae are thin. Greenwood (1976) noted that the first three abdominal vertebrae are the most individually distinguishable elements in the entire column; he described and figured them with details in some Recent species.

According to Johnson & Patterson (1993), the nomenclature of the accessory bones of the axial skeleton is established as follows: in all percomorphs the epineurals are on the ribs of all centra with ribs. The 'epipleurals' described by Greenwood (1976) and others are re-considered in the light of this analysis. Latids show the percomorph state, i.e. the tips of the first two pairs of epineurals lie in fossae at the antero-dorsal angle of the centra and their distal part is displaced ventrally; the posteriormost epineurals are displaced ventrally on to the ribs. The distribution of the epineurals varies depending on the species and/or the individual (Table 2). In *Psammoperca waigiensis*, epineurals develop on the seven or eight anteriormost vertebrae. In *Lates*, epineurals are present on the first

to the fifth through seventh vertebra, with the exception of *L. calcarifer*, which seems to possess four pairs of epineurals only (Patterson & Johnson, 1995). For the examined specimens we have: *L. stappersi* (five), *L. longispinis* (five to seven), *L. angustifrons* and *L. niloticus* (six or seven), and *L. albertianus*, *L. macrophthalmus*, *L. microlepis* and *L. mariae* (seven). In the fossil specimens with articulated skeletons, the epineural distribution pattern is the same as in Recent latids, e.g. epineurals are present from the first to the sixth abdominal vertebra in †*L. bispinosus*. The poorly preserved specimens of †*E. aquensis* do not permit any count to be made. On isolated fossil first and second vertebrae, the depressed areas in which the epineurals articulate are visible.

The striated ornamentation of the vertebrae is more apparent in Recent *Lates* (*Lates*) and fossil latids than in *Lates* (*Luciolates*) in which the vertebrae follow the general lengthening and weakening of the bones. Greenwood (1976) described these variations for Recent species. The vertebrae of †*Eolates gracilis* and †*Lates bispinosus* have the same shape as *L. niloticus*, and they show a strong striated ornamentation of the bone (mostly in †*L. bispinosus*).

Latid vertebrae are characterized by several fossae and ridges, which enable them to be distinguished from each other (Fig. 28A–H). The primary lateral fossa is present latero-dorsally on the first abdominal vertebra, absent on the second vertebra and occupies an increasingly ventral position from the third to the seventh vertebra; it disappears on the eighth. A ridge (future parapophysis) develops at the anterior part of the reduced primary fossa on the sixth and seventh vertebrae. The first ribs articulate directly in the primary lateral fossa of the third or fourth to fifth or seventh vertebra, on the anterior pad developed on the sixth or seventh vertebra, and then on the parapophyses of the seventh or eighth to the last abdominal vertebra. An upper lateral fossa deepens whereas the primary lateral fossa migrates ventrally. Both the primary lateral and the upper lateral fossae are separated by a very large striated horizontal bundle; its height decreases posteriorly. A lower lateral fossa deepens just above the parapophysis on the eighth vertebra. A ventral median fossa develops progressively: it appears on the third to fifth vertebra and is well developed on the eighth. It is present until the end of the vertebral column between the haemal arches. A single foramen generally opens at the base of each neural arch of the anteriormost vertebrae and two are present on the posteriormost vertebrae (Fig. 28A, F, G), but their respective number varies according to the individual. As well as these ridges and fossae, the vertebrae differ in shape and certain particularities according to their number.

The anterior face of the first vertebra is round (Fig. 28B) and the posterior face has a triangular shape. It is shorter than deep. In *Lates* and *Psammoperca*, the two anterior facets for the articulation with the exoccipitals are medially in contact with each other (Fig. 28B). The primary lateral fossa occupies a variable latero-dorsal position (Fig. 28A). Below this fossa, the bone is slightly striated, as on the ventral face. The postzygapophyses are more or less developed; they are very low in position, below the midpoint, and diagonally orientated.

The second vertebra (Fig. 28A, C, E, H) has a very short centrum particularly at the base, no primary lateral fossa, two additional small fossae developed laterally on the border of the anterior face (unique), and the neural spine is strongly enlarged and directed dorsally instead of posterodorsally. The postzygapophyses are developed laterally at the midpoint of the centrum, increasing the flattened diamond-shape of the centrum in anterior view. The prezygapophyses are strongly developed overlapping the first centrum. A lateral oblique ridge joins the pre- and postzygapophyses (Fig. 28A). In *Psammoperca* only, a single ventral longitudinal carina is present.

The third vertebra (Fig. 28A, D, H) has a long, enlarged neural spine, and a primary lateral fossa that develops in an oblique position between well-developed pre- and postzygapophyses (but less developed than in the anteriormost vertebrae). The first rib articulates in this fossa. The ventral part of the centrum is as deep as it is long, and both the anterior and the posterior surfaces are nearly parallel (in lateral view) and similar in shape (i.e. rounded and slightly flattened). The first median ventral fossa appears on this centrum in some individuals of *Lates*.

The fourth to seventh vertebrae (Fig. 28A) are slightly deeper than long to slightly longer than deep; the primary lateral fossa is located between the midpoint and the lower third of the centrum; the upper lateral and the ventral fossae appear and develop. The axis of the ventral fossa is not perfectly aligned with the axis on the anteriormost vertebrae. On the seventh centrum, a small process, in the rough shape of a parapophysis, appears in the anterior part of the primary lateral fossa. In *L. calcarifer*, the parapophyses develop on the sixth vertebra instead of the seventh.

The eighth to eleventh vertebrae (Fig. 28A) bear parapophyses. The centra are increasingly elongated, the transverse striated bundle becomes thinner and thinner (as on caudal vertebrae), and the length of the parapophyses increases. The ventral fossa is always parallel to the axis of the body. The well-defined upper lateral fossa occupies the upper part of the centrum and the ventral lateral fossa appears and develops posterior to and above the parapophyses. The dimensions of both upper and lower lateral fossae are similar on the last two abdominal vertebrae. The bony transverse bridge that appears between both parapophyses of the ninth vertebra is located very close to the centrum (Fig. 29B) and then moves to a more ventral position whereas the parapophyses are increasingly vertically directed.

The caudal vertebrae (Fig. 28A, F, G). The haemal spine of the first caudal vertebra (the twelfth vertebra) bears the first pterygiophore of the anal fin (see the modified haemal spine; Fig. 29C). The following caudal vertebrae are increasingly laterally flattened. The upper and lower fossae are equal in size, deep and separated by a reduced bundle of striated bone. The more posterior is a vertebra, the broader is the space between the prezygapophyses and the base of the haemal spine (Fig. 28F, G); they are close to each other or even in contact on the anteriormost caudal vertebrae.

There are two dorsal fins (Figs 26A, B, 27A, B, 30A, B; Table 2) separated by a gap of variable size. According to Greenwood (1976), a membrane bridges the two fins in *L. niloticus*, *L. calcarifer*, *L. longispinis*, *L. macrophthalmus*, *L. angustifrons* (in only some individuals), *Psammoperca* and †*Eolates aquensis*. This membrane is absent and the posterior dorsal fin is clearly separated from the anterior fin in *L. mariae* (in specimens longer than 0.7 m), *L. microlepis* and *L. stappersi*, which shows a larger gap.

Three predorsal bones lie in front of the first dorsal fin (predorsals and supraneurals were shown to be equivalent in the taxa studied by Mabee, 1988). The three predorsals and the first pterygiophore lie in front of the three anteriormost neural spines in two equivalent patterns depending on the species; the second and third pterygiophores lie between the third and the fourth neural spines in all latid fish (Figs 26A, B, 27A, B; Table 2). The first dorsal fin is spiny with seven or eight spines according to the species and/or the individuals, and the second fin is composed of a spine followed by soft branched rays (Table 2). The first spine articulates with the fused proximal and medial radials of the pterygiophore; the second articulates anteriorly (and serially) with the first distal radial, and posteriorly lies on the fused second proximal and medial radials (see also the anal fin). The following spines and rays articulate as does the second spine, with their serially associated pterygiophore. Patterson (1992) proposed starting the count from the fifth spine or ray where the serial association is always directly observable; the first spine is not serially associated with a pterygiophore and is thus supernumerary (Figs 26A, B, 27A, B). The formula 0/0/0+II/I+I/ is observed in all living latids and in †*Lates gregarius* [following Bannikov's (1992) drawings], whereas other fossil latids do not have a stable formula. The single known specimen of †*L. bispinosus* is 0+0//0+II/I+I/. A third formula,
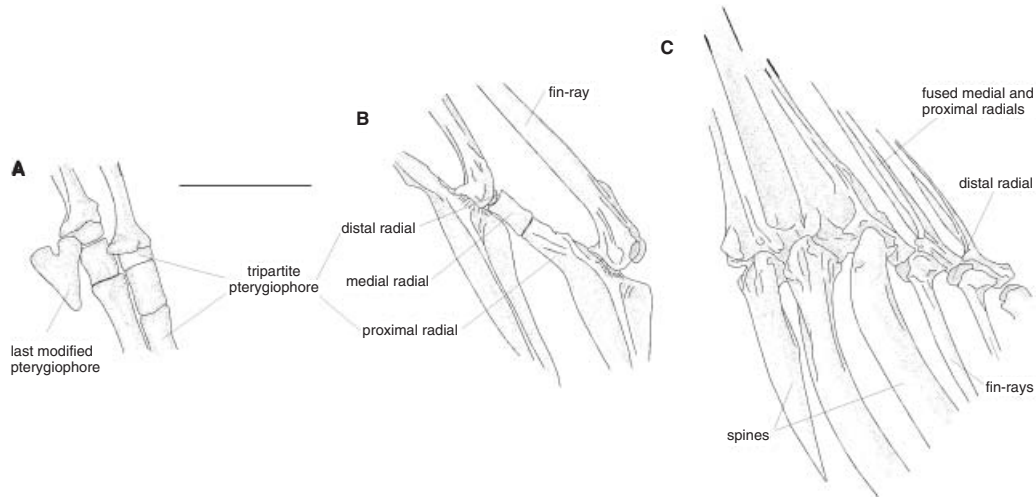
Figure 30. Bony elements of the median fins in latids: A, posteriormost pterygiophores of the second dorsal fin in *Lates calcarifer* (MG 26), in right lateral view; B, pterygiophores of the middle of the second dorsal fin of *L. niloticus* (NHM 28228[4]), in right lateral view; C, anteriormost elements of the anal fin of *L. niloticus* (NHM 28228[4]), in left lateral view. Scale bar = 2 mm.

/0/0+0+II/I+I/, is observed in †*Eolates aquensis*; †*E. gracilis* generally shows the most common formula but also the latter two or equivalents. The distal radials are wider, stronger and longer more posteriorly. The size of the spines increases from the first to the third, and then decreases. The fossil species †*Lates gregarius*, †*L. bispinosus* and †*Eolates aquensis*, and the living *Lates stappersi* and *Psammoperca waigiensis*, have an anterior dorsal fin with seven spines. †*Eolates gracilis* and living *Lates* species except *L. stappersi* have eight spines. *L. mariae* has 7–8 spines in the fin (Table 2). The first dorsal spine is reduced in *L. stappersi*. The spines of the unpaired fins are similar to those of other perciforms. One half is alternately more concave or convex and the spines fit together when lying on the back of the body.

The second dorsal fin starts with the last dorsal spine. Its spine and rays are all serially associated with their own pterygiophore. The anteriormost pterygiophores of the second dorsal fin are bipartite (with fused medial and proximal radials), as in the first dorsal fin. The medial radials of the five or six posteriormost (complete) pterygiophores are autogenous in *Lates*, not as Greenwood (1976: 45) noted '. . . distinct medial radials are also absent from those pterygiophores carrying the branched dorsal fin rays', except in *Lates stappersi* which 'do have distinct medial radials . . .'. The distal radial is a small ball placed between the right and left proximal parts of the rays. The last (reduced) pterygiophore is triangular in shape, short and ventrally rounded in all latid fish and bears two rays (Fig. 30A). The number of pterygiophores carrying rays and with an autogenous medial

radial varies depending on the individual (Table 2), except in *Lates mariae* and *L. angustifrons* (respectively five and six) but this could be due to the small number of specimens examined. The number of segmented rays in the posterior dorsal fin varies according to the species and/or the individuals (Table 2): eight in †*Lates bispinosus*; 9–10 in †*Eolates gracilis*; ten in *Lates stappersi*, *L. mariae*, *L. calcarifer* and †*L. gregarius*; 11–12 in *L. macrophtalmus* and *L. longispinis*; 10–12 in †*Eolates aquensis*; 12 in *Psammoperca waigiensis*, *Lates niloticus*, *L. angustifrons* and *L. microlepis* (one individual with 13 rays). The distal radial of the first pterygiophore of the second fin is always the longest. The spine of the posterior fin is always either longer or as long as the last spine of the anterior fin and is never of lesser size than the preceding spine.

The anal fin (Figs 26A–C, 27A–C, 30C, Table 2) is composed of three spines and 7–9 (usually eight) segmented rays. The first pterygiophore anteriorly bears two spines on a fused proximal and medial radial (Fig. 30C), and posteriorly one spine or one ray on the distal radial. Two supernumerary anal spines are consequently present, as is frequently observed in perciforms (Patterson, 1992). Most latid fish have the third (and last) spine serially associated with the first pterygiophore, except †*Lates bispinosus*, in which the first ray is the one serially associated with the first pterygiophore (there are just two spines, the supernumerary ones). The following pterygiophores carry one ray, on the distal radial. The anteriormost pterygiophores are bisegment, the posteriormost are tripartite depending on the species (the same distribution as in
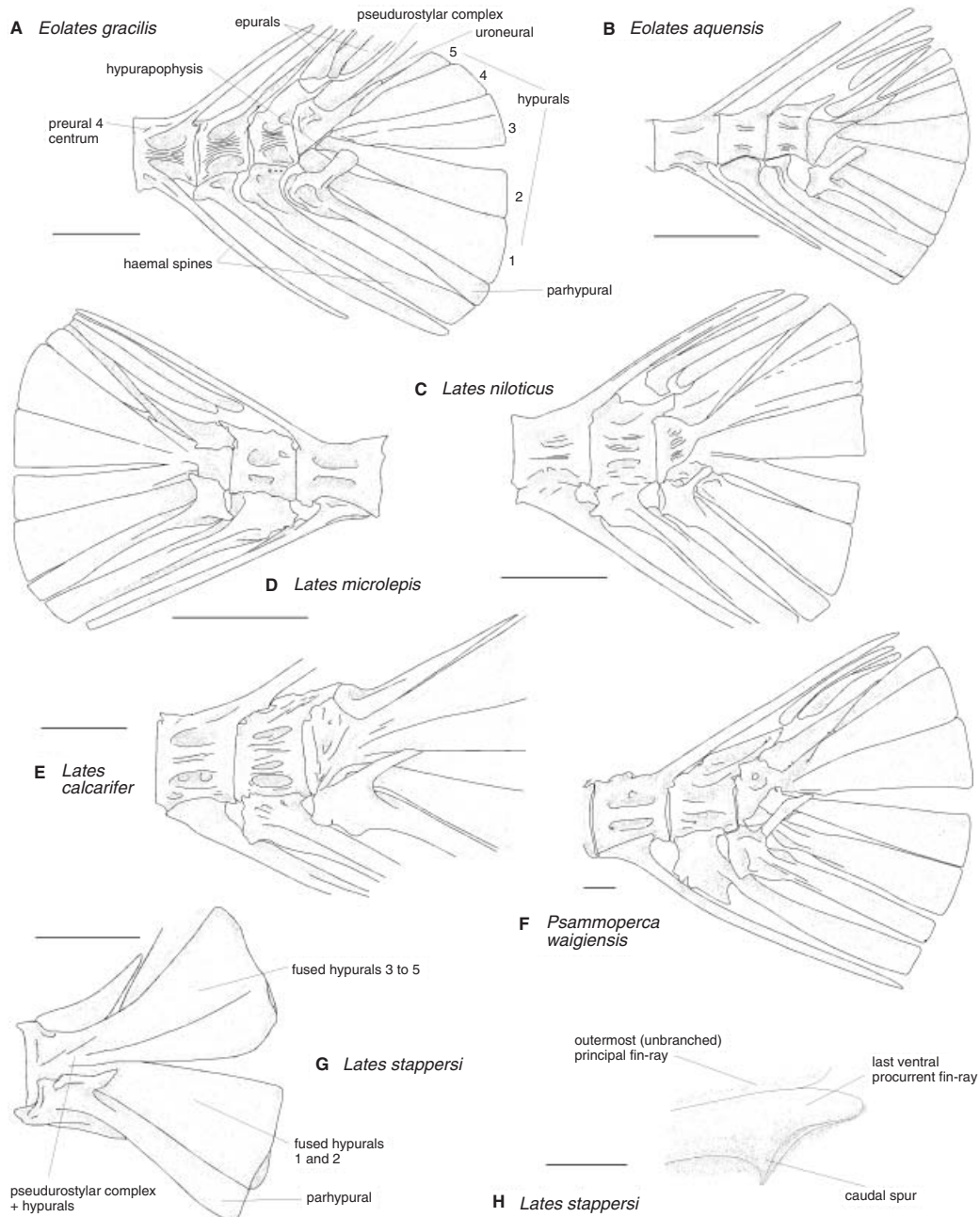
Figure 31. Caudal skeletons in Recent and fossil latids, in lateral view (A–G), and marginal ventral ray with the caudal spur, in right lateral view (H): A, †*Eolates gracilis* (NHM 3918b); B, †*E. aquensis* (NHM P3912); C, *Lates niloticus* (NHM 28228[4]); D, *L. microlepis* (NHM 28228 [1900-12-13:37]); E, *L. calcarifer*, caudal vertebrae and base of the hypurals (NHM 28228 [1985-11-14:1]); F, *Psammoperca waigiensis* (NHM 28228 [1888-11-6-6]); G, H, *L. stappersi* (NHM 28228 [1936-6-45: 1706]). Scale bars: A, B, H = 3 mm, and C–G = 10 mm.

the dorsal fin) and the last pterygiophore is reduced. The number of anal rays and of autogenous distal radials shows inter- and intraspecific variation (Table 2).

The caudal fin skeleton (Fig. 31; Table 3) is similar to the perciform generalized type (Gosline, 1961) with three centra, i.e. the preural centra 2 and 3 and a pseudourostylar complex (fused first preural and first ural centra), and no uroterminal complex (it has been lost or fused to the pseudourostylar complex). According to Greenwood (1976), all latid species have a parhypural, five hypurals and two or three epurals; a stegural and an uroneural are present except in *Psammoperca* (stegural only); the principal caudal fin

Table 3. Numerical characteristics of the caudal fin skeleton in latid species

	No. of epurals	Uroneural present	Fusion between the hypurals	Fusion of the hypurals with the centrum	Caudal formula
Eolates gracilis	3	yes	none	none	?
Eolates aquensis	3	yes	none	none	?
Lates bispinosus	?	yes	?	?	?
Lates gregarius	?	yes	?	?	?
Lates niloticus	2	yes	none	2–3–4(–5*)	(7/8)-I-8:7-I-(7/8)
Lates longipinis	2	yes	none	2–3–4	8/9)-I-8:7-I-(9)
Lates macrophtalmus	2	yes	none	2–3–5	(8/9)-I-8:7-I-(7/8)
Lates calcarifer	2	yes	none	2–3–6	(6)-I-8:7-I-(6)
Lates angustifrons	2	yes	none	2–3–7	(9)-I-8:7-I-(8)
Lates microlepis	2	yes	none	2–3–8	(7/8)-I-8:7-I-(6/7)
Lates mariae	2	yes	none	2–3–9	(10)-I-8:7-I-(9)
Lates stappersi	2	yes	[1–2] [3–4]	1–2–3–4–5	(9/11)-I-8:7-I-(8/9)
Psammoperca waigiensis	2	no	none	3–4	(7/8)-I-8:7-I-(7/8)

ray formula is I-7 : 8-I. The hypurapophysis of the parhypural is strongly developed. The caudal skeleton of †*Eolates gracilis* (Fig. 31A), †*E. aquensis* (Fig. 31B) and †*Lates gregarius* (incomplete) are known. The neural spines of preural vertebrae 1 and 2 are fused to their centra. Their haemal spines and the parhypural are autogenous. The neural spine of the preural vertebra 2 is very low. As there is no uroterminal complex, the pseudourostylar centrum alone bears the hypurals. In contrast to Greenwood (1976: fig. 26), no posterior hook or notch is present on the haemal spines of preural vertebrae 2 and 3 (Fig. 31C). However, apophyses develop on the anterior part of the parhypural and of the haemal spine of preural vertebra 2 in Recent latids (Fig. 31C–F). In †*Eolates*, such apophyses are absent but the haemal spine of the second preural vertebra is enlarged and meets the spine of the anterior vertebra. *Psammoperca waigiensis* has no uroneural (Fig. 31F), but in other species it is a thin, rod-like element. The stegural has an enlarged anterior part and its posterior part tapers to a sharp point. Only two epurals are present in *Lates* and *Psammoperca*. They lie close to each other and the anterior one has an enlarged proximal head. Three epurals are present in †*Eolates*. The two anterior epurals are enlarged and the third is a thin, rod-like element. All latid fish have five hypurals, with various patterns of fusion with the complex or each other (Table 3) depending on the species and/or the individuals (particularly during their growth). The hypurals of †*Eolates* are separate and autogenous (Fig. 31A, B). In *Psammoperca*, they are separate to each other but hypurals 3 and 4 are fused to the pseudourostylar complex (but not hypurals 2–4; *contra* Greenwood, 1976). This latter pattern is generally observed in *Lates* species (Fig. 31C–E)

except *L. stappersi* in which all hypurals are fused to the pseudurostylar complex (Fig. 31G). There is some exceptional individual variation, e.g. in a young *L. niloticus* all the hypurals are autogenous (Greenwood, 1976), whereas a *L. calcarifer* specimen shows hypurals 2–5 fused to the complex (Fig. 31E) and to each other distally. In *L. stappersi*, hypurals 1 and 2 on one hand, and 3 and 4 on the other hand are fused together (Fig. 31G). Greenwood (1976) described an unfused fifth hypural in *L. stappersi*. The parhypural process (= hypurapophysis) observed by Sorbini (1975) in †*Eolates gracilis* is present in all latid fish, with some individual or specific variation in size. It can cover the half the width of hypural 1, or it can reach the dorsal border of hypural 2 and even sometimes pass it. The number of procurrent rays differs among species and individuals (Table 3). A caudal spur (Johnson, 1975) is present on the first procurrent ventral ray of *Lates* (Fig. 31H) and †*Eolates* (observed in †*E. gracilis*). It is absent in *Psammoperca*. The outline of the posterior border of the caudal fin is rounded in †*Eolates* and, as described by Greenwood (1976), it varies in Recent species from rounded to truncated (*Psammoperca*, *Lates niloticus*, *L. calcarifer*, *L. longispinis*, *L. macrophthalmus*, *L. angustifrons*), to nearly straight to crescentic (*L. microlepis*, *L. mariae*). It differs from young to adult in *L. stappersi* (Greenwood, 1976). The ratio between the height and the length of the caudal peduncle allows latid species to be distinguished (Holden, 1967; Sorbini, 1975; Gaudant, 1977). The ratio varies from 1.5 to 2 in *L. macrophthalmus*, 1.4 to 1.9 in *L. angustifrons*, 1.9 to 2.3 in *L. microlepis*, 1.8 to 2.3 in *L. mariae* and 1 to 1.4 in *L. niloticus*; it is more than 1.5 in †*L. macrurus*, about 1 in †*E. aquensis* and less than 1 in †*E. gracilis*.

PAIRED FINS AND ASSOCIATED BONES

The pectoral girdle (Figs 32, 33) is very conservative among latids.

The posttemporals of *Lates* and †*Eolates* are similar in both their overall shape and ornamentation (Fig. 32A–C). Posteriorly, the shield-like body of the posttemporal bears 3–5 small spines depending on the individual. In *Psammoperca*, the posterior border is smooth (see Greenwood, 1976: fig. 24). A ligament links the tunica externa of the swimbladder and the posttemporal in *Psammoperca* and in Recent *Lates* (Greenwood, 1976). The functional purpose of this connection is unknown. However, the correlated morphological modifications are identified on the posttemporal, which differs from that of other percoids by the presence of a deep oval pit at the base of the intercalar limb (Fig. 32B; see Greenwood, 1976). This pit is present in all examined Recent latids and in fossil latids, where the posttemporal can be observed in medial view (disarticulated specimens). Thus its presence or absence is unknown in †*Eolates*. In †*Eolates gracilis* the epiotic limb of the posttemporal is longer than in *Lates niloticus*, with proportions similar to those of the Tanganyikan species.

The posterior angle of the cleithrum of *Lates* and †*Eolates* is expanded and its hind margin bears small spines (Fig. 33A, C–F). Their number was given by Greenwood (1976) for Recent species. In combination with observed data, there are three in †*Eolates* (Fig. 33A, D–F), *Lates microlepis*, *L. mariae*, *L. stappersi* and in fossil *Lates*, 5–7 in *L. macrophtalmus* and 5–10 in *L. calcarifer* and *L. niloticus*. Some of them are bifurcated (Fig. 33A, D–F). The cleithral posterior border is smooth in *Psammoperca*. In all latid species a ventral expansion of the cleithrum develops postero-ventrally toward the scapula and is probably occupied by the dorsal postcleithrum (Fig. 33A, C–F). The ventral limb of the cleithrum is thin and pointed.
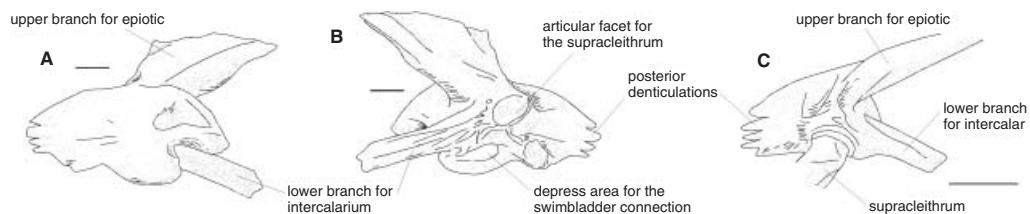
Figure 32. Posttemporals of certain Recent and fossil latids: A, B, right posttemporal of *Lates niloticus* (MG 25), in, A, lateral and, B, medial views; C, left posttemporal of †*Eolates gracilis* (MCSNV VI.N.59), in lateral view. Scale bars = 3 mm.
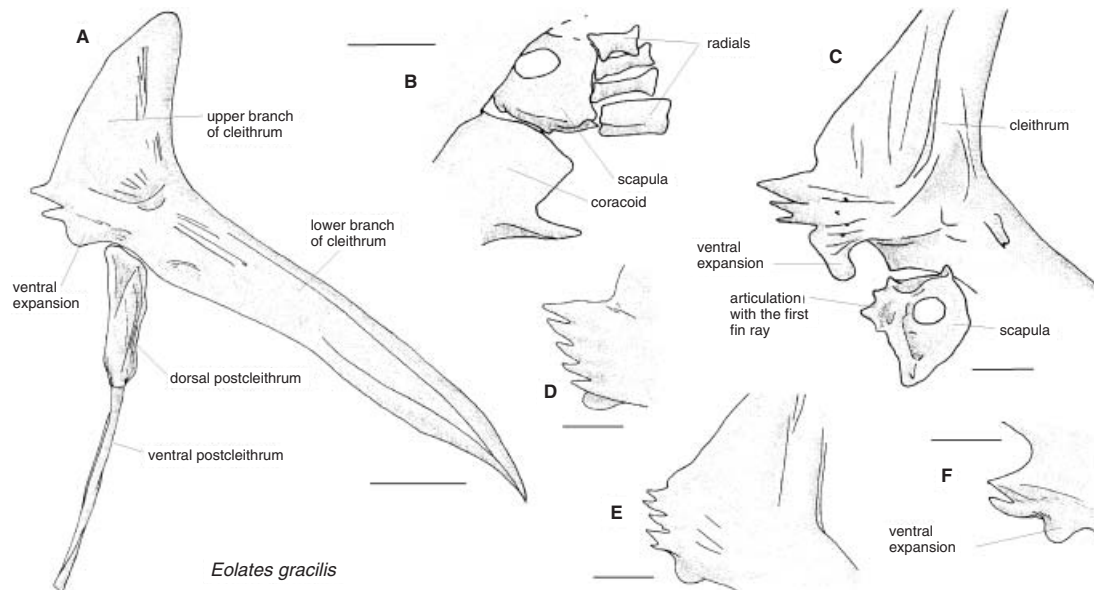
Figure 33. Elements of the pectoral girdle of †*Eolates gracilis*: A, cleithrum and dorsal and ventral postcleithra (MCSNV T.373), in lateral view; B, scapula, coracoid and radials (MCSNV Rom.Bo), in medial view; C, scapula and part of the cleithrum (23152), in lateral view; D–F, variations of the ventral expansion and number of small spines on the cleithrum, of, D (MCSNV TG 23200), E (VI.N.56 [reversed]) and, F (NHM P3918b), in lateral view. Scale bars = 3 mm.
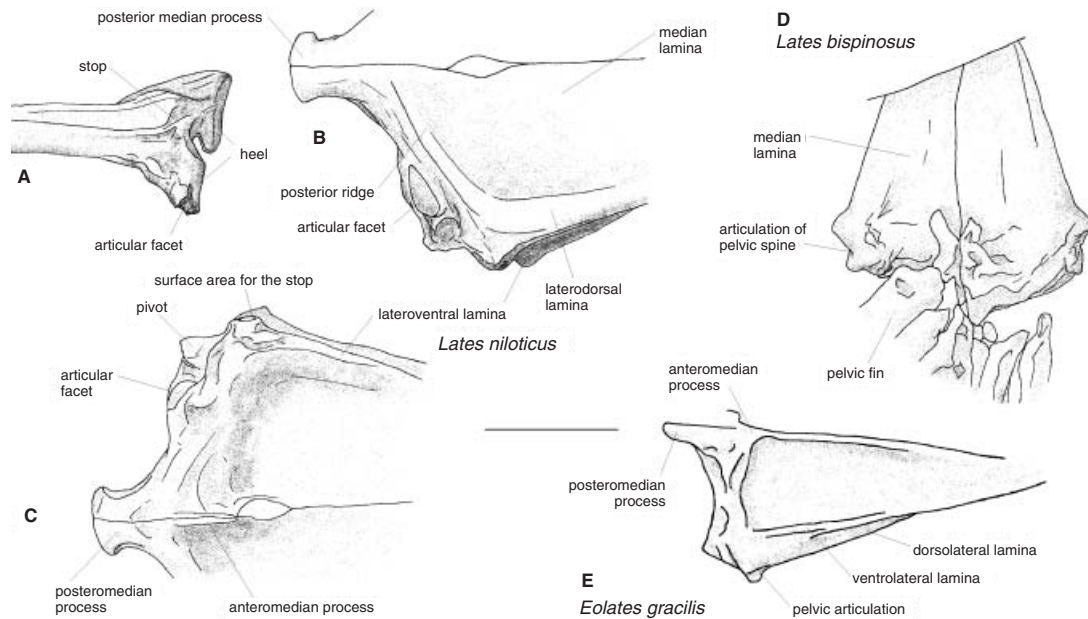
Figure 34. Pelvic bone and/or spine in certain Recent and fossil latids: A–C, *Lates niloticus* (NHM 28228[4]): A, proximal part of the pelvic spine, and, B, C, distal part of the pelvic bones, in, B, dorsal, and, C, ventral views; D, E, distal part of the pelvic bones in fossil latids: D, †*Lates bispinosus* (holotype), and, E, †*Eolates gracilis* (MCSNV VI.N.59)*, in ventral view. Scale bars = 5 mm.

Latids have a rod-like supracleithrum, a flat scale-like rectangular dorsal postcleithrum and an elongated robust ventral postcleithrum (Fig. 33A).

The coracoid of fossil and living *Lates* has a very strong posterior process (Fig. 33B) and differs from *Psammoperca*, which has a reduced process but is overall larger (see Greenwood, 1976). The first dorsalmost pectoral rays articulate with a small articular facet of the scapula (Fig. 33C), and the following rays articulate on the four radials (Fig. 33B). The total number of rays in *Lates* and †*Eolates* is 14, except in †*E. aquensis*, in which Gaudant (1977) counted 14–16 rays.

The formula of the pelvic fin is the typical perciform one, with one spine and five segmented rays, in both fossil (known in articulated skeletons) and living latids. Both pelvic bones are tightly joined along their whole length in *Psammoperca* and in *Lates* (Fig. 34B, C). The median lamella is without a ridge or crest on the ventral surface. The dorso- and ventro-lateral laminae are laterally developed. The posterior ridge bears the pelvic fin and has an anterior pointed process (the antero-median process) and a bulky and enlarged posterior process (the postero-median process). The latter process runs between the left and right pelvic fins. It results from the tight median juxtaposition of the two hemi-processes of the pelvic bones, and allows the insertion of the posterior infracarinalis muscles (Stiassny & Moore, 1992). The pelvic rays articulate

on the posterior ridge and the pelvic spine articulates on its lateral part in a complex articulation. The morphology of the pelvic spine articular head is typical for perciform fishes. Regarding the preserved parts of their pelvic bones and spines, the fossils †*Lates bispinosus* and †*Eolates gracilis* have this similar pattern (Fig. 34D, E).

PHYLOGENY

CHOICE OF IN- AND OUTGROUPS

To reconstruct the phylogenetic relationships of both Recent and fossil members of the family Latidae, the following taxa are included in the analysis:

Latidae
All Recent *Lates* species, *Psammoperca waigiensis* (the only species of the genus) and two of the three †*Eolates* species (i.e. †*E. gracilis*, †*E. aquensis* but not †*E. macrurus*, of which the fossils are too poorly preserved) are included in the analysis. Some latid taxa have the same character state pattern because autapomorphic characters were not coded. They are processed together under the following names: '*Lates* (*L.*) *nicaloma*' for *L. niloticus* + *L. calcarifer* + *L. longispinis* + *L. macrophthalmus*, '*Lates* (*L.*) *mima*' for *L. microlepis* + *L. mariae*; *L. stappersi* and *L. angustifrons* are coded alone. *Lates* fossil species are not

included, as their incomplete data coding is similar to 'Lates (L.) nicaloma' (see Discussion).

Centropomidae

In its old definition, this now monogeneric family included the latid species and the genus *Centropomus*. One *Centropomus* species, i.e. *C. unidecimalis*, is included in the analysis. The 11 other species have the same character state distribution in this analysis (O. Otero, pers. observ.; data from Fraser, 1968).

Two other 'ingroups' are included

Both these species have now been found to belong to two separate families, but they were included in the family Centropomidae by some previous authors.

Ambassis woolfi. Regan (1913) and Greenwood *et al.* (1966) included the genus *Ambassis* in the family Centropomidae *s.l.* A separate family Ambassidae including the genus and its two species, among others, is now considered to be monophyletic (Johnson, 1984).

Niphon spinosus. Rivas & Cook (1968) and then Nelson (1976) considered *Niphon spinosus* to be a Centropomidae (*s.l.*), closely related to *L. calcarifer*, whereas others (Gosline, 1966; Greenwood, 1976) included it in the Serranidae or in the Percichthyidae (see also Greenwood, 1977). More recently, *Niphon* was found to be a basal serranid (Johnson, 1983, 1984, 1988; Kendall, 1984; Baldwin & Johnson, 1993) and considered as such by others (Nelson, 1994).
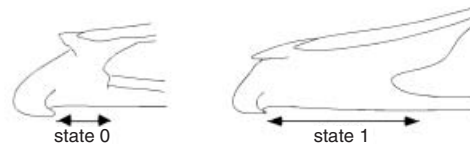
Polymixia lowei is the outgroup

This Recent species is a basal acanthomorph with few derived osteological characters. It is thus a good outgroup for phylogenetic reconstruction among basal percomorphs.

CHARACTER STATES AND THEIR DISTRIBUTION

The character states are described, discussed, figured (Figs 35–63) and summarized in the data matrix
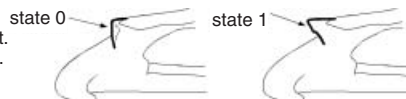
(Table 4). Their distribution is given for the taxa in the analysis and also for other examined species when the apomorphic state or another state was observed by the author or described elsewhere for basal acanthomorphs and perciforms. The character state(s) were described in detail for the latid species (Comparative anatomy).

1. Lengthening of the ethmovomerine region (Fig. 35). Non-perciform ctenosquamates, stromateoids and most percoids have a short ethmovomerine region. The lateral ethmoid, mesethmoid and vomer are tightly connected in beryciforms and perciforms. There is a strong lengthening of the whole region in the Latidae from Lake Tanganyika [*Lates* (*Luciolates*) species]. Such a lengthening is also observed in *Hapalogenys*, in the serranid *Aulocephalus temminckii*, and in the percid *Lucioperca*. The ethmovomerian region in †*Eolates gracilis* and †*E. aquensis* is as long as that of *Lates* (*Lates*) or *Psammoperca*.

2. Mesethmoid projections (Fig. 36). Anterior projections of the mesethmoid are not present in non-perciform ctenosquamates [except *Caproberyx* and *Homonotichthys* (Patterson, 1964)] nor in most percoids, except in the latid species (known in the fossil †*Eolates gracilis* and †*E. aquensis*) and also the Recent percid *Percina caprodes*, where two strong projections develop anteriorly on the mesethmoid. Arratia (1982) also described such projections in the percichthyid *Percilia*, and very slight lateral projections develop in *Niphon*.

3. Openings of the sensory canal on the frontal (Fig. 37). In primitive ctenosquamates and in most perciforms, the sensory canal runs in a tube on the frontal with opened canaliculi, including the interfrontal branch opening medially between the two bones. This state is also that of *Niphon*, whereas (1) the sensory canal runs in an open groove with bony bridges in *Centropomus* and *Ambassis* [and also in *Lateolabrax* (Katayama, 1959) and percichthyid fish], and (2) the sensory canal runs in a bony tube,

```
code for the character 1 states:
    0 => no lengthening of the ethmovomerine region.
    1 => lengthening of the ethmovomerine region.
```


state 0   state 1

Figure 35. States of character 1. Lengthening of the ethmovomerine region.

```
code for the character 2 states:
    0 => anterior projections of the mesethmoid reduced or absent.
    1 => anterior projections of the mesethmoid largely developed.
```


state 0   state 1

Figure 36. States of character 2. Mesethmoid projections.

Table 4. Data matrix of the cladistic analysis. The states of the following characters are described and discussed in the text: (1) Lengthening of the ethmovomerine region, (2) Mesethmoid projections, (3) Openings of the sensory canal on the frontal, (4) Openings of the sensory canal on the sphenotic, (5) Openings of the sensory canal on the pterotic, (6) Anterior development of the supraoccipital, (7) Fronto-parietal crests, (8) Posterior process of the epiotic, (9) Sphenotic shelf, (10) Pleurosphenoid pedicle, (11) Shape of the exoccipital articular facets, (12) Metapterygoid lamina, (13) Noteworthy spine(s) at the posterior angle of the preoperculum, (14) Ornamentation of the preopercular horizontal branch, (15) Sensory canal on the ascending limb of the preoperculum, (16) Sensory canal on the horizontal limb of the preoperculum, (17) Articular process of the premaxilla, (18) Vertebral formula, (19) Configuration of the first haemal spine, (20) Dorsal and anal pterygiophores, (21) Dorsal supernumerary spines, (22) Association between the epaxial musculature and the dorsal skeleton, (23) Epural count, (24) Uroneural, (25) Hypurals, (26) Connection between the tunica externa and the posttemporal, (27) Ornamentation on the posterior border of the cleithrum, (28) Ventral expansion on the posterior plate of the cleithrum, and (29) Medio-posterior process of the pelvic bone

Character number (text)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Eolates gracilis	0	1	?	?	?	1	?	?	?	?	?	2	1	1	2	1	0	1	1	?	1	?	0	0	0	?	1	1	3
Eolates aquensis	0	1	?	?	?	1	?	?	?	?	?	?	1	1	?	1	?	3	?	?	1	?	0	0	0	?	1	1	?
Lates (L.) except angustifrons	0	1	2	1	1	1	1	1	1	1	1	2	1	1	2	1	1	3	1	1	1	1	1	0	1	1	1	1	3
Lates angustifrons	1	1	2	1	1	1	1	1	1	1	1	2	1	1	2	1	1	3	1	1	1	1	1	0	1	1	1	1	3
Lates microlepis & mariae	1	1	2	1	1	1	1	1	1	0	1	2	1	1	2	1	1	3	1	1	1	1	1	0	1	1	1	1	3
Lates stappersi	1	1	2	1	1	1	1	1	1	0	0	2	1	0	2	1	1	3	1	1	1	1	1	0	2	1	1	1	3
Psammoperca waigiensis	0	1	2	1	1	1	1	1	1	0	0	2	1	0	2	1	0	3	1	2	1	1	1	1	1	0	1	1	3
Centropomus unidecimalis	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	2	0	0	0	0	1	0	0	0	2
Ambassis woolffii	0	0	1	1	0	1	0	0	0	0	0	1	0	0/1	0	0	0	1	0	2	0	0	1	0	1	0	0	1	1
Niphon spinosus	0	0	0	1	1	0	0	0	1	1	0	1	1	1	1	1	0	2	0	1	0	1	0	1	0	0	1	0	1
Polymixia lowei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

code for the character 3 states:
    0 => the sensory canal runs in a tube on the frontal except the interfrontal branch opened medially.
    1 => the sensory canal runs in a groove on the frontal.
    2 => the sensory canal runs in a tube on the frontal including the interfrontal branch.
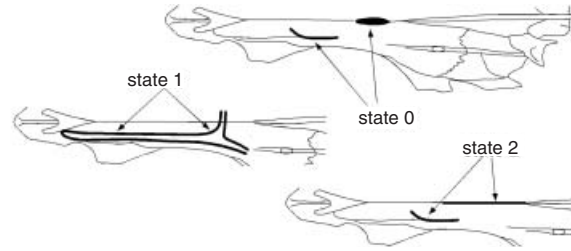
Figure 37. States of character 3. Frontal branch of the sensory canal.

code for the character 4 states:
    0 => the sensory canal runs in an open groove on the sphenotic.
    1 => the sensory canal runs in tube on the sphenotic.
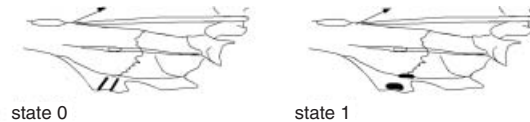
Figure 38. States of character 4. Sphenotic branch of the sensory canal.

code for the character 5 states:
    0 => the sensory canal runs in an open groove on the pterotic.
    1 => the sensory canal runs in a tube on the pterotic.

Figure 39. States of character 5. Pterotic branch of the sensory canal.

code for the character 6 states:
    0 => supraoccipital confined posteriorly.
    1 => anteriorly developed supraoccipital.
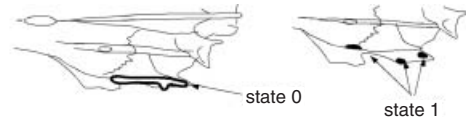
Figure 40. States of character 6. Anterior development of the supraoccipital.

including the interfrontal branch, in *Lates* (including †*L. bispinosus*) and *Psammoperca* [and also in *Hapalogenys*, in some derived serranids such as the epinephelines and in other perciform lineages such as the lutjanids (e.g. *Lutjanus chrysurus*)].

4. Openings of the sensory canal on the sphenotic (Fig. 38). A sensory canal running in an open groove on the sphenotic is observed in the examined non-perciform ctenosquamates and in numerous percoids (e.g. *Centropomus*, *Ambassis*). Some percoids show another state, with the sensory canal running in a tube on the sphenotic, including Recent latids (unknown in fossil species), most serranids (including *Niphon*) and some other perciforms such as lutjanids.

5. Openings of the sensory canal on the pterotic (Fig. 39). The sensory canal runs in an open groove with or without bridges, in non-perciform ctenosquamates except ctenothrissiforms (Patterson, 1964) and in most percoids. By contrast, it runs in a bony tube with three primary openings in latids and *Niphon* (at least †*Lates bispinosus* for fossil species; and also in *Hapalogenys*, *Siniperca*, epinephelines, *Percina*

caprodes and lutjanids). Some supernumerary openings may be present (see Anatomy).

6. Anterior development of the supraoccipital (Fig. 40). In basal ctenosquamates [e.g. pattersonichthyiforms (Gaudant, 1978)], the supraoccipital does not extend anteriorly to reach the frontals. In more derived taxa [beryciforms (except the Diretmidae), and most percoid fish], the supraoccipital inserts between the parietals and reaches the frontal posterior border. In some perciforms, the supraoccipital largely develops anteriorly in front of the parietals between the frontals. Greenwood (1976) considered the extensive interfrontal penetration of the supraoccipital as a derived feature for latids compared with berycoids. This state is present in all the Recent latid species and in †*Lates bispinosus*, †*Eolates aquensis*, †*E. gracilis* (unknown in the other fossil species) and *Ambassis*. It has also been observed in *Hapalogenys* and in lutjanids.

7. Fronto-parietal crests (Fig. 41). Fronto-parietal crests are not found in primitive ctenosquamates nor in several percoids (e.g. *Siniperca*, percichthyids,

code for the character 7 states:
  0 => no frontal and/or parietal crests.
  1 => fronto-parietal crests present.
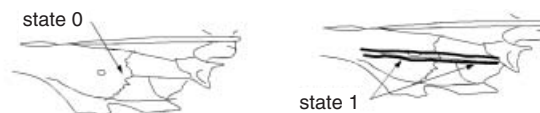
Figure 41. States of character 7. Development of fronto-parietal crests.

code for the character 8 states:
  0 => no posterior process of the epiotic.
  1 => posterior process of the epiotic present.

Figure 42. States of character 8. Epiotic posterior process.

code for the character 9 states:
  0 => no sphenotic shelf.
  1 => sphenotic shelf developed.

Figure 43. States of character 9. Sphenotic shelf.

code for the character 10 states:
  0 => no pleurosphenoid pedicle.
  1 => pleurosphenoid pedicle present.

Figure 44. States of character 10. Pleurosphenoid pedicle.

Ambassis, *Niphon*, percids). In some percoids, two different types of frontal/parietal crests develop: (1) parietal crests in *Morone* and in many serranids; (2) fronto-parietal crests in latids and *Centropomus* [in *C. poeyi*, *C. pectinatus* and *C. parallelus* the crests develop separately on the parietal and on the frontal (Fraser, 1968)] among others. Parietal crests develop as well in *Berycopsis* [polymixiiforms (Patterson, 1964)] and Greenwood (1976) considered the presence of fronto-parietal crests to be the primitive condition, because they develop in berycoids. However, the homology between the perciform and the beryciform crests is doubtful, because in the latter they are linked with the presence of mucus cavities, which are absent in the former.

8. Posterior process of the epiotic (Fig. 42). In nonperciform ctenosquamates, there is no posterior process developed medial to the articular facet of the epiotic. Such a process develops frequently among percoids, e.g. in latids (†*Lates bispinosus*) and serranids except *Niphon*; it is absent in *Centropomus* and *Ambassis* [and *Siniperca* (Katayama, 1959)].

9. Sphenotic shelf (Fig. 43). Primitively, a small process of the dermosphenotic develops anterior to the pterotic surfaces for the hyomandibular muscles. This is the state observed in non-percoid ctenosquamates and in many percoid fish, such as *Centropomus*, and *Ambassis* (and many serranids). By contrast, a horizontal shelf develops laterally from the sphenotic roof in some percoid taxa such as latids (unknown in fossil species) and *Niphon* (and also in some other percoids, including percids where it is more or less reduced).

10. Pleurosphenoid pedicle (Fig. 44). There is no pleurosphenoid pedicle in basal ctenosquamates, nor generally in perciform fish. Such a pedicle develops within some percoid families or genera: in some *Lates* species (all Recent ones except *L. microlepis*, *L. mariae* and *L. stappersi*). It is assumed to be present in †*Lates bispinosus* and absent in †*Eolates gracilis*. It develops feebly in one of the centropomid species (*Centropomus ensiferus*), and was also observed in *Epinephelus* (*E. tauvina*) and in all examined percid fish except *Perca fluviatilis* and *Percina caprodes*. Rognes (1973; in Greenwood, 1976) described the pleurosphenoid pedicle in some labrid fish and listed its frequency in teleosts. Within percoids, he noted it in some *Epinephelus* species, *Perca fluviatilis* and *Stizostedion volgensis* [which is corroborated by Greenwood (1976) for those species].

code for the character 11 states:
    0 => rounded exoccipital articular surfaces.
    1 => bean-shaped exoccipital articular surfaces.
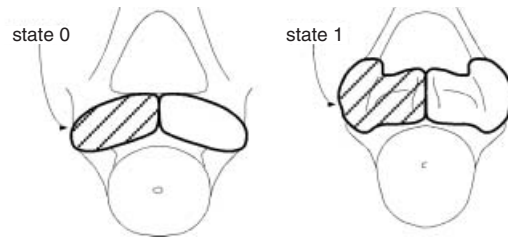
Figure 45. States of character 11. Shape of the exoccipital articular facets.

code for the character 12 states:
    0 => metapterygoid lamina present.
    1 => metapterygoid lamina strongly reduced.
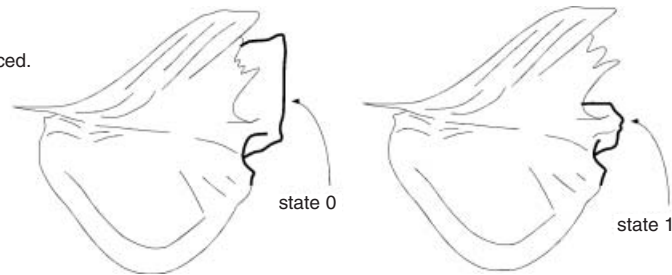
Figure 46. States of character 12. Metapterygoid lamina.

11. Shape of the exoccipital articular facets (Fig. 45). The exoccipital facets for the articulation with the first vertebra are rounded and they only contribute to the floor of the foramen magnum in non-perciform ctenosquamates as well as in many perciforms, except *Lates* within the examined taxa. The articular facets of latid exoccipitals are bean-shaped, developing laterally to the foramen magnum and contributing to the basal part of its walls (unknown in fossil species).

The suspensorium
Johnson (1980) considered that the suspensorium may prove to be one of the most important complexes in the elucidation of percoid relationships, because despite the role of this apparatus and the strong plasticity of the jaws, a similar configuration of the suspensorium appears to be retained between closely related taxa whatever their feeding habits. According to this author, the generalized configuration of the percoid suspensorium is that of his Percichthyidae (i.e. *Morone*, which he included with the percichthyids) with a minimal osseous contact between bones, a symplectic without an extension behind the ascending process of the hyomandibula, and a metapterygoid lamina (*sensu* Matsubara, 1943) articulating with the hyomandibular ascending process and providing an interosseous space between the metapterygoid ascending lamina and the hyomandibula, whereas derived taxa have an ectopterygoid posterior projection that separates the quadrate and the entopterygoid. The projection exists in latid fish and also in a few species of each order of examined basal ctenosquamates.

12. Metapterygoid lamina (Fig. 46). The metapterygoid lamina (*sensu* Matsubara, 1943) is not present in non-percomorph ctenosquamates [although Patterson (1964) described a double dorsal lamina in the metapterygoid of the ctenothrissiform *Aulolepis*]. A metapterygoid lamina is present in beryciform and most of the examined percoid fish. Its presence thus appears to be a percomorph apomorphy. Among others, *Centropomus*, *Ambassis* and *Niphon* have a well-developed lamina, whereas it is reduced to a notch and a ridge in latids (known in †*Lates bispinosus*, †*Eolates gracilis*), and also in three of the other examined species (i.e. *Perchichthys trucha*, *Eupomotis aureus* and *Priacanthus arenatus*).

13. Northworthy spine(s) at the posterior angle of the preopercululm (Fig. 47). Except for some beryciforms (the holocentrid *Holocentrus* and the trachichthyid *Gephyroberyx*), neither non-perciform ctenosquamates nor most percoid fish possess a strong spine at the posterior angle of the preopercululm. Thus, even if a strong preopercular posterior spine develops in many perciform larvae, the absence of such a spine in adults is considered primitive (Baldwin & Johnson, 1993). Furthermore, these authors noted the development of such a spine in niphoninine adults as an autapomorphy for the tribe, and the absence of an elongated spine at the preoperculum in the larval diplopriinines, liopropomines and grammistinines as a synapomorphy (those tribes are serranids). *Centropomus* and *Ambassis* [and also *Morone* and *Lateolabrax* (Katayama (1959)] show the primitive state of the character (no spine).

code for the character 13 states:
    0 => no large triangular spine at the posterior angle of the two limbs of preoperculum.
    1 => large triangular spine (or several strong spines) at the posterior angle of the two limbs of preoperculum present.
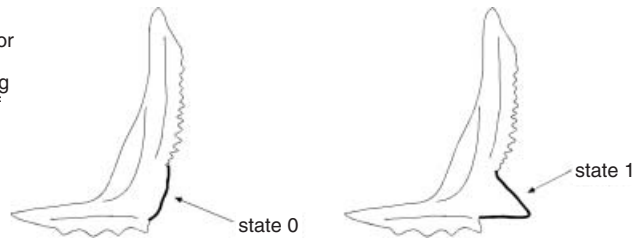
state 1

state 0

Figure 47. States of character 13. Posterior spine of the preoperculum.

code for the character 14 states:
    0 => denticulation along the ventral border of the horizontal limb of the preoperculum.
    1 => strong triangular spines along the ventral border of the horizontal limb of the preoperculum.
    2 => smooth border of the horizontal limb of the preoperculum.

state 0   state 1   state 2
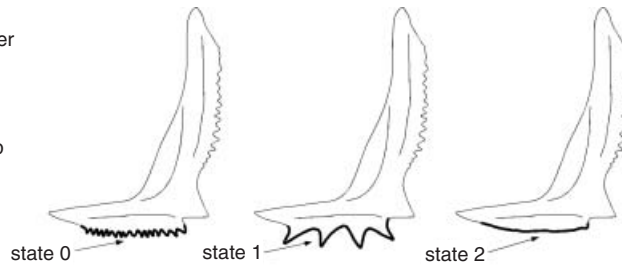
Figure 48. States of character 14. Ventral border of the preopercular horizontal limb.

code for the character 15 states:
    0 => the sensory canal runs in an open groove along the vertical limb of the preoperculum.
    1 => the sensory canal runs in a tube opened by numerous openings.
    2 => the sensory canal runs in a close tube.

state 0   state 1   state 2
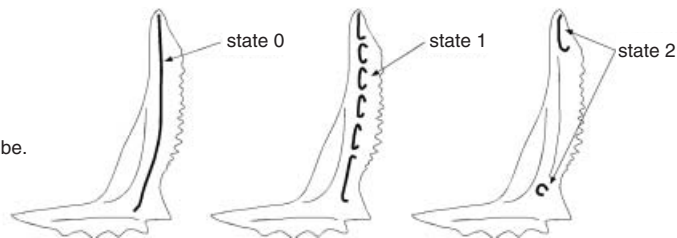
Figure 49. States of character 15. Sensory canal on the ascending limb of the preoperculum.

Latids and *Niphon* (and some others such as *Siniperca*) have a strong spine at the posterior angle of the preoperculum.

14. Ornamentation of the preoperculum horizontal limb (Fig. 48). In basal acanthomorphs and most percoids, like *Centropomus* and some latids, the ventral border of the horizontal limb of the preoperculum is smooth (*Psammoperca*) or feebly serrated (*Lates stappersi*). In other latids and in *Niphon* [and in some other percoid taxa such as *Hapalogenys* and *Lateolabrax* (Katayama (1959)] strong spines develop ventrally on the preopercular horizontal limb. *Ambassis woolffii* is polymorphic for this character. Greenwood (1976) noted that large and well-separated spines are rare among perciforms, and are only known in serranids, *Percalates*, *Siniperca* and in his 'centropomids'. In the latter family, he interpreted both *Centropomus* and *Lates stappersi* as derived taxa for this character, considering that the smooth ventral border is due to a reduction of the ornamentation.

The preopercular branch of the sensory canal
In basal ctenosquamates (ctenothrissiforms, pattersonichthyiforms, aipichthyoids, polymixiiforms and beryciforms), the preopercular branch of the sensory canal runs in an open groove with or without a bony bridge at the angle of the two limbs of the bone. In some percoids, the sensory canal runs in a bony tube. The extent and distribution of the sensory canal bony cover is different on the horizontal branch and on the vertical one, depending the taxa (*Niphon*), so that two different characters are considered.

15. Sensory canal on the ascending limb of the preoperculum (Fig. 49). This runs in an open groove in *Centropomus* and *Ambassis*. In most of the examined percoids, the open groove is covered by several bridges (*Siniperca*, *Hapalogenys* and in percids, serranids and centrarchids, for example). In *Lates*, †*Eolates* and *Psammoperca*, the sensory canal runs in a bony tube.

16. Sensory canal on the horizontal limb of the preoperculum (Fig. 50). It runs in an open groove on the horizontal limb of the preoperculum in *Centropo-*

code for the character 16 states:
    0 => the sensory canal runs in an open groove along
the horizontal limb of the preoperculum.
    1 => the sensory canal runs in a groove with numerous
bony bridges.

state 0   state 1
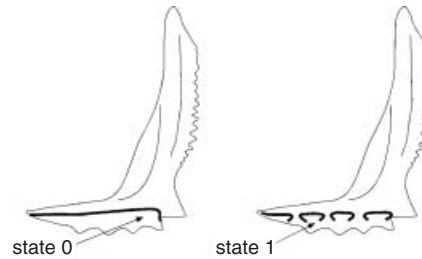
Figure 50. States of character 16. Sensory canal on the horizontal limb of the preoperculum.

code for the character 17 states:
    0 => flat articular process of the premaxilla, with or without
a vertical gutter.
    1 => ridge along the anterior border of the articular
process of the premaxilla.

state 0   state 1
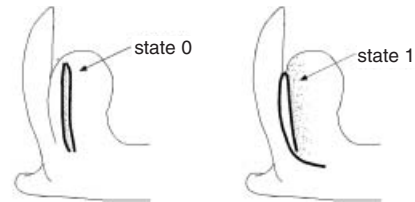
Figure 51. States of character 17. Articular process of the premaxilla.

code for the character 18 states:
    0 => more than 12 abdominal vertebrae.
    1 => 10 abdominal vertebrae.
    2 => 12 abdominal vertebrae.
    3 => 11 abdominal vertebrae.

state 1
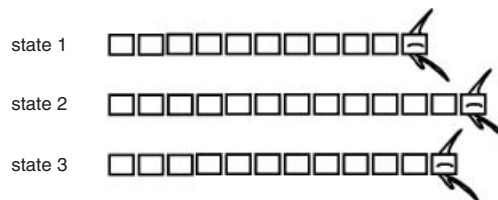
state 2

state 3

Figure 52. States of character 18. Vertebral formula (see also Table 2).

mus and *Ambassis*, whereas the groove is covered by several large bony bridges in many percoids, including Latidae, *Siniperca* and *Niphon*.

17. Articular process of the premaxilla (Fig. 51). The lateral surface of the articular process of the premaxilla is flat (with or without a vertical groove) in non-percoid ctenosquamates and in most of the examined perciforms, particularly †*Eolates gracilis* (unknown in other fossil latid species), *Psammoperca*, *Centropomus*, *Ambassis* and *Niphon* [as well as many others, such as percids, lutjanids and most serranids (except *Grammistes*)]. In *Lates* a strong vertical ridge develops anteriorly on the articular process (it is also present in *Morone* and *Siniperca*).

18. Vertebral formula (Fig. 52). The variation in the number of caudal vertebrae is not significant for the concerned taxa (14 or 15), whereas the number of abdominal vertebrae is quite stable within families. In non-perciform ctenosquamates, the abdominal count is higher than 12 [except in the beryciform Berycidae (10) and Holocentridae (11) (Zehren, 1979), and in the aipichthyids (11) (Otero & Gayet, 1996)]. Among percoids, the most common vertebral count is 10+14/15.

Gosline (1968) considered that this latter formula (10+14/15) is primitive for his percoids, and Johnson (1984) found such a count in half of the percoid families. However, some families differ in their vertebral count [e.g. Centrarchidae (11/14+15/19; Johnson, 1984), *Percichthys* (usually >30), Percidae (> 40)]. *Centropomus*, *Ambassis* and †*Eolates gracilis* show the percoid general state of the character with ten abdominal vertebrae, whereas other latids (observed in †*E. aquensis*, †*Lates bispinosus* and †*L. gregarius*) have 11 abdominal vertebrae. Some other percoid taxa show different abdominal counts; for example, Baldwin & Johnson (1993) noted a count of 30 vertebrae as an autapomorphy of *Niphon* among serranids (the members of this family normally show 24 vertebrae, of which ten are abdominal). Among Grammistini, they used the abdominal count as a synapomorphy of *Grammistes* and *Pogonoperca*, despite the strong variations of the vertebral count in the family. Finally, they considered a count of 26–28 vertebrae as a synapomorphy for *Aporops*, *Pseudogramma* and *Suttonia*.

19. Configuration of the first haemal spine (Fig. 53). In non-perciform ctenosquamates and in many perci-

code for the character 19 states:
      0 => first haemal spine totally fused to the
parapophyses (simple).
      1 => first haemal spine partially fused to the
parapophyses (enlarged or trifid).
      2 => first haemal spine not fused to the
parapophyses.
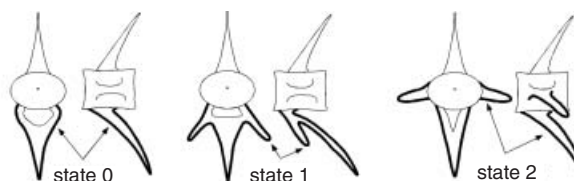
Figure 53. States of character 19. Configuration of the first haemal spine.

code for the character 20 states:
      0 => one dorsal pterygiophore
supporting rays is bipartite,
others tripartite.
      1 => several dorsal pterygiophores
supporting rays are bipartite,
several tripartite.
      2 => all dorsal pterygiophores supporting
rays are bipartite.
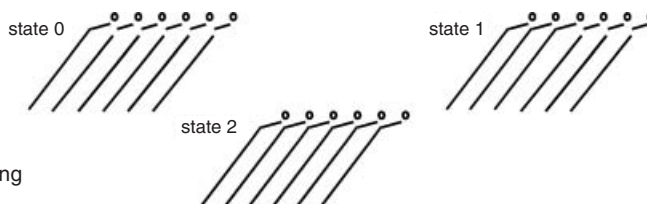
Figure 54. States of character 20. Pterygiophores (see also Table 2).

code for the character 21 states:
      0 => two supernumerary dorsal spines.
      1 => only one supernumerary dorsal spine.
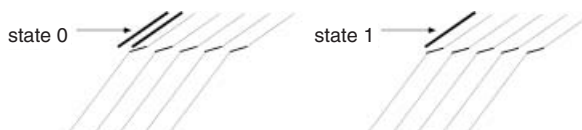
Figure 55. States of character 21. Dorsal supernumerary spines (see also Fig. 30, Table 2).

forms, the first haemal spine is fused with the two parapophyses and the observed structure is similar to that of the following haemal spines. This is observed in *Centropomus*, *Ambassis* and *Niphon* [as well as all the serranids, and Johnson (1980) described the parapophyses of the first caudal vertebra as fused in the midline to form the first haemal spine in the Lutjanoidea]. By contrast, latids (known in the fossils †*L. bispinosus* and †*E. gracilis*) show a modified haemal spine, trifid in anterior view, as if a fusion had occurred between the parapophysis, the bony bridge and an haemal spine. The latter state was observed elsewhere only in some percid fish (*Lucioperca* and *Perca*) and in *Terapon*. The development of the very broad haemal arches of the examined percichthyids could represent an intermediate stage between the two preceding ones (haemal spine simple/trifid). This is supported by Arratia (1982), who figured this latter stage in *Percichthys lonquimayensis* and the trifid configuration in other *Percichthys* and *Percilia* species.

20. Dorsal and anal pterygiophores (Fig. 54). Bridge (1896; in Johnson, 1980) first elucidated the tripartite nature of the teleost median fin support. Primitively, in lower teleosts, there is a proximal, a medial and a distal radial, the three parts forming a pterygiophore, but there is a tendency for these supports to become bipartite through the fusion of the proximal and medial radials (Bridge, 1896; in Johnson, 1980). In most of the examined percoids, the pterygiophores are bipartite in the anterior part of the fin and tripartite in the posterior part. In another state, the medial radial is fused to the (bipartite) pterygiophores supporting the rays. Here the focus is on the presence of the tripartite pterygiophore. In *Polymixia*, only the first pterygiophore is bipartite and all others are tripartite. In *Lates* and *Niphon* (and also in most of the percoids studied, e.g. *Morone*, *Siniperca* and *Hapalogenys*), the anteriormost rays are bipartite and the posteriormost tripartite. Additionally, Baldwin & Johnson (1993) noted the lack of an autogenous first distal radial to be an epinephelin apomorphy, the first pterygiophore being primitively bipartite in percoids and other serranids. All the pterygiophores are bipartite in *Psammoperca*, *Centropomus* and *Ambassis*. The distribution of the character states is similar for the anal fin for the analysed taxa and unknown in fossil species.

21. Dorsal supernumerary spines (Fig. 55). Johnson (1984) considered the presence of two supernumerary spines to be the most common and primitive state for percoids. By means of an outgroup analysis of teleosts, Patterson (1992) demonstrated that two supernumerary elements is the primitive perciform number. This is the state in *Centropomus*, *Niphon*; according to Johnson (1984), the predorsal formula of *Ambassis*, with one supernumerary fin spine is homologous. By

code for the character 22 states:
  0 => type 0 association.
  1 => type 1 association.
  2 => type 2 association.
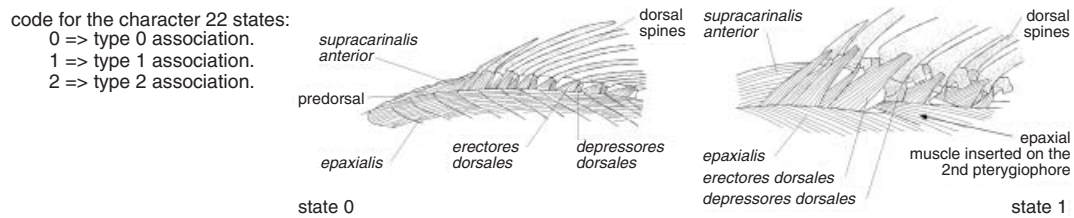
Figure 56. States of character 22. Epaxial musculature, after Mooi & Gill (1995).

code for the character 23 states:
  0 => 3 epurals.
  1 => 2 epurals.

Figure 57. States of character 23. Epural count (see also Table 3).

code for the character 24 states:
  0 => one uroneural and one stegural.
  1 => stegural only.
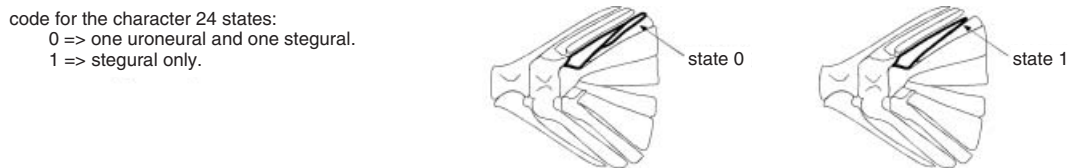
Figure 58. States of character 24. Uroneural (see also Table 3).

contrast, there is only one supernumerary spine in both Recent and fossil latids. The reduction in the anal supernumerary spine count does not vary among the taxa in the analysis. They all have two supernumerary anal spines.

22. Association between the epaxial musculature and the dorsal skeleton (Fig. 56). This character and its phylogenetic implications have been defined and studied by Mooi & Gill (1995) in all extant acanthomorph families, generally including several species. Among other results, it enabled them to question the phylogenetic relationships between the Latidae and the Centropomidae. They defined four types of association, with type 0 shown to be the plesiomorphic state, and the rest not polarized (although the structural complexity increases with the number of the type of association). Two types are of concern here. Their data are included in this analysis without any modification and the taxa they used are given in parentheses.

type 0: there is no insertion of the epaxial muscles on the distal tips of the pterygiophores. This plesiomorphic state is observed in *Polymixia*, *Centropomus* (*C. armatus*, *C. ensiferus*, *C. pectinatus* and *C. unidecimalis*), and in Ambassidae (*Ambassis* sp. and *Chanda ranga*) among others.

type 1: there is a separate slip of epaxial musculature that inserts dorsally on the second pterygiophore, directly posterior to the second spine. This apomorphic state is that of the Latidae (*Lates calcarifer*, *L. mariae*, *L. niloticus* and *Psammoperca waigiensis*) and of *Niphon spinosus* (and the serranids). According to the authors, this apomorphic state is the easiest to identify.

23. Epural count (Fig. 57). The primitive state of three epurals is observed in all non-perciform ctenosquamates and in half the percoids studied. Among the latter, this is the state in *Centropomus*, *Niphon* and †*Eolates* (observed in †*E. gracilis* and †*E. aquensis*), whereas *Lates*, *Psammoperca* and *Ambassis* have two epurals.

24. Uroneural (Fig. 58). The state comprising a well-developed stegural and one uroneural is observed in non-perciform ctenosquamates and most percoids. Regarding the lack of the uroneural, Johnson (1983) stressed that there is no argument to support the idea that the distal process of the stegural is a relic of the lost uroneural. I agree, on the basis that a well-developed posterior part of the stegural is observed in taxa that still have a uroneural. A stegural plus a uroneu-

code for the character 25 states:
  0 => autogenous hypurals.
  1 => hypurals 3 and 4 fused
to the pseudurostylar complex.
  2 => hypurals 2, 3 and 4 fused
to the pseudurostylar complex.
  – => others.
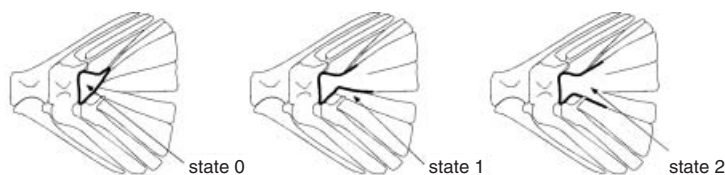
Figure 59. States of character 25. Hypurals (see also Table 3).

code for the character 26 states:
  0 => no modification of the posttemporal.
  1 => modification of the posttemporal due
to the connection with the *tunica externa.*
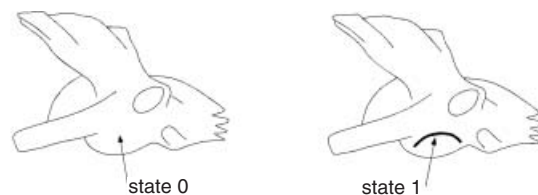
Figure 60. States of character 26. Connection between the tunica externa and the posttemporal.

code for the character 27 states:
  0 => smooth posterior border of the cleithrum.
  1 => posterior border of the cleithrum with one or several spines.
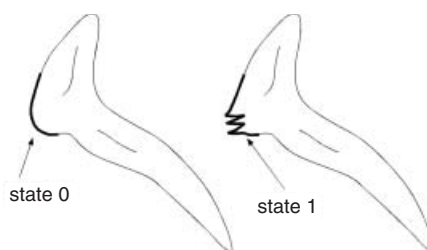
Figure 61. States of character 27. Posterior border of the posterior plate of the cleithrum.

ral is found in *Lates*, †*Eolates*, *Centropomus* and in most of the percoids studied. *Psammoperca* and *Niphon* (and also all the other serranids and some percids) have one stegural but no uroneural [the loss of the uroneural was noted by Greenwood (1976) as a common character for *Psammoperca* and the Serranidae *sensu* Gosline (1966)].

25. *Hypurals* (Fig. 59). The five hypurals are generally separate and autogenous in basal ctenosquamates and also in most of the percoids studied, including †*Eolates* and *Niphon*. This state is observed in the young of some species in which the adults show hypural fusion. Different types of hypural fusion are observed: hypurals 3 and 4 [in *Psammoperca*, *Lates*, adult *Centropomus* and *Ambassis* (*A. wolffii*)], and all hypurals except the fifth are fused to the centrum in *Lates stappersi*.

26. *Connection between the tunica externa and the posttemporal* (Fig. 60). In *Lates* and *Psammoperca*, the swimbladder and the posttemporal are connected by a connective tissue from an antero-dorsal point on the tunica externa to a depression on the ventral part of the posttemporal medial face (Greenwood, 1976). According to this author, this is a characteristic of the family Latidae among percoids. Because of working

mostly with dry skeletons and fossils, the connective tissue itself has not been observed. Therefore, it is the presence of the depression on the medial face of the posttemporal that defines this original state [observed in all Recent species and in disarticulated fossils (†*Lates* sp. cf. *niloticus* from the Pliocene of the Natronal)]. This modification was not observed in any other fish examined.

27. *Ornamentation on the posterior border of the cleithrum* (Fig. 61). The border of the cleithral posterior plate is either ornamented with one to several small spines or smooth. It is smooth in non-perciform ctenosquamates (in the beryciform *Ostichthys*, small spines are present but limited to the upper part of the posterior border of the ascending limb). The posterior plate of the cleithrum bears one or several spines in the Latidae, both extant and fossil (known in †*Eolates gracilis*, †*E. aquensis*, †*Lates gregarius,* †*L. bispinosus*), and in *Niphon* (one spine), whereas it is smooth in *Centropomus*, *Ambassis* and in other percoids such as non-niphonine serranids and lutjanids.

28. *Ventral expansion on the posterior plate of the cleithrum* (Fig. 62). In non-perciform ctenosquamates, perciforms and some percoid fish, the ventral border of the cleithral plate is smooth, whereas in the

code for the character 28 states:
    0 => no ventral expansion on the posterior plate
of the cleithrum.
        1 => ventral expansion on the posterior plate
of the cleithrum present.
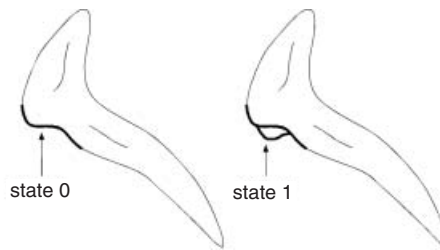
Figure 62. States of character 28. Ventral expansion on the posterior plate of the cleithrum.

code for the character 29 states:
    0 => no median posterior process
    1 => median posterior process
of the pelvic bone rod-like or spear-head shaped.
    2 => median posterior process
of the pelvic bone with a sharp point.
    3 => median posterior process
of the pelvic bone in short massive expansion.
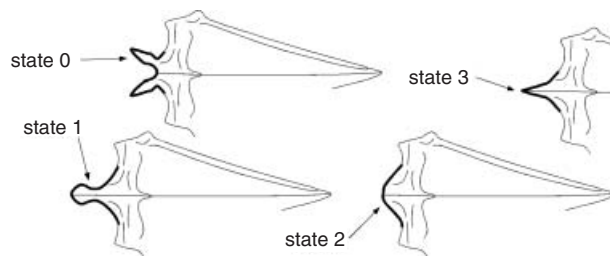
Figure 63. States of character 29. Medio-posterior process of the pelvic bone.

other percoids, a small bony expansion develops ventrally on that plate. *Centropomus* and *Niphon* show the former generalized state, whereas both Recent and fossil Latidae and *Ambassis* show the latter state.

29. Medio-posterior process of the pelvic bone (Fig. 63). In percomorphs and holocentrids only, there is a posterior suture between the two pelvic bones (Stiassny & Moore, 1992; O. Otero, pers. observ.) and a suture between the two hemi-processes in their proximal part, whereas in more primitive groups the two hemi-processes remain separated (*Polymixia*). The length of the postero-median process was used by Gosline (1966) as a difference between his perichthyids (long process) and serranids (short process). In fact, the variations appear to be more complex within families; moreover, Arratia (1982) noted some intraspecific variations in the lengthening, and Johnson (1980) considered the comparison of the posterior process length as a poor taxonomic character. By contrast, the shape of the posterior process appears to be more reliable. It is a sharp, pointed process in the Latidae, both Recent and fossil (observed in †*Eolates gracilis* and †*Lates bispinosus*), whereas it is a spear-head-like posterior process in *Ambassis* and *Niphon* (and also *Siniperca*, *Hapalogenys* and *Morone*) and the process is reduced to a massive expansion between the two fins in *Centropomus*.

RESULTS, DISCUSSION AND CONCLUSION

The cladistic analysis is based on 29 characters, 28 of which are osteological and one myological (insertion of the epaxial muscles of the dorsal fin; data from Mooi & Gill, 1995). The character states were coded in a data matrix using MacClade, and processed with PAUP 3.1.1 with an exact search method algorithm (exhaustive search) to obtain the most parsimonious hypothesis. The trees are rooted with an outgroup (*Polymixia lowei*).

By processing the data matrix with the character states unordered and of equal weight, five most parsimonious trees were retained; their length is 49 steps [CI = 0.796; RI = 0.848; RC = 0.675].

Figure 64 shows the consensus tree, and Figure 65 the conflicting arrangements, both with the distribution of the character states (including equivocal positions). The main results are: the paraphyly of the family Centropomidae *s.l.*; the monophyly of the family Latidae (*Psammoperca,* †*Eolates* and *Lates*); the monophyly of the group (*Psammoperca* + *Lates*); and the polyphyly of the genus †*Eolates* as a stem group at the base of the family. The distribution and the support for the nodes are critiqued below with reference to the character descriptions. The differing hypotheses for the *Lates* species intrarelationships are discussed. Moreover, a synthetic table (Table 5) of the diagnostic characteristics of both the Recent and the fossil latids highlights the 'resemblances' between the taxa and gives the autapomorphic characters for the species.

'PERCOID' (FIG. 64)

This group is monophyletic in the analysis and unites the perciform fishes of the analysis, separate from the
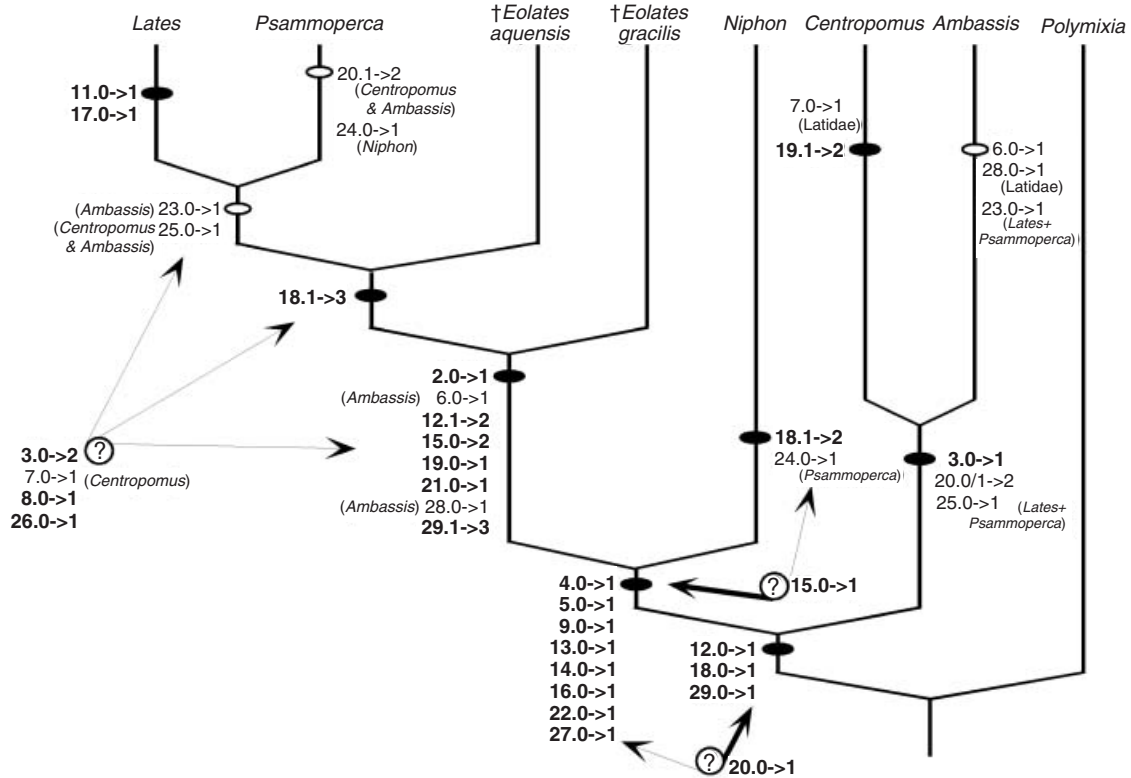
Figure 64. Strict consensus of the five most parsimonious trees (indices in the text) obtained by a cladistic analysis of character states summarized in the data matrix (Table 4). The character state changes are given. Apomorphies are in bold type. See Fig. 65 for the area of disagreement.

outgroup, *Polymixia lowei*. The monophyly of the suborder Percoidei itself is not discussed and the attribution of the species to the suborder is accepted as defined by Johnson (1984). Three characters unite the percoid taxa in the analysis.

- A metapterygoid lamina (character 12, state 1) is present in the beryciforms and perciforms studied. It appears to be a percomorph apomorphy.
- An abdominal vertebrae count of ten (character 18, state 1) is generally considered as the percoid primitive condition.
- The presence of a spear-head-like median posterior process of the pelvic bone (character 29, state 1) appears to be apomorphic at that node. A median process exists in the percomorph and holocentrid fish, and its shape may be a character available at the family level; the roughly spear-head-like pattern is observed in some other basal percoids and could be a primitive/generalized state.

A fourth character is highly probably an apomorphy at this node rather than at the '*Niphon* + latid' node.

- The anteriormost pterygiophores of the dorsal fin are bipartite, the posteriormost are tripartite (character 20, state 1). This character has an ambiguous position in the analysis. However, I assume that the

state of several bipartite pterygiophores preceded the state in which all the pterygiophores are bipartite (which exists in *Ambassis* + *Centropomus*, and in *Psammoperca* and is then interpreted as a more derived state). This agrees with the hypothesis made by Patterson (1992) of a general tendency towards the fusion of the pterygiophore radials, as well as with Baldwin & Johnson (1993), who considered (state 1) to be the primitive condition for the character in percoids.

THE PARAPHYLY OF THE FAMILY CENTROPOMIDAE *S.L.* (FIG. 64)

The distribution of the ingroups within the family Centropomidae *s.l.* clearly demonstrates its paraphyly. '*Ambassis* + *Centropomus*' appears to be the sister-group of '*Niphon* + Latidae', both taxa being defined by three and eight character states, respectively, which could be apomorphies for upper level taxa of percoids.

Greenwood (1976) considers that the broad shape of the first neural spines in *Lates*, *Psammoperca* and *Centropomus* indicates their common phylogenetic origin, whereas, according to Mooi & Gill (1995), this

Table 5. Osteological differences between Recent and fossil latid species. All data detailed in the text. Some characters are accepted as described in the literature: *from Holden (1967), Sorbini (1975) and Gaudant (1977); from Greenwood (1976); **this latter character is only seen in Recent species. ***†*Lates karungae* was defined on the basis of a cavity posterior to the anterior facet of the first centrum and the third vertebra with the fossae for the articulation of the rib as long as deep +, ++, +++: increasing narrowing and elongation of body and bones

	Age	Distribution	Environment	Narrow elongated body & bones	Snout/neuro-cranial length	Braincase/snout	Orbit	Vomerine tooth patch	Pleuro-sphenoid pedicle	Para-sphenoid	Supraoccipital development/neuro-cranium	Frontal lateral plate	Supernumerary opening on the pterotic	Walls of the braincase	Exoccipital facet shape
†*Eolates gracilis*	Lower Eocene	Monte Bolea	marine	no	<20%			?	no(?)	straight	?	reduced	no	flat	?
†*Eolates aquensis*	Oligocene	South France	marine to FW(?)	no	<20%			?	no(?)	straight	?	reduced	no	?	?
†*Eolates macrurus*	Lower Eocene	Paris Basin	coastal water	no	?			?	?	straight(?)	?	?	?	?	?
†*Lates (L.) bispinosus*	Neogene	Turkey	freshwater	no	?			?	yes(?)	straight	?	strong	no	flat	?
†*Lates (L.) partshii*	Middle Miocene	Wien Basin	freshwater	no	<20%			?	?	straight(?)	?	?	?	?	?
†*Lates (L.) macropterus*	Oligocene	Italy	freshwater(?)	no	?			?	?	straight(?)	?	?	?	?	?
†*Lates (L.) gregarius*	Upper Miocene	Moldavia	freshwater	no	<20%			?	?	straight	?	?	?	?	?
†*Lates (L.) croaticus*	Miocene	Croatia	freshwater(?)	?	?			?	?	straight(?)	?	?	?	?	?
†*Lates (L.) karungae****	Lower Miocene	Kenya	freshwater	?	?			?	?	?	?	?	?	?	?
Lates (L.) niloticus	UpMio-Recent	Africa(+ Italy)	freshwater	no	<20%			shape variable	yes strong	straight	0.3–0.25	strong	no	flat	bean
Lates (L.) longipinis	Recent	L. Rodolph (Afr)	freshwater	no	<20%		large	yes	slightly curved	straight	#0.3	yes	flat	bean	
Lates (L.) macrophtalmus	Recent	L. Albert (Afr)	freshwater	no	<20%		large	yes	straight	straight	#0.25	yes	inflated	bean	
Lates (L.) calcarifer	Recent	Indo-Pacific	coastal water	no	#15%			strong	straight	straight	#0.25	no	flat	bean	
Lates (Ll.) angustifrons	Recent	L. Tanganyika (Afr)	freshwater	+	>20%			yes	slightly curved	slightly curved	> 0.3	strong	flat	bean	
Lates (Ll.) microlepis	Recent	L. Tanganyika (Afr)	freshwater	++	>20%		large	no	strongly bent	strongly bent	#0.3	yes	inflated	bean	
Lates (Ll.) mariae	Recent	L. Tanganyika (Afr)	freshwater	++	>20%		large	no	strongly bent	strongly bent	#0.25	yes	inflated (small)	bean	
Lates (Ll.) stappersi	Recent	L. Tanganyika (Afr)	freshwater	+++	>25%		caniniform teeth	no	strongly bent	strongly bent	#0.5	reduced	no	flat	bean
Psammoperca waigiensis	Recent	Indo-Pacific	coastal water	no	<20%	large/thin	projects ventrally	no	slightly curved	slightly curved	#0.5	no	yes +++	inflated	drop

	Supernumerary opening on infraorbitals	Pads and subocular shelf on infraorbitals	Serrations on the infraorbitals	Pre-operculum horizontal limb	Branchiostegal ray number	Branchiostegal ray position on ceratohyal	Other hyoid characteristics	Jaw teeth	Premaxilla ascending articular process	Articular process of premaxilla	Premaxilla posterior border	Single supramaxilla anterior process	Dentary sensory canal openings	Dentary symphysial striae	Ventral notch of dentary	Angulo-articular shape	Angulo-articular glenoid cavity
†*Eolates gracilis*	iorb2, 3	pad on iorb1	iorb 1, 2, 3	4 (3) spines	7 + 1(?)	?	short & deep bones	villiform	#1.5	with groove	concave	yes	4	no	yes	deep	deep
†*Eolates aquensis*	?	?	?	4 spines	?	?	?	villiform	#1.5	with groove	?	yes	?	?	?	mid	?
†*Eolates macrurus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Lates (L.) bispinosus*	?	?	?	3 spines	?	?	?	villiform	?	?	?	?	?	?	?	?	?
†*Lates (L.) partshii*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	flat	flat
†*Lates (L.) macropterus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Lates (L.) gregarius*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Lates (L.) croaticus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Lates (L.) karungae****	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lates (L.) niloticus	iorb3	sos iorb3	iorb 1, 2, 3	4(3) spines	7	cerato & epihyal	basibr. toothless	villiform	1.3–1.6	with ridge	notch	yes	4(5)	yes	yes	mid	mid
Lates (L.) longipinis	iorb3	sos iorb3	iorb 1, 2	3 or 4 spines	7	cerato & epihyal	basibr. toothless	villiform	1.3–1.6	with ridge	notch	yes	4	no	yes	mid	mid

Table (continued from previous page) — osteological characters, last 7 taxa

Species	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14
Lates (L.) macrophtalmus	iorb3	sos iorb3	3 or 4 spines	7	basibr: toothless	villiform	cerato & epihyal	4	notch / with ridge	1.3–1.6	villiform	yes	mid	mid
Lates (L.) calcarifer	iorb3	sos iorb3	3 spines	7	basibr: toothless	villiform	cerato & epihyal	5	notch / with ridge	1.3–1.6	villiform	yes	mid	deep
Lates (Ll.) angustifrons	iorb3	sos iorb3	3 spines	7	basibr: toothless	villiform	cerato & epihyal	4	notch / with ridge	1.3–1.6	villiform	yes	mid	mid
Lates (Ll.) microlepis	iorb3	sos iorb3	4(3) spines	7	basibr: toothless	villiform	cerato & epihyal	4	notch / with ridge	1–1.3	villiform	yes	mid	mid
Lates (Ll.) mariae	iorb3	sos iorb3	4(3) spines	7	basibr: toothless	villiform	cerato & epihyal	4	notch / with ridge	1–1.3	villiform	yes	mid	mid
Lates (Ll.) stappersi	iorb3	sos iorb3	serrations	7	basibr: toothless	caniniform	cerato & epihyal	4	notch / with ridge	#1	villiform	no	shallow	mid
Psammoperca waigiensis	no	no	collapsed	7	basibr: toothed	villiform	cerato & epihyal	4	notch + / with ridge	#1.1	villiform	yes	flat	flat

Table — vertebral and fin characters

Species	No. of abdominal vertebrae	No. of post-abdominal vertebrae	No. of epineural pairs	Abdominal vertebrae without parapophysis	Ventral carena on vertebra 2	Vertebra 3 longer than high	Predorsal formula	Dorsal fin formula	Dorsal fin gap	Bipartite dorsal pterygiophores supporting rays	Anal formula	Post-temporal spines	Bipartite anal pterygiophores supporting rays
†Eolates gracilis	10	14	7	5	no	no	0/0/0 + II/I + I/(+)	VIII – I + 10(9)	weak	?	III + 8	yes	?
†Eolates aquensis	11/12	13/14(15)	7	7	?	?	/0/0 + 0 + II/I + I/	VI-I + 10/12	weak	?	III + 7/8	yes	?
†Eolates macrurus	?	?	?	?	?	?	?	?	weak	?	?	?	?
†Lates (L.) bispinosus	11	?	6	7	no	no	0 + 0//0 + II/I + I/	VII-I + 8	weak	?	II + 7(?)	?	?
†Lates (L.) partishii	?	?	?	?	?	?	?	?	?	?	?	?	?
†Lates (L.) macropterus	?	14	6	7	?	?	0/0/0 + II/I + I/	VII-I + 10	?	?	III + 8	?	?
†Lates (L.) gregarius	11	?	?	?	?	?	?	?	mid	?	?	?	?
†Lates (L.) croaticus	?	?	?	?	?	?	?	?	?	?	?	?	?
†Lates (L.) karungae***	?	?	?	?	no***	no***	?	?	?	?	?	?	?
Lates (L.) niloticus	11	14	6/7	6/7	no	no	0/0/0 + II/I + I/	VII-I + 12(11)	mid	(5)6 (7)	III + 8	yes	2/4
Lates (L.) longipinis	11	14	5/7	6	no	?	0/0/0 + II/I + I/	VI-I + 11/12	mid	5/7	III + 8(7)	yes	3/5
Lates (L.) macrophtalmus	11	14	7	6/7	no	?	0/0/0 + II/I + I/	VI-I + 12/11	mid	6 (7)	III + 7/8	yes	3
Lates (L.) calcarifer	11	14	?	6/7	no	no	0/0/0 + II/I + I/	VI-I + 10	mid	4/5	III + 8	yes	2/3
Lates (Ll.) angustifrons	11	14	6 (7)	7	no	no	0/0/0 + II/I + I/	VI-I + 12	mid	6	III + 8	yes	3
Lates (Ll.) microlepis	11	14	7	6/7	no	slightly	0/0/0 + II/I + I/	VII-I + 12(13)	mid	7	III + 8	yes	2/4
Lates (Ll.) mariae	11	14	7	6/7	no	slightly	0/0/0 + II/I + I/	VII(VIII) – I + 10	mid	6	III + 8	no	3
Lates (Ll.) stappersi	11	14	5	5	no	yes +++	0/0/0 + II/I + I/	VIII – I + 10	wide	4/5	III + 9	yes	2/4
Psammoperca waigiensis	11	14	7/8	5/6	yes	no	0/0/0 + II/I + I/	VI-I + 12	mid	all	III + 8	yes	6

Table — caudal and other characters

Species	No. of epurals	Uroneural present	Fusion between the hypurals	No. of post-hypurals	Fusion of the hypurals with the centrum	Other hypurals characteristics	Caudal formula	Caudal fin spur	Predorsal formula	Caudal fin outline	Dorsal fin formula	Height/length of caudal peduncle*	Lateral line on caudal fin	Count of spines on the cleithral plate	Pectoral fin rays	Post-temporal spines	Nostril position**
†Eolates gracilis	3	yes	none	none	none	Hpu2 enlarged	(8)-I-8:7-I-(7)	yes	0/0/0 + II/I + I/(+)	rounded	VIII – I + 10(9)	< 1	simple	2(3)	14	yes	?
†Eolates aquensis	3	yes	none	none	none	Hpu2 enlarged	(8)-I-8:7-I-(7)	?	/0/0 + 0 + II/I + I/	rounded	VI-I + 10/12	# 1	?	3	14–16	yes	?
†Eolates macrurus	3	?	?	?	?	?	?	?	?	rounded	?	> 1.5	?	2(3)	?	?	?
†Lates (L.) bispinosus	?	yes	?	?	?	?	?	?	0 + 0//0 + II/I + I/	?	VII-I + 8	?	?	3	14	?	close
†Lates (L.) partishii	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	close
†Lates (L.) macropterus	?	yes(?)	?	none (?)	?	?	?	?	0/0/0 + II/I + I/	?	VII-I + 10	?	?	2(?)	?	?	close
†Lates (L.) gregarius	?	?	?	?	?	?	?	?	?	rounded	?	?	?	?	?	yes	close
†Lates (L.) croaticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	close
†Lates (L.) karungae***	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	close
Lates (L.) niloticus	2	yes	none	2-3-4	2-3-4	apo parhyp & Hpu2	(7/8)-I-8:7-I-(7/8)	yes	0/0/0 + II/I + I/	round-truncated	VII-I + 12(11)	1–1.4	triple	5–10	14	yes	close
Lates (L.) longipinis	2	yes	none	2-3-4	2-3-4	apo parhyp & Hpu2	8/9)-I-8:7-I-(9)	yes	0/0/0 + II/I + I/	round-truncated	VI-I + 11/12	?	triple	3	14	yes	close
Lates (L.) macrophtalmus	2	yes	none	2-3-4	2-3-4	apo parhyp & Hpu2	(8/9)-I-8:7-I-(7/8)	yes	0/0/0 + II/I + I/	round-truncated	VI-I + 12/11	1.5–2	triple	5–7	14	yes	close
Lates (L.) calcarifer	2	yes	none	2-3-4	2-3-4	apo parhyp & Hpu2	(6)-I-8:7-I-(6)	yes	0/0/0 + II/I + I/	round-truncated	VI-I + 10	1.5–2	triple	5–10	14	yes	close
Lates (Ll.) angustifrons	2	yes	none	2-3-4	2-3-4	apo parhyp & Hpu2	(9)-I-8:7-I-(8)	yes	0/0/0 + II/I + I/	round-truncated	VI-I + 12	1.4–1.9	triple	6–10	14	yes	close
Lates (Ll.) microlepis	2	yes	none	2-3-4	2-3-4	apo parhyp & Hpu2	(7/8-I-8:7-I-(6/7)	yes	0/0/0 + II/I + I/	straight-crescent	VII-I + 12(13)	1.9–2.3	triple	3–4	14	yes	close
Lates (Ll.) mariae	2	yes	none	2-3-4	2-3-4	apo parhyp & Hpu2	(10)-I-8:7-I-(9)	yes	0/0/0 + II/I + I/	straight-crescent	VII(VIII) – I + 10	1.8–2.3	triple	3–4	14	yes	close
Lates (Ll.) stappersi	2	no	[1–2] [3–4]	3-4	3-4	apo parhyp & Hpu2	(9/11)-I-8:7-I-(8/9)	ye	0/0/0 + II/I + I/	crescent	VIII – I + 10	>2	triple	3	14	yes	close
Psammoperca waigiensis	2	no	none	3-4	1-2-3-4-5	apo parhyp & Hpu2	(7/8)-I-8:7-I-(7/8)	no	0/0/0 + II/I + I/	round-truncated	VI-I + 12	?	simple	0	14	no	widely separated

character is not homologous. Following Mooi & Gill (1995), I do not consider this character in the analysis because of (1) the high subjectivity in its determination as the fact that it is a continuous character, and (2) its wide distribution among studied taxa. According to Greenwood, a second character supports the monophyly of the Centropomidae *s.l.*, the presence of pored lateral-line scales extending to the posterior border of the caudal fin. My study was based on osteological characters and not on scale characters; however, Mooi & Gill (1995) suggested that this scale character is possibly the plesiomorphic state within Perciformes.

THE *CENTROPOMUS* + *AMBASSIS* GROUP (FIG. 64)

This group is supported by three character states, the first being apomorphic and the two latter being homoplasic in the analysis. Moreover, all of them have been observed elsewhere among percoids.
- The frontal branch of the sensory canal running in an open groove is observed in *Centropomus* and *Ambassis* (character 3, state 1) and also in *Lateolabrax* and percichthyids.
- A fused proximal and median radial on all the pterygiophores (character 20, state 2) is also observed in *Psammoperca* (see also 'Percoid').
- The fusion of hypurals 3 and 4 with the pseudourostylar complex (character 25, state 1) is also known in *Psammoperca* and *Lates* species.

The latter two characters are also currently observed in different lineages and could be convergent for *Centropomus* and *Ambassis*. The first one could be uniting a larger group among basal percoids. In my opinion, these shared character states are far too weak to support alone a possible sister-group relationship between the families Centropomidae and Ambassidae, which appear to be plesiomorphic when compared with the other percoids in the analysis.

Although the aim of the study was not to define them, *Centropomus unidecimalis* and *Ambassis woolffii* exhibit autapomorphies. Those of *C. unidecimalis* are shared by the other species of the family Centropomidae.
- The presence of frontoparietal crests (character 7, state 1) is convergent with latids. Moreover, identifying this as convergence is supported by the different type of frontoparietal crests in *C. poeyi*, *C. pectinatus* and *C. parallelus*, in which they are not continuous between the frontal and parietal.
- The median posterior process of the pelvic bones forming a short and massive expansion is only present in Centropomidae among all the studied taxa (character 29, state 2).

Ambassis woolffii is convergent with latids or with '*Lates* + *Psammoperca*' by three characters (discussed below).

- An anteriorly developed supraoccipital bone (character 6, state 1).
- A ventral expansion on the cleithral plate (character 28, state 1).
- The presence of two epurals (character 23, state 1).

THE LATIDS + *NIPHON* GROUP (FIG. 64)

The group is supported by eight apomorphies.
- The sphenotic branch of the sensory canal runs in a tube (character 4, state 1).
- The pterotic branch of the sensory canal runs in a tube (character 5, state 1). (Both these character states have the same distribution for the analysed taxa but not among percoids.)
- A sphenotic shelf developing laterally and posteriorly (character 9, state 1). This is also observed in percids and its presence in *Niphon* is an exception among serranids, many of which show a small process instead of a shelf.
- There is a strong posterior spine at the angle of the preopercular limbs (character 13, state 1). This character state could be a convergence as it is considered to be an autapomorphy for niphonines by Baldwin & Johnson (1993) among serranids and is also present in a few other percoids.
- Strong triangular spines develop ventrally on the horizontal preopercular limb (character 14, state 1), in latids, in *Niphon* and more generally in serranids, and also in few other percoids.
- The sensory canal runs in a groove with several bony bridges on the horizontal preopercular limb (character 16, state 1). This is generally observed in percoids except, among the species studied, *Ambassis*, *Centropomus*, and also *Morone* and *Percichthys jordanops*.
- The epaxial musculature shows an association of type 1, according to Mooi & Gill's (1995) definition (character 22, state 1); this association is the same as that of latids and serranids among other percoids. It was the first argument to contradict the monophyly of the family Centropomidae *s.l.* (Mooi & Gill, 1995).
- One or several spines develop at the posterior border of the cleithral plate (character 27, state 1). This is also observed in some other percoids but not in serranids other than *Niphon*.

Moreover,
- the sensory canal running in a groove covered by several bony bridges on the vertical preopercular limb (character 15, state 1) is probably an apomorphy at this node if we assume it is an intermediate state between an open groove (state 0) and a bony tube (state 2), which is a latid apomorphy.

Finally, another character (character 20, state 1) has an ambiguous position. The 'percoid' position is preferred (see 'Percoid').

The number of apomorphies, first, underlines the paraphyly of the family Centropomidae *s.l.*, and, second, suggests a possible percoid group uniting at least the families Latidae and Serranidae. However, I chose *Niphon* as a representative of the family Serranidae, and, logically, among the eight apomorphies, five are shared by all serranids and latids (and sometimes other percoids). However, three apomorphies (character 9, state 1; character 13, state 1; character 27, state 1) are only shared by *Niphon* and latids, and not by any other serranid fish. So, either *Niphon* and latids are convergent, or the Serranidae is paraphyletic (or should exclude *Niphon*). The serranid–latid interrelationships are not discussed further. The aim of the study was not to place the family Latidae among a hypothetical 'serranoid' group, and thus the serranid apomorphies identified by different authors (e.g. Johnson, 1983, 1984, 1988; Baldwin & Johnson, 1993) were not taken into account.

In the analysis, *Niphon spinosus* has one autapomorphy, the increase in the number of abdominal vertebrae to 12 (character 18, state 2), which agrees with Baldwin, who noted the vertebral formula as a niphonine apomorphy.

THE MONOPHYLY OF THE FAMILY LATIDAE (FIG. 64)

The latid fish share six apomorphies. They are not or only rarely found in any other perciform species. The data are lacking in at most one fossil latid species.

- The presence of mesethmoid projections (character 2, state 1) is known in the beryciform *Caproberyx*, in the polymixiiform *Homonotichthys* (Patterson, 1964) and in percid fish of the genera *Percina* and *Percilia*. The state is unknown in †*Lates bispinosus*.
- The reduction of the metapterygoid lamina to the relict ridge and notch (character 12, state 1) is observed in *Percichthys trucha* (Percichthyidae), and in the studied species of *Eupomotis* (Centrarchidae) and *Priacanthus* (Priacanthidae). The state is unknown in †*Eolates aquensis*.
- A sensory canal on the ascending limb of the preoperculum in a bony tube (character 15, state 2) was not observed in any other taxa. The state is unknown in †*Eolates aquensis*.
- A trifid first haemal spine (character 19, state 1) is present in some percid and percichthyid species (among the following genera: *Lucioperca*, *Perca*, *Percichthys* and *Percilia*). The state is unknown in †*Eolates aquensis*.
- A single dorsal supernumerary spine is observed in the Latidae (character 21, state 1). The count of the supernumerary spines is made following Patterson

(1992) [see Anatomy: the first spine(s), which are not serially associated with a pterygiophore, are supernumerary spine(s)]. I agree with Johnson (1984) that the ambassid single dorsal supernumerary fin spine is equivalent to the generalized percoid state with two supernumerary spines (when considering the whole predorsal formula). This hypothesis is supported by the distribution of the character among percoids. The state is known in all latid fossil species.

- A medio-posterior pelvic process (apomorphic for percomorphs) is sharp and pointed in shape (character 29, state 3) in two other species of the study, *Serranus unicolor* and *Terapon trivittatus*. The state is unknown in †*Eolates aquensis*.

Two latid characters are homoplasic in the analysis. They are both convergent with *Ambassis*, and also, with *Hapalogenys* and lutjanids for the first, and with *Morone* and *Hapalogenys* for the second.

- An anteriorly developed supraoccipital (character 6, state 1).
- The development of a ventral expansion on to the cleithral posterior plate (character 28, state 1). The use of this expansion is unknown (is it to reinforce the support of the dorsal postcleithrum?); moreover, its primitive absence and its later loss cannot be distinguished.

Furthermore, four apomorphies have an ambiguous position among basal latids, because their state is unknown in †*Eolates gracilis* and in †*Eolates aquensis*. Only new fossil material would enable us to fix their position.

- The sensory canal running in a bony tube on the frontals, including the interfrontal branch (character 3, state 2), has been observed in latid fish, including †*Lates bispinosus*. It also exists in *Hapalogenys*, in some derived serranids like the epinephelines, and in other perciform lineages such as lutjanids (e.g. *Lutjanus chrysurus*).
- Fronto-parietal crests (character 7, state 1) exist in latid fishes and also in *Centropomus*.
- A posterior process of the epiotic (character 8, state 1) has been described and observed in latid fish, including †*Lates bispinosus*; it sometimes develops among percoids, including some serranid fish (but not *Niphon*).
- Connection between the tunica externa and the posttemporal (character 26, state 1) has only been described and observed in the extant latid fish, but its presence or absence in fossil species is unknown.

Finally, the material of a proposed latid fish from the Maastrichtian and Early Upper Palaeocene of Bolivia was reported by Gayet (1991) and described by Gayet & Meunier (1998). Apart from bones belonging to a perciform fish (quadrates, pterygiophores) and tentatively referred to the same fish, they assigned

vertebrae, dentaries, premaxillae, basioccipitals, cleithra, and dorsal and pelvic spines to a latid fish, on the basis of the characters discussed. The enlarged neural spine of the second vertebra, defining the Centropomidae *s.l.* in Greenwood's (1976) opinion, is not valid in my opinion (see discussion on The paraphyly of the family Centropomidae *s.l.*). A concave border of the dentary is related to the notch present in *Lates* and *Eolates*, but the general shape of the bone figured by the authors also resembles some percoid jaws (e.g. as figured by Arratia, 1982) and could correspond to the presence of a ventral plate on the dentary. The dentary striae that are present in some *Lates* species and in the Bolivian fossil are also present in other taxa. The spines on the horizontal limb of the preoperculum are not only a latid character but also a serranid one (character 14, state 1). Moreover, on the figured bone, the spines are not massive and shaped as in *Lates* or *Eolates*, and their orientation is also different. So, lacking more data, I propose to keep this unnamed perciform in Perciformes *incertae sedis*.

BASAL LATID INTERRELATIONSHIP: †*EOLATES* POLYPHYLY (FIG. 64)

†*Eolates* is polyphyletic. †*Eolates gracilis* is the sister-group of all other fossil and Recent latids (i.e. †*Eolates aquensis* + '*Lates* + *Psammoperca*'), which are united on the basis of one apomorphy:

- An abdominal vertebral count of 11 centra (character 18, state 3).

Some of the four 'latid' apomorphies with an ambiguous position could support this node instead (see The monophyly of the family Latidae).

The genus †*Eolates* was created by Sorbini (1975) on the basis of the presence of three epurals (two in *Lates*) and of a low number (three) of spines on the posterior border of the cleithral plate. Gaudant (1977) and Gaudant & Sen (1979) rejected the validity of the genus and argued using only the genus *Lates*: they considered that the epural count is not always observable in fossil species and moreover that it is variable in some Recent species (Vladikov, 1962, in Gaudant, 1977). In my opinion, the problem of the genus †*Eolates* is that it was defined by a plesiomorphy, i.e. three epurals (the count of cleithral spines is variable among species, but remains low in †*Eolates*). However, †*E. gracilis* and †*E. aquensis* clearly do not belong in the group formed by *Lates* + *Psammoperca*. †*Eolates* is not a monophyletic genus, *Lates* is monophyletic, and together they form a paraphyletic group. So, we keep †*Eolates* as a valid genus for the 'basal' latids, i.e. the non-*Lates* and non-*Psammoperca* latids. The genus is polyphyletic and contains at least two species: †*Eolates gracilis* and †*E. aquensis*. †*Eolates macrurus* is kept in the genus as defined by Sorbini (1975).

THE *LATES* + *PSAMMOPERCA* GROUP AND THE MONOPHYLY OF BOTH GENERA (FIG. 64)

Two characters unite *Lates* and *Psammoperca* in a monophyletic group. They are both homoplasic in the analysis but apomorphic for the family.

- The reduction in the number of epurals from three to two (character 23, state 1). This epural number is also observed in *Ambassis*, *Morone* and *Siniperca*.
- The fusion of hypurals 3 and 4 with the pseudourostylar complex (character 25, state 1). This fusion is also observed in *Ambassis* + *Centropomus* (see above).

There is a tendency to the reduction of the epural number (and more generally of number of caudal elements) and also a tendency to the fusion of hypurals. This is observed in other percoid lineages and elsewhere, e.g. in basal acanthomorphs (Otero & Gayet, 1996). Nevertheless, they could be interesting characters to resolve intrafamiliar relationships. Moreover, some of the four 'latid' apomorphies with an ambiguous position could reinforce this node (see The monophyly of the family Latidae).

Lates is monophyletic and presents two apomorphies that are only observed in its species among the analysis.

- The presence of bean-shaped exoccipital facets (character 11, state 1). This character state is unknown in fossil species.
- The presence of a ridge lateral on the premaxilla articular process (character 17, state 1).

Psammoperca is monotypic. Two homoplasic characters are apomorphic at the familial level.

- The fusion of the proximal and median radial of all anal and dorsal pterygiophores, which are then bipartite (character 20, state 1). This state is also shared by *Centropomus* and *Ambassis* (see also 'Percoid').
- The absence of an uroneural (character 24, state 1). This reduction also occurs in *Niphon* (the comment made above on the epural count can be extended to this character).

LATES FOSSIL SPECIES (FIG. 64; TABLE 5)

Seven fossil species are attributed to the genus *Lates*. Some show apomorphies of the family. Their other known characteristics are discussed in Table 5.

(1) †*L. bispinosus* is known from a single specimen lacking the posterior half of the body and the anterior part of the head. It shows the apomorphic state for most of the family characters, and a count of 11 abdominal vertebrae (a character of the unnamed taxon). The state is unknown for the identified *Psammoperca* + *Lates* characters. However, the presence of the *Lates* pleurosphenoid pedicle is probable. Furthermore, it does not share any of the *Psammo-*

perca apomorphies. So, it may be a *Lates*, but it is certainly not a *Psammoperca*.

(2) †*L. partshii* (Heckel, 1856; Middle Miocene of Austria) shows one *Lates* + *Psammoperca* character state: the presence of two epurals. Furthermore. it resembles *Lates* with the presence of three spines on the posterior border of the cleithrum.

The states for the four other fossil *Lates* species is unknown for any of the latid characters.

(3) †*L. gregarius* (Bannikov, 1992; Upper Miocene of Northern Moldavia) has the predorsal formula 0/0/ 0 + II/I + I/, which is the formula shared by the percoid fish in this analysis except *Ambassis* and some autapomorphic taxa.

(4) & (5) †*L. macropterus* (Bassani, 1889; Oligocene of Chiavon, Italy) and †*L. croaticus* (Kramberger,

1902; Miocene of Croatia) are too badly preserved to determine any character state.

(6) †*L. karungae* (Greenwood, 1951; Miocene, Lake Victoria, Kenya) is only known by isolated vertebrae. Lacking any contradictory characters, the species is left in the genus *Lates*.

NB. (7) Another species of *Lates* has just been described in the Lower Oligocene of Egypt (Murray & Attia, 2004).

LATES INTRAGENERIC RELATIONSHIPS (FIG. 65, TABLE 5)

Despite the weakness of morphological information for most of the fossil taxa (Table 5), a phylogenetic hypothesis, based on osteological characters, enables
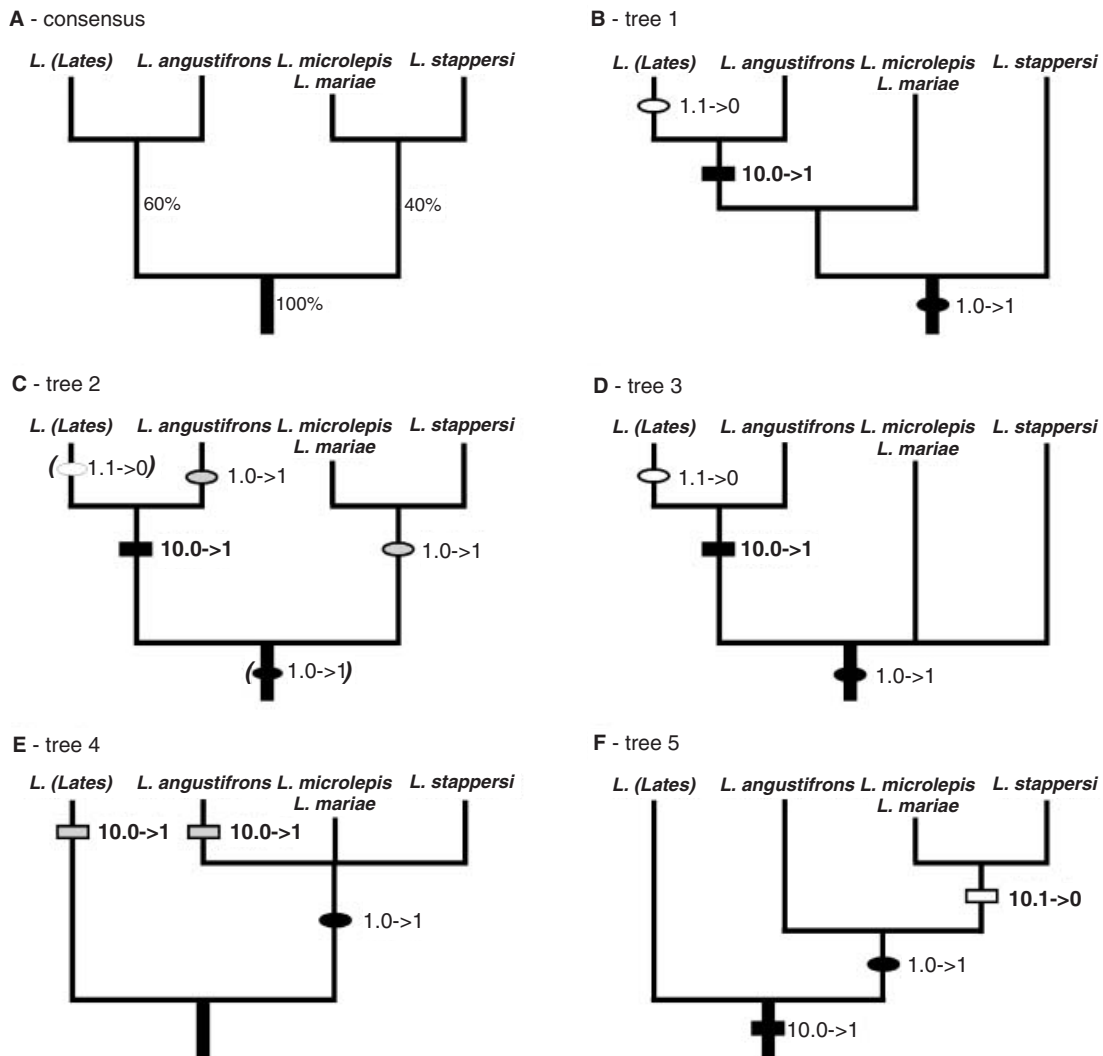
Figure 65. The hypothesis of *Lates* intrarelationships: the majority rule consensus tree and the five most parsimonious trees. The characters creating the conflict are character 1, oval shape: (0) short ethmovomerine region, (1) long ethmovomerine region; character 10, rectangular shape: (0) pleurosphenoid pedicle absent, (1) pleurosphenoid pedicle present. Apomorphies are in black, reversals in white and convergences in grey.

us to resolve the intrarelationships of both Recent and fossil Latidae. This monophyletic family is known since (at least) the Eocene, with the fossil genus *Eolates*; the Recent genera, i.e. *Lates* and *Psammoperca*, are sister-groups. However, the cladistic analysis does not resolve the Recent *Lates* species interrelationships.

The genus *Lates* is monophyletic, and *Lates* (*Luciolates*) unites the four Recent species of the genus which are endemic to Lake Tanganyika, i.e. *L. angustifrons*, *L. microlepis*, *L. mariae* and *L. stappersi*, whereas *Lates* (*Lates*) gathers *L. macrophthalmus*, *L. longispinis*, both endemic to Lake Rudolf, *L. calcarifer* from Indo-Pacific coastal waters, and *L. niloticus* from Miocene to Recent African freshwaters, and, by default, six supposed *Lates* fossil species (see *Lates* fossil species, above). However, the five most parsimonious trees of the cladistic analysis of the family differ in *Lates* intrarelationships (Fig. 65B–F). A majority rule consensus tree (Fig. 65A) indicates the paraphyly of *Lates* (*Luciolates*) as *Lates angustifrons* forms a monophyletic group with *Lates* (*Lates*) in three of the five most parsimonious trees. The conflict is based on the interpretation of two characters. The majority rule tree unites *Lates* (*Lates*) with *Lates angustifrons* because *L. microlepis* + *L. mariae* and *L. stappersi* are coded the same for both the concerned characters.

The elongation of the ethmovomerine region (see also Anatomy) is observed in all the Tanganyikan species. However, this character is not properly discrete: for examined specimens of a similar neurocranial length (around 100–120 mm), the ratio d/a (Table 1), which characterizes the length of the ethmovomerine region compared with the total neurocranial length, is around 18–19% in *Lates niloticus*, 23% in *L. angustifrons* and up to 28% in *L. stappersi*, but only 14–15% in *L. calcarifer*. Furthermore, if the ratio is stable in some species (e.g. *L. niloticus*), it is variable between young and adults in other species (e.g. *L. calcarifer*). Nevertheless, the choice of 20% as the limit between short and long snouts, which seems so subjective, reflects the limit under which the specimens do not show modification of the snout morphology, i.e. no lateral ethmoid posterior border that slopes backward from the parasphenoid to the frontal in a sharp angle. This is the situation in all the fossil *Lates*. Whether they are European complete specimens or Afro-Arabian disarticulated fossils, and from the Lower Miocene to the Late Pliocene, they do not show any elongation of the ethmovomerine region. So, the appearance of the apomorphic state of the elongate snout at the genus level, which makes the Tanganyikan species a stem polyphyletic group [trees 1 and 3 and solution in italic of tree 2 (Fig. 65B–D); these trees are the same as the branches of *L. microlepis* + *L mar-*

iae are not supported] seems weakly probable. Therefore, either the elongation of the snout appears once and *Lates* (*Luciolates*) is valid (trees 4 and 5, Fig. 65E, F), or it appears twice and we find the majority-rule consensus situation (tree 2, normal type, Fig. 65C).

The pleurosphenoid pedicle (see also Anatomy) is developed in the *Lates* (*Lates*) species and in *L. angustifrons*. The presence or absence of a pleurosphenoid pedicle is a discrete character, but its development is more or less obvious according to the species, and reduced in *Lates angustifrons*. Moreover, although its presence or absence is unknown in most *Lates* fossil species (as the pleurosphenoid pedicle area is often hidden or crushed), it is probably present in †*L. bispinosus*. This indicates an earlier presence of the apomorphic state in the genus.

Therefore, the discussion of the concerned characters leads us to suspect the probable monophyly of the subgenus *Lates* (*Luciolates*) as defined by Greenwood (1976); in which case *Lates* (*Lates*) is the *Lates* stem group and is either supported by the homoplastic development of a pleurosphenoid pedicle (tree 4, Fig. 65E), or is not supported by any apomorphy (tree 5, Fig. 65F) and might then be polyphyletic. No information supports one hypothesis over another.

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APPENDIX

LIST OF THE EXAMINED MATERIAL OF LATIDAE, CENTROPOMIDAE AND COMPARATIVE SPECIES

Order Beryciformes Regan, 1909
Trachichthyidae Bleeker, 1859 (*Gephyroberyx darwini*, DS, MG 16; *Hoplostetus mediterraneus*, DS, MG 31); Berycidae Gill, 1862 (*Beryx splendens*, MG 24); Holocentridae Richardson, 1846 (*Holocentrus seychellensis*, MG 63); Myripristidae Nelson, 1955 (*Myripristis murdjans*, MG 59).

Order Perciformes Bleeker, 1859. Suborder Percoidei Bleeker, 1859
incertae sedis: †*Semlikiichthys rhachirhynchus* (Greenwood & Howes, 1975), Rift (Zaire), Pliocene (MRAC 17.501–17.600); †*Weilerichthys fajumensis* (Weiler (1929), Fajum (Egypt), Oligocene (NKM unnumbered holotype, SI P. 1898–99, P. 1904, P. 1906); *Hapalogenys* Richardson, 1844 (*Hapalogenys guentheri*, NHM 28.060 [1895-5-27:20], DS, Mazatlan); *Lateolabrax* Bleeker, 1857 (*Lateolabrax*); *Siniperca* Gill, 1862 (*Siniperca chuatsi*: NHM 28.070 [88-3-23-3], DS, Kiu Kiang).

Latidae Jordan, 1923. Recent material: •*L. niloticus*: NHM 28228 [4], DS (Red Sea); NHM 28228 [1971-2-8:186], DS (London Zoo); NHM 28228 [84-6-9-21], DS (Niger); NHM unnumbered, DS; NHM 31170 [1900-6-28: 291-5], X-rays 294, five individuals (Senegal); NHM 31170 [1929-1-24], X-rays A311, *L. albertianus* type; MG 205, DS; MG 206, DS; MG 207, DS. •*L.* cf. *niloticus*: NHM 28228, DS (Lake Kwano, Niger). °*L. longispinis*: NHM 28228, DS; NHM 31170 [1932-6-13: 102-6], X-rays 296, five paratypes (Lake Turkana).

•*L. macrophtalmus*: NHM unnumbered, DS (Lake Albert = Mobutu); NHM 31170 [1929-1-24: 340-4], X-rays A301, 12 individuals (six types). •*L. calcarifer*: NHM 28228 [1873-1-21:2], DS (Fitzroy river); NHM 28228 [1985-11-14:1], DS (Darwin Fish Market); NHM 31170 [1891-11-30: 1-8], X-rays 299, eight individuals (Sittany river); MG 26, DS. •*L. angustifrons*: NHM 28228 [1955-12-20: 1722], DS (Lake Tanganyika); NHM 31170 [1936-6-15: 1987-97], [1906-9-8: 87-88], X-rays 293, eight individuals. •*L. microlepis*: NHM 28228 [1900-12-13:37], DS (Albertville); NHM 31170 [1955-12-20: 1753-85], X-rays 292, 13 individuals (Lake Tanganyika); NHM 31170 [1906-9-8: 89], X-rays 292 (Lake Tanganyika). •*L. mariae*: NHM [1936-6-15:1672-86], DS (Lake Tanganyika); NHM [1955-12-20:1667], DS, two individuals (Lake Tanganyika); NHM 31170 [1906-9-6: 7], X-rays 291, two individuals (Lake Tanganyika); NHM 31170 [1955-12-20: 1928-29, 1936-38, 1955-56, 1972-86], X-rays 290, 16 individuals. •*L. stappersi*: NHM 28228 [1975-4-23:1], DS (Lake Tanganyika); NHM 28228 [1936-6-15: 1705-6], DS (Lake Tanganyika); NHM 28228 [1955-12-20:1672], DS (Lake Tanganyika); NHM 31170 [1955-12-20: 1669-71, 1680], [1936-6-15: 1705-6], [1971-6-23: 76-78], [Tervuren 129887-889], X-rays 289, eight individuals. •*Lates* sp. NHM unnumbered, hyoid arches and infraorbital series. •*Psammoperca waigiensis*: NHM 31160 [1872-10-18:90], DS (with 1892-9-2:10-11); NHM 31160 [1892-9-2:10-11], DS; NHM 31160 [88-11-6-6], DS (Mavras); NHM 31060 A [1892-9-2: 10-11], B [1870-12-27: 17], C [1888-11-6: 5], D [1872-10-18: 90], E [1939-1-17: 11], X-rays, six individuals.

Fossil material: •†*Eolates gracilis* (Agassiz, 1883), Monte Bolca (Italy), Lower Eocene: MCSNV IG 23151-152 (part and counter-part, ex NS1-2); IG 23153 (ex NS3 Vr); IG 23176 (ex NS25 Vr); IG 23199-200; IG 135672-673; IG 43388-389; II B 79; T 373; VI N 55-VI N 56; VI N 57-58; VI N 59; VI N 61-62; VI N 63-64; VI N 65; VI N 66; S1 (ex S65); S81-S82*; S85; S86; S180; S183 (2 individuals). NHM unnumbered Young †*Eolates*; P 1913; P 2095-P 3818a; P 3918b-c; P 9461a-b; P 16128; P 16377; P 19007 (ex †*L. notaeus*); P 23798; P 23802-803; P 36203 (ex †*L. gibbus*); P 37225 (ex †*L. gibbus*); P 62112a-b (two individuals). MNHN Bol 0267*; Bol 0223. •†*Eolates aquensis* (Gaudant, 1977), Aix-en-Provence (France), Oligocene: NHM P 3912 (ex †*Perca*). MNHN 1909-30 (0236) (ex †*Smerdis macrurus*); 4903 (EMP Aix 52); 11253 (loan of the MCSNV). •*Lates* (*Lates*) sp., Ghaba (Sultanate of Oman), Miocene (loan to the MNHN, site reference in Roger et al., 1994): Site 1: Gb-P1. Site 3: Gb-P2, Gb-P3. Site 5: Gb-P4, Gb-P5, Gb-P6. Site unknown: Gb-P7, Gb-P8, Gb-P9, Gb-P10. •*Lates* (*Lates*) sp., Negev (Israel), Miocene (loan of the Hebrew University of Jerusalem (Israel): AH 0305, 1244, 1260, 1270, 1282, 1313, 1340,

1356, AH 1392, AH 1452, AH 1451, and unnumbered material. •*Lates* sp. cf. *niloticus*, As-Sarrar (Saudi Arabia), Lower Miocene (loan to the MNHN; site reference in Thomas *et al.*, 1982): Site 6: As-P1. Site 7: As-P2-9. Site 9: As-P10-P49. Site 16: As-P50. Site 21: As-P51-P56. Site 23: As-P57. Site unknown: As-P58-P64. •†*Lates* sp. cf. *niloticus*, Natronal (Egypt), Pliocene: SI 5728-5748 [see also Greenwood (1972)]. Other poor material of †*Lates* sp. from the Miocene of Tunisia has been described by Greenwood (1973) (Greenwood (1974) reviewed the African fossil localities which have yielded latid material]. •†*Lates niloticus*, Monte Castellaro (Italy), Miocene (Messinian): MCSN T.1088-1092. •†*Lates bispinosus* (Gaudant & Sen, 1979), Altinova (Turkey), Neogene: MNHN 1952-12 (holotype and only material). •†*Lates karungae* Greenwood (1951), Kenya, Miocene: NHM 24 D [see Greenwood (1951) for details].

Centropomidae Poey, 1868: *Centropomus armatus* (NHM 31.190 [1938-11-18: 7-8], X-rays 317, two individuals, Ecuador); *C. ensiferus* (NHM 31.190 [1861-12-2:13], DS; MG 296, DS; NHM 31.190 [1903-5-15: 3-5], X-rays 316, three individuals, Panama); *C. parallelus* (NHM 31.190 [1865-3-25: 8-9], X-rays 319, two individuals, Mexico, [1923-7-30: 115], X-rays 319, one individual, Rio de Janeiro); *C. pectinatus* (NHM 31.190 [1920-12-22: 57-58], X-rays 317, two individuals, Tobago); *C. pedimaculata*: (NHM 31.190 [1894-12-10-5], DS, Jamaica; NHM 31.190 [1895-5-27: 3-5], [1903-5-15: 1], X-rays 315, three individuals, Mazatlan); *C. unidecimalis* (NHM 31.190 [1883-12-16:1-2], DS, Jamaica; NHM 31.190 X-rays 320 [1895-5-27: 2], Mazatlan, [1936-1-31: 8], Trinidad, [1924-2-29: 16], Marajo Island).

Other percoids: Percichthyidae Jordan and Evermann, 1896: *Percalates colonarum* (NHM 27.960 [1890-9-23:180], DS, Sydney); *Percichthys jordanops* (NHM 27.950 [1894-9-12:2], DS, Santiago); *Percichthys trucha* (NHM 27.950 [1894-9-12:1], DS, Santiago). Moronidae Fowler, 1907: *Morone americana* (NHM 27.990 [1850-11-14:168], DS). Acropomatidae Gill, 1891: *Acropoma*. Ambassidae, Boulenger, 1904: *Ambassis commersonii* (NHM 31.200 [55-9-19:359], DS, India); *A. wolffii* (NHM 31.200 [1898-4-2-67], DS, Siam). Serranidae Swainson, 1839: Serraninae: *Serranus humeralis* (NHM 28.260 [69-11-12:4], DS, Cinchas Ld.); *S. radians* (NHM 28.260 [1904-3-15:27], DS, Margarita); *S. unicolor* (NHM 28.260 [1904-3-15:12], DS, St Thomas); Epinephelinae Niphonini: *Niphon spinosus* (NHM 27.980 [1890-2-26:26], DS, Yokohama); Epinephelini: *Epinephelus aeneus* (NHM 28.220 [1907-12-22:81], DS, Menzaleh); *E. fasciatus* (NHM 28.220, DS, Chine); *E. tauvina*: (NHM 28.220, DS; Java); Grammistini: *Grammistes sexlineatus* (NHM 28.470 [71-3-29:5], DS, Salomons Island); *Aulocephalus temminckii* (NHM 28.190, DS, Siam). Centrarchidae Bleeker, 1859: *Eupomotis aureus* (NHM 29.070 [1], DS, North America); *Centrarchus macropterus* (NHM 29.010 [1895-10-14:27], DS, North Carolina). Percidae Cuvier, 1817: *Percina caprodes* (NHM 29.520 [1907-12-22:81], DS, North America); *Perca fluviatilis* (NHM 29.500 [139.a], DS); *Lucioperca vitrea* (NHM 29.510 [1876-9-25:13], DS, Lake Erie); *L. volgensis* (NHM 29.510 [1879-11-14:2], DS; Astrachan); *Stizostedion lucioperca* (NHM 29.510 [m. 150a], DS). Priacanthidae Gill, 1872: *Priacanthus arenatus* (NHM 29.190, DS, Madeire). Apogonidae Jordan and Gilbert, 1882: *Apogon maximus* (NHM 29.500 [1887-11-11:68], DS, Muscat). Lutjanidae Gill, 1884: *Lutjanus aya* (NHM 31.540, DS, Florida); *L. chrysurus* (NHM 31.540 [1852-9-13:108], DS); *L. macolor* (NHM 31.540 [1858-4-21:217 Y], DS, Amboyna). Glaucosomatidae Jordan, 1923: *Glaucosoma burgeri* (NHM 31.150 [1864-2-26: 60-A], [1864-2-26: 10-B], X-rays, two individuals).

Suborder Stromateoidei Regan, 1929 s.l.
Teraponidae Richardson, 1856: *Terapon servus* (NHM 28.040 [51-12-27:55], DS, China sea); *T. trivittatus* (NHM 28.040 [57-10-28:1], DS, Sydney). Kuhliidae Jordan and Evermann, 1896: *Kuhlia malo* (NHM 28.890 [1876-3-11:24], DS, Rodriguez); *K. taeniura* (NHM 28.890 [1898-10-29:10], DS, Socorro).