

A REVIEW OF THE FAMILY CENTROPOMIDAE
(PISCES, PERCIFORMES)



BY
PETER HUMPHRY GREENWOOD

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By P. H. GREENWOOD

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INTRODUCTION

THE Centropomidae, a family of tropical estuarine, marine and freshwater percoid fishes, is represented in the New World, Africa and Asia by a total of at least 18 species (the number varying mainly with the taxonomic limits set for the family by different authors). Of the 18 species recognized, 9 occur in the New World, 7 – all freshwater species – occur in Africa and 2 in Asia.

Temporally the family has a good fossil record extending from the Eocene to prehistoric times. Geographically, however, the fossil record is restricted to Africa and Europe, and only one taxonomic division of the family, the closely related genera *Lates* and *Eolates*, is represented; see Sorbini (1973) and Greenwood (1974).

It was, in fact, a new fossil centropomid from the neogene of Africa (Greenwood & Howes, 1975) that led to this revision. Our attempts to identify the new fossil soon made it clear that the African centropomids are more varied anatomically than had been realized previously. Also, it became obvious that the current taxonomic arrangement of the family does not reflect the probable phyletic relationships of its constituent taxa. Indeed, except for Fraser's (1968) analysis of the New World *Centropomus* species, no fully reasoned attempt has been made to interpret intra-familial relationships along phyletic lines. Also, the presumed relationships of the Centropomidae with the Serranidae (Regan, 1913; Berg, 1947; Gosline, 1966; Greenwood, Rosen, Weitzman & Myers, 1966) appear to be based more on intuitive than on critical taxonomic reasoning, and need reappraisal.

Although it was for these reasons mainly that the present review was undertaken, I also hope that it may provide a step towards the clearing of that taxonomic rag-bag, the 'lower percoid fishes' (see Greenwood *et al.*, 1966; Gosline, 1966).

MATERIALS

GLAUCOSOMIDAE

Osteological material :

| | | | |
|---------------------------|-------------------|-------|-------------|
| <i>Glaucosoma burgeri</i> | BMNH 1884.2.26:60 | China | 293 mm S.L. |
|---------------------------|-------------------|-------|-------------|

CENTROPOMIDAE

Osteological material :

| | | | |
|--------------------------------|-----------------------------|-----------------|---|
| <i>Lates calcarifer</i> | BMNH 1873.1.21:2 | Fitzroy R. | 360 mm S.L. (skeleton) |
| <i>Lates niloticus</i> | Unregistered | No locality | (alizarin preparation) |
| <i>Lates niloticus</i> | BMNH 1971.2.8:186 | No locality | (disarticulated skeleton) |
| <i>Lates niloticus</i> | Unregistered | 'Red Sea' | (disarticulated skeleton) |
| <i>Lates niloticus</i> | BMNH 1864.6.29:5 | 'West Africa' | (skull and pectoral girdle) |
| <i>Lates niloticus</i> | Unregistered | Lake Rudolf | (alizarin preparation) |
| <i>Lates niloticus</i> | Unregistered | No locality | (alizarin preparations) |
| <i>Lates niloticus</i> | Unregistered | Lake No | (alizarin preparation) |
| <i>Lates macrophthalmus</i> | Unregistered | Lake Albert | (skeleton, 102 mm S.L.) |
| <i>Lates longispinis</i> | Unregistered | Lake Rudolf | (skull) |
| <i>Lates microlepis</i> | BMNH 1900.12.13:37 | Albertville | (disarticulated skeleton) |
| <i>Lates angustifrons</i> | BMNH 1955.12.20:1722 | Lake Tanganyika | (skull and pectoral girdle) |
| <i>Lates mariae</i> | BMNH 1955.12.20:1667 | Lake Tanganyika | (skull and pectoral girdle) |
| <i>Luciolates stappersi</i> | BMNH 1955.12.20:1672 | Lake Tanganyika | (disarticulated skeleton) |
| <i>Luciolates stappersi</i> | BMNH 1936.6.15: 1705-6 | Lake Tanganyika | (skull) |
| <i>Luciolates stappersi</i> | BMNH 1971.6.23:76-8 | Lake Tanganyika | (alizarin preparation) |
| <i>Luciolates stappersi</i> | BMNH 1975.4.23:2 | Lake Tanganyika | (disarticulated skeleton from a fish 390 mm S.L.) |
| <i>Psammoperca waigiensis</i> | BMNH 1892.9.2:10-11 | Borneo | (skull and pectoral girdle) |
| <i>Psammoperca waigiensis</i> | BMNH 1872.10.18:90 | Cebu | (circumorbital series) |
| <i>Centropomus undecimalis</i> | BMNH 1883.12.16:1-2 | Jamaica | (skull) |
| <i>Centropomus ensiferus</i> | BMNH 1861.12.12:13 | No locality | (skeleton, disarticulated) |
| <i>Centropomus pectinatus</i> | BMNH 1894.12.1:5 | Jamaica | (skull and pectoral girdle) |
| Dissected specimens : | | | |
| <i>Lates niloticus</i> | BMNH 1907.12.2: 2915-6 | Nile | 227 mm S.L. |
| <i>Lates niloticus</i> | BMNH 1907.12.2: 2952-3 | Nile | 165 mm S.L. |
| <i>Lates niloticus</i> | BMNH 1931.11.20:1-2 | Merowe | 218 mm S.L. |
| <i>Lates macrophthalmus</i> | BMNH 1929.1.24:341-4 | (Paratype) | 275 mm S.L. |
| <i>Lates macrophthalmus</i> | BMNH 1975.1.18:1 | Lake Albert | 315 mm S.L. |
| <i>Lates longispinis</i> | BMNH 1932.6.13: 102-106 | (Syntype) | 250 mm S.L. |
| <i>Lates angustifrons</i> | BMNH 1906.9.8:87-88 | Lake Tanganyika | 300 mm S.L. |
| <i>Lates mariae</i> | BMNH 1955.12.20: 1628-29 | Lake Tanganyika | 220 mm S.L. |
| <i>Luciolates stappersi</i> | BMNH 1955.12.20: 1669-71 | Lake Tanganyika | 215 mm S.L. |

| | | | |
|--------------------------------|-------------------------------------|----------------------------|-------------------|
| <i>Psammoperca waigiensis</i> | BMNH 1892.9.2:10-11 | Borneo | 150 mm S.L. |
| <i>Psammoperca waigiensis</i> | BMNH 1872.10.13:90 | Cebu | 240 mm S.L. |
| <i>Centropomus undecimalis</i> | BMNH 1883.12.16:1-2 | Jamaica | 280 mm S.L. |
| <i>Centropomus undecimalis</i> | BMNH 1923.7.30:114 | Rio de Janeiro | 175 mm S.L. |
| <i>Centropomus pectinatus</i> | BMNH 1895.5.27:3-5 | Mazatlan | 245 mm S.L. |
| Specimens examined: | | | |
| <i>Lates calcarifer</i> | BMNH 1863.2.23:29 | Amoy | 190 mm S.L. |
| <i>Lates calcarifer</i> | BMNH 1936.8.6:43 | Queensland | 260 mm S.L. |
| <i>Lates niloticus</i> | Major part of the entire collection | | |
| <i>Lates macrophthalmus</i> | BMNH 1929.1.24: | | |
| | 340-344 | (Paratypes) | 145-283 mm S.L. |
| <i>Lates longispinis</i> | BMNH 1932.6.13: | | |
| | 102-106 | (Syntypes) | 115-270 mm S.L. |
| <i>Lates angustifrons</i> | Entire collection | | |
| <i>Lates mariae</i> | Entire collection | | |
| <i>Lates microlepis</i> | Entire collection | | |
| <i>Luciolates stappersi</i> | Entire collection | | |
| <i>Luciolates stappersi</i> | RGMARC 129887-889 | (Tervuren Museum specimen) | 407 mm S.L. |
| <i>Psammoperca waigiensis</i> | BMNH 1933.3.11:312 | Culion, Philippines | 110 mm S.L. |
| <i>Psammoperca waigiensis</i> | BMNH 1883.11.28:14 | Singapore | 165 mm S.L. |
| <i>Psammoperca waigiensis</i> | BMNH 1891.10.29:66 | Ceylon | 132 mm S.L. |
| <i>Psammoperca waigiensis</i> | BMNH 1939.1.17:11 | Hong Kong | 215 mm S.L. |
| <i>Psammoperca waigiensis</i> | BMNH 1888.11.6:5 | Madras | 175 mm S.L. |
| <i>Centropomus undecimalis</i> | BMNH 1936.1.31:8 | Trinidad | 290 mm S.L. |
| <i>Centropomus undecimalis</i> | BMNH 1906.6.23:82 | Trinidad | 180 mm S.L. |
| <i>Centropomus pectinatus</i> | BMNH 1920.12.22: | Trinidad | 230 & 240 mm S.L. |
| | 57-58 | | |
| <i>Centropomus ensiferus</i> | BMNH 1903.5.15:3-5 | Panama | 183-230 mm S.L. |
| Specimens radiographed: | | | |
| <i>Lates calcarifer</i> | BMNH 1891.11.30:1-8 | | |
| <i>Lates niloticus</i> | BMNH 1900.12.2: | | |
| | 2329-38 | | |
| <i>Lates macrophthalmus</i> | BMNH 1929.1.24: | | |
| | 340-344 | | |
| <i>Lates macrophthalmus</i> | BMNH 1929.4.16:39-41 | | |
| <i>Lates macrophthalmus</i> | BMNH 1929.1.24: | | |
| | 341-344 | | |
| <i>Lates longispinis</i> | BMNH 1932.6.13:102-6 | | |
| <i>Lates angustifrons</i> | BMNH 1936.6.15: | | |
| | 1687-97 | | |
| <i>Lates angustifrons</i> | BMNH 1906.9.8:87-88 | | |
| <i>Lates mariae</i> | BMNH 1955.12.20:1636; | | |
| | 1628-9; 1655-6; | | |
| | 1672-86 | | |
| <i>Lates mariae</i> | BMNH 1906.9.6:7 | | |
| <i>Lates microlepis</i> | BMNH 1906.9.8:89 | | |
| <i>Lates microlepis</i> | BMNH 1955.12.20: | | |
| | 1753-85 | | |
| <i>Luciolates stappersi</i> | BMNH 1955.12.20: | | |
| | 1669-71; 1680 | | |

| | |
|--------------------------------|---------------------------|
| <i>Luciolates stappersi</i> | BMNH 1936.6.15: 1705-6 |
| <i>Luciolates stappersi</i> | BMNH 1971.6.23:76-78 |
| <i>Psammoperca waigiensis</i> | BMNH 1872.10.18:90 |
| <i>Psammoperca waigiensis</i> | BMNH 1939.1.17:11 |
| <i>Psammoperca waigiensis</i> | BMNH 1892.9.2:10-11 |
| <i>Psammoperca waigiensis</i> | BMNH 1870.12.27:17 |
| <i>Psammoperca waigiensis</i> | BMNH 1888.11.6:5 |
| <i>Centropomus unionensis</i> | BMNH 1903.5.15:8 |
| <i>Centropomus robalito</i> | BMNH 1895.5.27:6 |
| <i>Centropomus nigrescens</i> | BMNH 1883.7.28:14 |
| <i>Centropomus ensiferus</i> | BMNH 1903.5.15:3-5 |
| <i>Centropomus undecimalis</i> | BMNH 1895.5.27:2 |
| <i>Centropomus undecimalis</i> | BMNH 1936.1.31:8 |
| <i>Centropomus undecimalis</i> | BMNH 1924.2.29:16 |

Fossil material :

| | | | |
|-------------------------|-------------|-------------|----------------|
| <i>Eolates gracilis</i> | BMNH P23803 | Monte Bolca | 130 mm S.L. |
| <i>Eolates gracilis</i> | BMNH P16137 | Monte Bolca | 121 mm S.L. |
| <i>Eolates gracilis</i> | BMNH P3918 | Monte Bolca | 139 mm S.L. |
| <i>Eolates gracilis</i> | BMNH P23798 | Monte Bolca | c. 135 mm S.L. |
| <i>Eolates gracilis</i> | BMNH P16374 | Monte Bolca | 41 mm S.L. |
| <i>Eolates gracilis</i> | BMNH P16756 | Monte Bolca | 29 mm S.L. |
| <i>Eolates gracilis</i> | BMNH P37225 | Monte Bolca | 124 mm S.L. |

SERRANIDAE

Osteological material :

| | | | |
|------------------------------|--------------------|----------|-------------------------|
| <i>Epinephelus tauvina</i> | Unregistered | Java | (skeleton, 225 mm S.L.) |
| <i>Epinephelus areolatus</i> | BMNH 1888.12.29:24 | Muscat | (skeleton, 280 mm S.L.) |
| <i>Epinephelus afer</i> | Unregistered | St Croix | (skeleton, 140 mm S.L.) |
| <i>Epinephelus itajara</i> | BMNH 1883.12.16:9 | Jamaica | (skeleton, 355 mm S.L.) |

Dissected specimens :

| | | | |
|---------------------------------|------------------|-------|-------------|
| <i>Epinephalus alexandrinus</i> | BMNH 1964.7.14:1 | Malta | 243 mm S.L. |
|---------------------------------|------------------|-------|-------------|

Specimens examined :

| | | | |
|--------------------------|----------------------|----------------|-----------------|
| <i>Serranus radialis</i> | BMNH 1923.7.30:77-79 | Rio de Janeiro | 115-140 mm S.L. |
|--------------------------|----------------------|----------------|-----------------|

AMBASSIDAE

Osteological material :

| | | |
|-----------------------------|---------------------|---------------------------|
| <i>Ambassis urotaenia</i> | BMNH 1928.1.17:8-15 | (alizarin preparation) |
| <i>Ambassis commersonii</i> | BMNH 1855.9.19:359 | (disarticulated skeleton) |
| <i>Ambassis wolffii</i> | BMNH 1898.4.2:67 | (skeleton, 85 mm S.L.) |

Specimens examined:

The major part of the collections of *Ambassis* and *Chanda*

GERREIDAE

Osteological material :

| | | |
|---------------------|----------------------|-------------------------|
| <i>Gerres oyena</i> | BMNH 1965.4.4:125-38 | (alizarin preparations) |
| <i>Gerres oyena</i> | BMNH 1960.3.15:670-5 | (alizarin preparations) |

ABBREVIATIONS USED IN THE TEXT-FIGURES

| | | | |
|---------------------------------|--|-----------------------------------|---|
| AA | Anguloarticular | OCS | Occipito-spinal nerve foramen |
| ART P | Articular process of the pre-maxilla | OP | Operculum |
| ASC P | Ascending process of the pre-maxilla | PAL | Palatine |
| AHYF | Anterior facet for hyomandibula | PAR | Parietal |
| | | PARC | Parietal crest |
| Bb 1-3 | Basibranchial | Pb1-Pb4 | Pharyngobranchials of the first to fourth gill arches |
| 'BcF' | 'Berycoid foramen' | Pb2 TP- | |
| BOC | Basioccipital | Pb4 TP | Tooth plates associated with pharyngobranchials of the second to fourth gill arches |
| BrR | Branchiostegal ray | PC ₁ , PC ₂ | Upper and lower postcleithra |
| BSP | Basisphenoid | PFR | Pectoral fin ray |
| Cb 1-5 | Ceratobranchial of first to fifth arch | PH | Parhypural |
| Ch | Ceratohyal | PHYF | Posterior facet for hyomandibula |
| CL | Cleithrum | | |
| COR | Coracoid | PMAXP | Posterior maxillary process |
| D | Dentary | PMXP | Premaxillary process of the maxilla |
| Dhh | Upper hypohyal | POP | Preoperculum |
| D PROC | Dorsal process of the maxilla | PRO | Prootic |
| E | Mesethmoid | PS | Parasphenoid |
| E1-E4 | Epibranchials of the first to fourth arches | PTF | Posttemporal fossa |
| E2TP, | Tooth-plates associated with the | PTO | Pterotic |
| E3TP | second and third epibranchials | PTS | Pterosphenoid |
| ECT | Ectopterygoid | PTSP | Pterosphenoid pedicle |
| Eh | Epihyal | PTSS | Pterosphenoid spur |
| ENT | Entopterygoid | PU ₁ +U ₁ | Fused first ural and preural centra |
| EP | Epural | Q | Quadrate |
| EPI | Epioccipital (= epiotic <i>auct.</i>) | R | Radial for pectoral ray |
| EXO | Exoccipital | RA | Retroarticular |
| FR | Frontal | SC | Supracleithrum |
| FRC | Frontal crest | Sc | Scapula |
| FRR | Frontal ridge | SLP | Supralamellar tooth plate |
| GF | Gill filament | SOC | Supraoccipital |
| Gh | Glossohyal | SOC S | Supraoccipital shelf |
| Gr | Gill raker | SOP | Suboperculum |
| H ₁ , H ₅ | First and fifth hypurals | SOS | Subocular shelf |
| Hb1 | Hypobranchial of first gill arch | SPO | Autosphenotic |
| HsPU ₂ | Haemal spine of second preural vertebra | SY | Symplectic |
| HY | Hyomandibula | TP | Tooth plate |
| IC | Intercalar | UR | Uroneural |
| IOP | Interoperculum | UR1, UR2 | Upper and lower uroneurals |
| LAC | Lachrymal (first circumorbital bone) | V | Vomer |
| LATE | Lateral ethmoid | VHh | Lower hypohyal |
| LAT SP | Latero-sensory canal openings | II-V | Second to fifth circumorbital bones |
| LC | Lateral commissure | IX | Foramen for glossopharyngeal nerve |
| LIG | Ligament | X | Foramen for vagus nerve |
| MET | Metapterygoid | 1st APTY | First anal pterygiophore |
| NaPU ₂ | Neural arch and spine of second preural vertebra | 2nd Asp | Second anal fin spine |

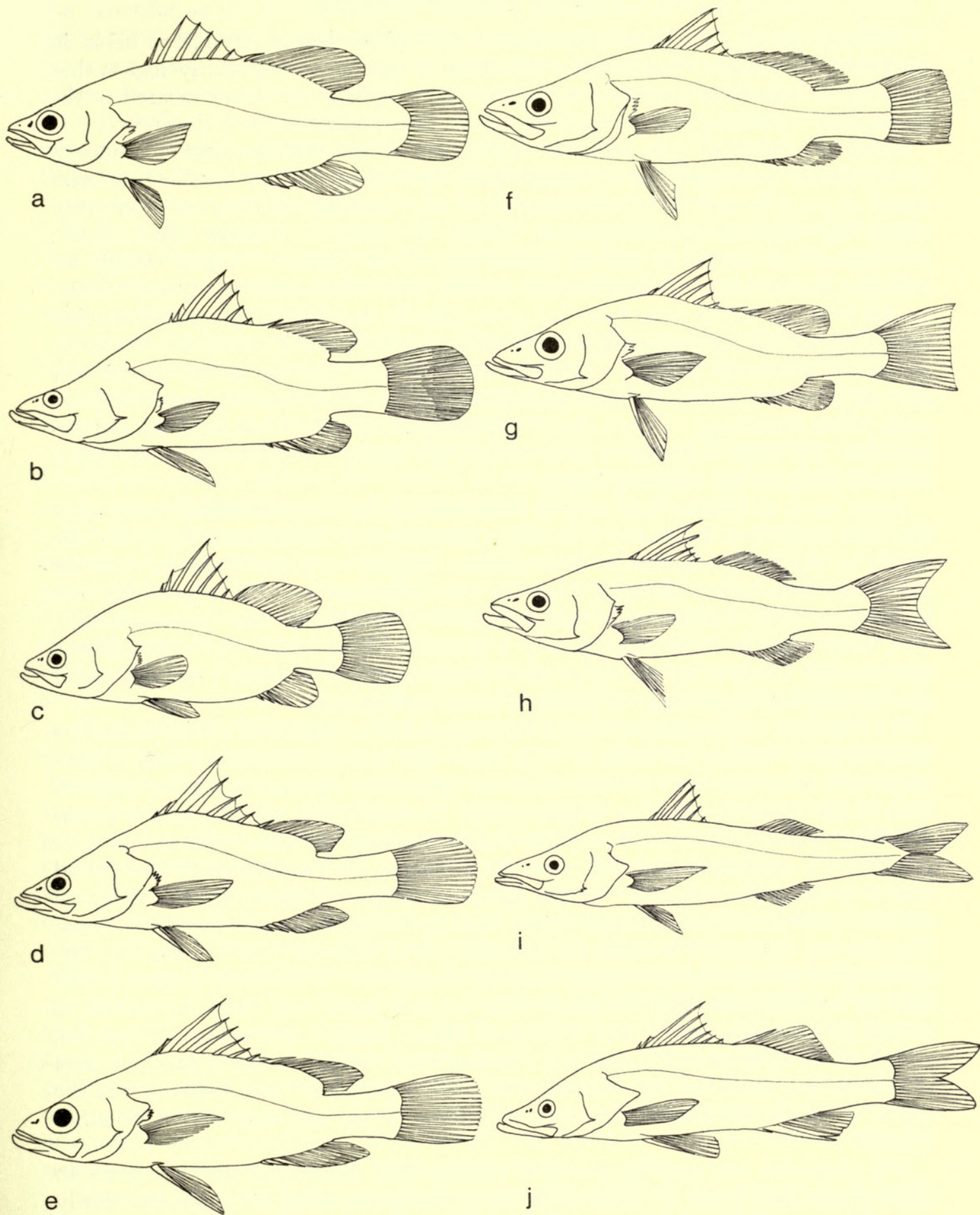


FIG. 1. Outlines of : (a) *Psammoperca waigiensis*, (b) *Lates calcarifer*, (c) *L. niloticus*, (d) *L. longispinis*, (e) *L. macrophthalmus*, (f) *L. angustifrons*, (g) *L. mariae*, (h) *L. microlepis*, (i) *L. stappersi*, (j) *Centropomus undecimalis*.

THE FAMILY CENTROPOMIDAE

Although in 1955 Matsubara classified several of the genera considered below in the family Serranidae, there is still a consensus of opinion among ichthyologists that these fishes constitute a natural taxonomic group, albeit one closely related to the Serranidae. (See Katayama (1956) for a short taxonomic history of the group.)

There has, however, been rather less agreement on the definition and delimitation of the family Centropomidae in which these various genera are classified, or with which they are thought to be most closely related. In particular there is uncertainty about the affinities of *Glaucosoma* Temm. & Schl., of *Chanda* Ham. Buch. (= *Ambassis* of authors), and of genera related to *Chanda*. Regan (1913), for example, included both *Glaucosoma* and *Chanda* (as *Ambassis*) in the Centropomidae, as did Norman (1966) who, however, gave *Chanda* and related genera subfamilial rank (Chandinae) and placed *Glaucosoma* with *Lates* Cuv., and *Psammoperca* Richardson in the subfamily Latinae. Other views were expressed by Jordan (1923) who gave familial rank both to *Chanda* and its related taxa (Ambassidae), and to *Glaucosoma* (Glaucosomidae). Berg's (1947) classification returned *Chanda* to the Centropomidae, but kept *Glaucosoma* as a monotypic family. Greenwood *et al.* (1966) followed Berg, as did Lindberg (1971).

There have, of course, been several definitions of the Centropomidae, both *sensu latu* and *stricto* (see especially Gill, 1883, and Meek & Hildebrand, 1925, for the family as restricted to species of *Centropomus*; Regan, 1913, and Norman, 1966, for the family *sensu latu*; Munroe, 1961, for the Chandidae and Centropomidae, and Katayama, 1954, for the only comprehensive definition of the Glaucosomidae). Yet, from none of these definitions is it possible to determine the synapomorphic features that could establish the phyletic relationships of the taxa involved, either as a holophyletic assemblage or as two or even three lineages.

With the aim of establishing such relationships I have examined all the characters listed in these various definitions; as is inevitable in such revisionary work I have discovered other characters which were not taken into account by earlier authors. Most of the characters used by Regan (1913), Norman (1966) and Katayama (1954) are either primitive features widely distributed amongst the lower percomorphs and percoids (i.e. symplesiomorphies), or, if derived ones, are characteristics also shared with several percoid families. In the symplesiomorphic category are the vertebral number, presence of frontoparietal crests, and the dentition and other jaw characters. The derived characters include the presence of an axillary pelvic scale, and the extension of lateral line pore scales onto the caudal fin. This latter character is of interest because, although the lateral line extends some way onto the caudal in several percoid taxa, rarely does it reach or almost reach to the margin of that fin, as it does in *Centropomus*, *Lates* and *Psammoperca*. (Only in the Sciaenidae does the lateral line extend as far posteriorly as in these genera.) This distinction in the degree to which the lateral line extends posteriorly has not been drawn by other workers.

One character not used by previous authors (but mentioned with reference to *Centropomus* and *Lates* by Gosline, 1966) is the presence of an anteroposteriorly expanded neural spine on the second vertebra. Indeed, this feature, combined with

the extension of the lateral line far onto the caudal fin, provide the only synapomorph characters at all widely distributed amongst taxa currently classified with the Centropomidae. Because the caudal lateral line character also occurs in the Sciaenidae, the neural spine character is the sole truly synapomorph feature of the centropomids. Currently recognized genera with such an expanded neural spine are *Lates*, *Luciolates*, *Psammoperca* and *Centropomus* (Fig. 1). Except for *Luciolates*, these genera also have the caudal lateral line scale row extending or almost extending to the fin margin. (The lateral line in *Luciolates* is discussed on p. 48.)

Neither *Glaucosoma* nor *Chanda* (and its related genera) has either of these features. The lateral line extends only onto the basal third, or less, of the caudal fin, and the second neural spine is no wider than that of the first vertebra (in other words, the usual percomorph condition).

Thus, on the basis of these characters, and the lack of any other unifying features, it would seem that *Glaucosoma* and *Chanda* cannot belong to the same lineage as *Centropomus*, *Lates*, *Luciolates* and *Psammoperca*. These latter taxa alone are therefore retained in the family Centropomidae.

Questions now arise as to the relationships and status of *Glaucosoma* and the *Chanda*-like genera, of their relationship to the Centropomidae as here defined, and of the interrelationships of the Centropomidae within the Percoidei.

Nothing I have yet discovered suggests that *Glaucosoma* is a close relative of *Chanda* (and its immediate relatives). Both taxa are readily defined by various autapomorphies, but I cannot find any synapomorph characters uniting them. Unfortunately, the sort of detailed information needed for phyletic studies amongst percoid fishes is not yet available for many taxa, and I cannot suggest where the relationships of *Chanda* and *Glaucosoma* may lie. For the moment the only course available is to recognize two families, the Glaucosomidae and the Chandidae, and to consider both as of uncertain affinity amongst the Percoidei. The dorsal gill arch skeleton in the Chandidae I have examined (several species of *Chanda*) is certainly more derived than are those of the Centropomidae and Serranidae (see Rosen, 1973, for a discussion of the gill arches in percoid fishes). In the morphology of the pharyngobranchials, especially the second, *Chanda* is very similar to *Eucinostomus argenteus* (Gerridae) as figured by Rosen (op. cit., text-figs 98 & 99). *Glaucosoma* also shows more derived characters in its gill arch skeleton than does any member of the Centropomidae. I suspect that it will be from the gill arch skeleton that the relationships of these two families will ultimately be determined.

Similar problems and lack of data limit the formulation of hypotheses regarding the phylogeny of the Centropomidae. It is generally thought, or implied, that the centropomids are closely related to the Serrandiae (see Regan, 1913; Katayama, 1954; Gosline, 1966; Greenwood *et al.*, 1966; Norman, 1966). Again it has so far proved impossible to demonstrate within these families any but symplesiomorph or autapomorph features, none of which provides acceptable information for confirming or refuting this relationship. Thus, for the time being the Centropomidae too must remain as a family *incertae sedis* amongst the lower percoids.

However, with the limits of the Centropomidae defined (see above) it is now possible to turn to problems of infrafamilial relationship and taxonomy.

AN ANATOMICAL AND TAXONOMIC REVIEW OF THE *LATES* AND
LUCIOLATES SPECIES

The present taxonomic status of several *Lates* species must be reviewed before considering their anatomy and phyletic relationships. The probably monotypic genus *Luciolates* Blgr. is also included in this review, although a discussion of its ultimate status is deferred until p. 49.

With one exception, namely *Lates calcarifer* (Bloch), all extant *Lates* species are confined to Africa but fossil remains of this genus are known from southern Europe as well as from several areas in Africa (Sorbini, 1973; Greenwood, 1974). The extinct taxon *Eolates gracilis* (Agassiz) from Monte Bolca will be considered later (p. 70), together with the extinct 'species' of *Lates*.

Lates calcarifer, a coastal and estuarine species, is widely distributed in the Indo-Pacific region (India, Bangladesh, Burma, Malay Peninsula, Java, Sumatra, Borneo, Celebes, Sarawak, Philippines, Papua-New Guinea, northern and western Australia, southern China, and Japan). According to Weber & de Beaufort (1929), this species also occurs in the Persian Gulf; their reference to *L. calcarifer* entering the mouths of the Nile, Niger and Senegal, and ascending these rivers, is clearly an error stemming from a confusion of this species with *L. niloticus*. Although essentially a marine fish, *L. calcarifer* freely enters and remains in rivers but always returns to estuarine or marine environments for spawning (Dunstan, 1959; Lake, 1971).

Lates niloticus (L.) is widely distributed in the rivers and lakes of tropical Africa (Nile, Niger, Senegal, Volta and Zaire [= Congo] rivers; Lakes Chad, Albert, Rudolf and some of the Ethiopian lakes). Not surprisingly in such a widespread taxon there are indications of some geographically limited morphotypes. As yet there has been insufficient study of these populations to determine the significance of their morphological differences, and none of the fluviatile populations has been given the formal status of a subspecies (see Daget (1954) on Pellegrin's (1922) *L. niloticus* var. *macrolepidotus* from Zaire). Worthington (1932), however, has described two subspecies, *L. niloticus rudolfianus* and *L. n. longispinis* from Lake Rudolf.

Lates niloticus rudolfianus, a form attaining a large size (up to 148 cm total length) and apparently confined to inshore regions of Lake Rudolf (Worthington, 1932), is acknowledged by Worthington to be morphologically intermediate between *L. niloticus* of the Nile and populations of that species inhabiting Lake Albert (named *L. albertianus* by Worthington [1929], but shown by Holden [1967] to be indistinguishable from *L. niloticus*). I have re-examined the type material of *L. n. rudolfianus* and can find no reason for maintaining the subspecific status of this population. In all morphometric, meristic and gross morphological characters the type specimens lie within the range of variability determined for *L. niloticus* over its entire range. Thus, at least until larger samples are available from numerous localities in Lake Rudolf, I would consider *L. niloticus rudolfianus* to be a synonym of the nominate species.

The second subspecies from Lake Rudolf, *L. n. longispinis*, presents a somewhat different problem. Apparently it is separated ecologically from the other *Lates*

species in the lake, being a fish of the deeper waters (Worthington, 1929; Hopson, unpublished report). Furthermore, it is morphologically differentiable from *L. niloticus*, and does not attain such a large adult size.

The principal morphometric differences distinguishing the taxon '*longispinis*' from *L. niloticus* are its larger eye (diameter 22.6–39.9 per cent of head in fishes 118–273 mm standard length, cf. 18.3–22.9 per cent in *L. niloticus* of a comparable size; in both taxa eye size is negatively correlated with standard length) and longer third spine in the dorsal fin (78.0–84.0 per cent of head, cf. 55.0–70.0 per cent). The larger eye in '*longispinis*' is most clearly manifest when small specimens of both species are compared; for example the eye is 21.8 per cent of the head in a 107 mm S.L. *L. niloticus* but is 32.9 per cent in a 118 mm specimen of '*longispinis*'.

Another difference, but one correlated with relative eye size, lies in the less marked posterior extension of the maxilla in '*longispinis*'. In specimens of *L. niloticus* more than 125 mm S.L. the posterior tip of the maxilla lies at a point clearly behind a vertical through the posterior orbital margin; in '*longispinis*' above 125 mm long the maxillary tip lies in or a little anterior to that vertical. In fishes less than 120 mm S.L., the distinction is much less obvious (or even non-existent) because of the relatively larger eye in *L. niloticus* of that size.

Since, in Lake Rudolf, '*longispinis*' and *L. niloticus* are sympatric (albeit allotopic), and because the two taxa show various and consistent morphological differences, I can find no grounds for considering '*longispinis*' to be a subspecies of *L. niloticus*. The obvious expedient of raising Worthington's (1932) *L. n. longispinis* to full specific rank, however, requires further consideration when the taxon is compared with *L. macrophthalmus* Worthington, 1929 (see above; also Holden, 1967). *Lates macrophthalmus* is the endemic ecological counterpart in Lake Albert of '*longispinis*' in Lake Rudolf (see Holden, 1967), and closely resembles that species as well, sharing with it the presumably derived features of enlarged eyes and elongate third spine in the dorsal fin. The only differential feature I can find is the relatively longer spine of '*longispinis*' (78.0–85.0, mean 82.0 per cent of head, cf. 65.0–84.0, $m = 74.4$ per cent, in *L. macrophthalmus*). There also appear to be slight differences in the relative proportions of certain head parts, e.g. the vertical limb of the preoperculum lies slightly further forward in '*longispinis*'. Detailed comparisons are hampered by the paucity of study material, there being only the five syntypes of *L. n. longispinis** and the eleven syntypes of *L. macrophthalmus* available.

Basically, the problem raised by '*longispinis*' in Lake Rudolf and *L. macrophthalmus* in Lake Albert is whether each should be considered a distinct and endemic species evolved locally from a population of *L. niloticus* (the generally accepted hypothesis, see Worthington, 1932, and Holden, 1967) or whether they should be looked upon as sister taxa derived from a common ancestor distinct from *L. niloticus*. This hypothetical species presumably invaded the developing Lakes Rudolf and Albert alongside *L. niloticus*. If this latter relationship could be determined it would, on the morphological evidence available, be more realistic to

* The sixth syntype of *L. n. longispinis* mentioned by Worthington (1932) cannot be located, and neither is it recorded in the Museum's register. This suggests that the word 'six' in the original description is a *lapsus* for 'five'.

treat '*longispinis*' as a subspecies of *L. macrophthalmus* rather than as a distinct species. Unfortunately I do not have enough material at my disposal to test the two hypotheses, even assuming that anatomical criteria alone would be suitable for this purpose. For the moment then, and without prejudice to an ultimate solution of the taxon's true phyletic position, I propose treating Worthington's subspecies as a full species, namely *L. longispinis* Worthington (1932).

The three other *Lates* species, *L. angustifrons* Blgr., *L. microlepis* Blgr. and *L. mariae* Steindachner (see Poll, 1953), require no further comment at this stage. All are morphologically distinct from the other species and from one another.

A fourth *Lates*-like taxon from Lake Tanganyika is currently placed in the genus *Luciolates** Blgr., principally because of the wide separation of the two dorsal fins (Boulenger, 1914; Poll, 1953, 1957). *Luciolates* is closely related to *Lates*, in particular to *L. mariae*. As I hope to demonstrate in the next section of this paper I believe that *Luciolates* should be included in *Lates* if the principles of phyletic classification are not to be violated.

The anatomy of *Lates* and *Luciolates*

The anatomy, and especially the osteology, of *Lates* and *Luciolates* has never been subject to a general review encompassing all known species. Gregory (1933) has given a rather superficial account of the syncranial osteology in *Lates niloticus*,† and Katayama (1956) a more detailed description of *Lates calcarifer* which included some details of its soft anatomy.

The account which follows is based on the examination of at least two skeletons of each species, and in the case of *L. niloticus* on several specimens over a wide size range. Radiographs of several specimens of every species were also examined.

In all intrageneric comparisons made below the conditions found in *L. calcarifer* and *L. niloticus* are, with few exceptions, taken to be those primitive for the genus. This conclusion regarding the status of the two species was reached after all the species had been examined and a comparison made with members of other percoid groups apparently related to the Centropomidae (Gosline, 1966; Greenwood *et al.*, 1966). Within the Centropomidae as a whole, *L. calcarifer* and *L. niloticus*-type cranial osteology should also be taken to represent the primitive condition.

The neurocranium

The overall morphology of the neurocranium in *Lates* and *Luciolates* can be judged from Figs 2-8.

Basically, the neurocranium in *Lates* differs little from that of most serranids (*sensu* Greenwood *et al.*, 1966). It has, however, well-developed and continuous frontoparietal crests with a sensory canal pore located at or near the junction of the crests, and the exoccipital facets are contiguous (separated in most serranids,

* A second species, *Luciolates brevior*, has been described (Boulenger, 1914), but is known only from the holotype and has never been recorded again. In all probability *L. brevior* should be treated as a synonym of *Luciolates stappersi* Blgr., 1914, and is treated as such in this paper.

† The neurocranium supposedly of *Luciolates stappersi*, figured by Gregory (1933), is wrongly identified; as far as I can judge it is from a specimen of *Lates angustifrons*.

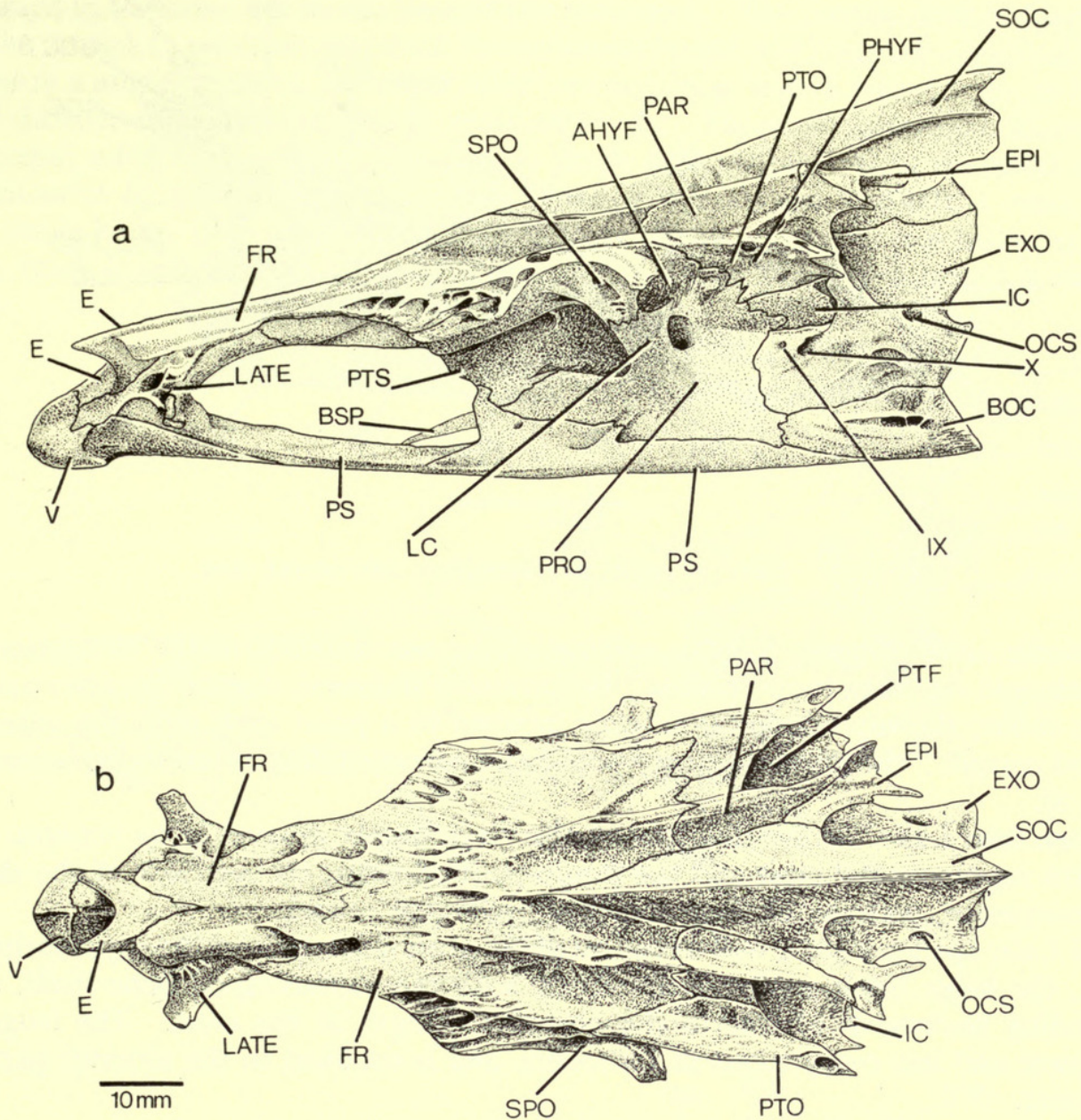


FIG. 2. *Lates niloticus*, neurocranium. (a) Left lateral view. (b) Dorsal view. (From Greenwood & Howes, 1975.)

personal observations; see also Gosline, 1966). Since continuous frontoparietal crests (usually incorporating a sensory pore) occur in berycoid fishes (see Patterson, 1964), this condition must be considered a primitive one. Likewise, the medially contiguous exoccipital facets are also a primitive feature found in berycoids. The extensive interfrontal penetration of the supraoccipital, however, must be ranked as a derived feature.

The dorsicranium shows some slight interspecific differences in detail but not in basic layout. The supraoccipital extends forward to the level of the median sensory pore of the supraorbital lateral line cross-commissure, and clearly separates the frontals posteriorly. The bone's relative anterior extension appears to be least marked in *L. angustifrons*, *L. mariae* and *L. microlepis*; this is attributable to the

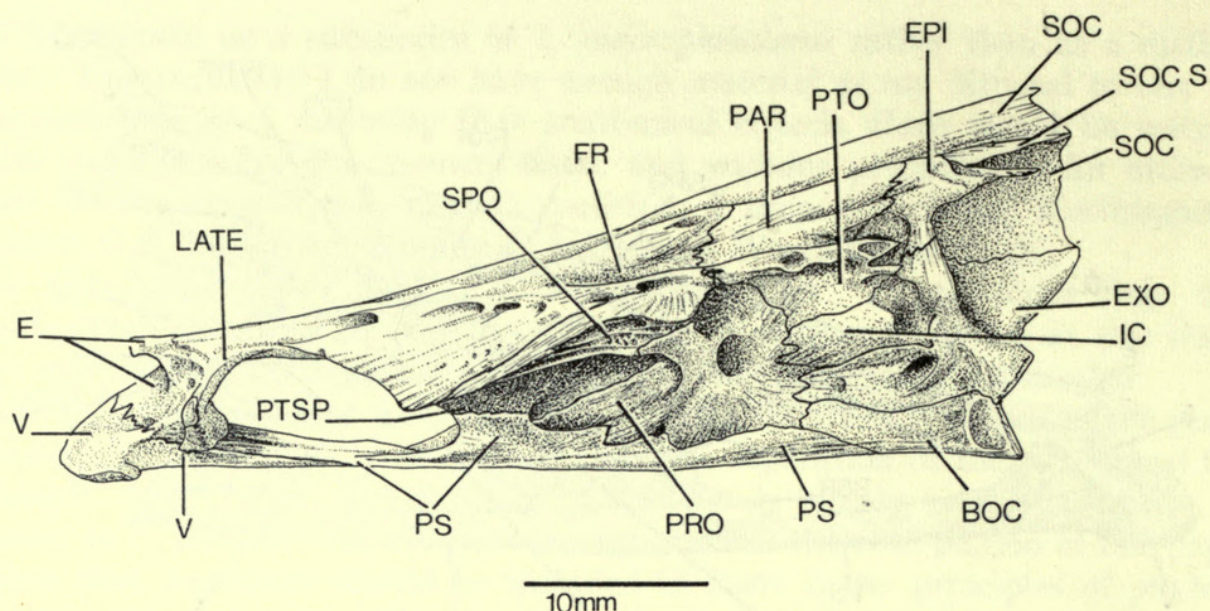


FIG. 3. *Lates calcarifer*, neurocranium, left lateral view.

anteriorly more elongate frontals, a lengthening associated with the elongation of the ethmoid region in these species. In *Luciolates stappersi*, despite the attenuation of its snout, the supraoccipital extends forward to a point level with the anterior orbital margin; the median sensory pore has a corresponding anterior displacement (Fig. 8).

These four Lake Tanganyika species also have deeper grooves lying between the median supraoccipital crest and the fronto-parietal ridges on each side of the skull, a consequence, perhaps, of their narrower skulls (see below).

All *Lates* species have a well-demarcated ledge on either side of the supraoccipital crest, the ledge being confluent anteriorly with the supraoccipital bone itself, and extending backwards almost to the posterior margin of the crest. The ledge is narrower and less conspicuous in *Luciolates*, and is confined to the anterior part of the crest.

The posttemporal fossa is deep in all species except *Luciolates stappersi*, and in none do its constituent bones meet at the centre of the fossa; even in the largest specimen examined the fossa is still open, its aperture closed off from the cranial cavity by a tough membrane. Amongst members of the Serranidae the *Lates-Luciolates* condition is characteristic of small and apparently juvenile fishes; in larger individuals (many of which are, nevertheless, considerably smaller than adult *Lates*) the fossa has a completely bony floor. This interfamilial difference would suggest that the *Lates* condition is the primitive one.

The wide cephalic lateral line canals of the dorsicranium are completely bone enclosed in all species (including *Luciolates*). On each side of the skull the continuous supraorbital-temporal canal opens to the exterior through several pores.

Dorsal and lateral skull outlines are essentially similar in *L. calcarifer*, *L. niloticus*, *L. macrophthalmus* and *L. longispinis* except for a marked narrowing of the inter-orbital region in the two latter species, and a more forward position of the orbit in *L. calcarifer*. The ethmoid region is relatively short, and the parasphenoid runs

forward in the same line as the base of the braincase. The preotic skull proportions of the largest *L. niloticus* examined (neurocranial length 228 mm) are very similar to those in a much smaller *L. calcarifer* skull (103 mm long, from a fish of c. 40 cm S.L.), and differ from those in smaller *L. niloticus* skulls. The most noticeable differences apparent when these smaller *L. niloticus* skulls are compared with the skull of an equal-sized *L. calcarifer* are the relatively more anterior position of the orbit, and the much longer precommissural skull region in the latter species (see below, p. 20). The skull proportions of large *L. niloticus* (i.e. skulls > 150 mm long), however,

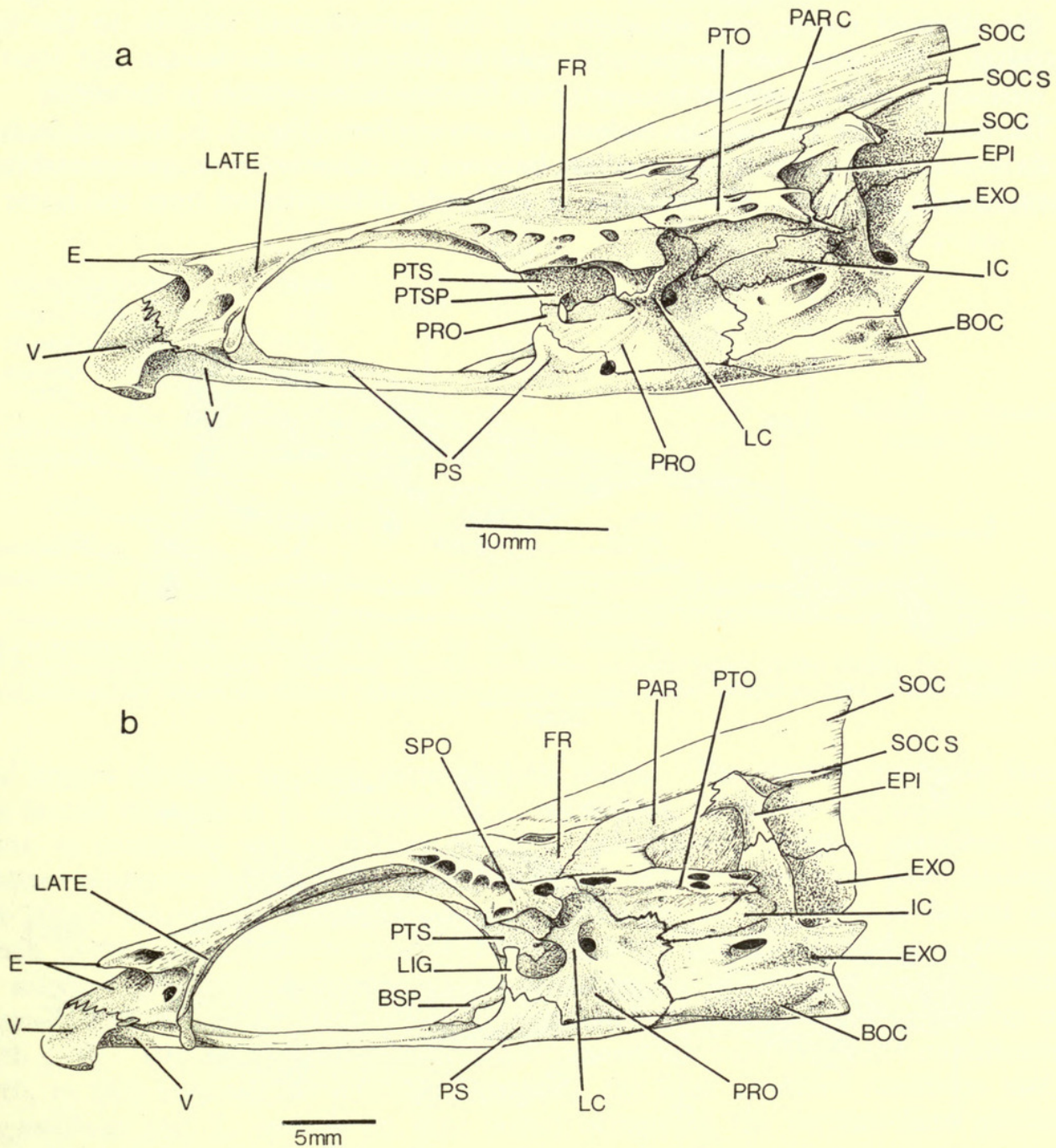


FIG. 4. (a) *Lates longispinis*. (b) *L. macrophthalmus*. Neurocranium in left lateral view. For nomenclature of *L. longispinis* see p. 12 *et seq.*

come to resemble those of *L. calcarifer* more closely, the resemblance increasing with the size of the skull. Katayama (1956) figures the neurocranium from a *L. calcarifer* of 28.6 cm S.L. ; judging from this figure there is little difference between a skull of that size and one from a *L. niloticus* of comparable length. Seemingly the orbital and precommissural skull proportions change much more rapidly in *L. calcarifer* ; compare, for example, the 103 mm skull of *L. calcarifer* (S.L. c. 40 cm) with the 123 mm skull of *L. niloticus* (S.L. c. 48 cm) in Figs 3 and 2.

Compared with the four species from outside Lake Tanganyika, three endemic Tanganyikan species, *L. microlepis*, *L. mariae* and *Luciolates stappersi* (Figs 5–8) show a distinct narrowing of the skull (particularly the braincase), an elongation of the ethmoid region, and an angling of the parasphenoid relative to the basioccipital. The slope of the parasphenoid is steepest in *L. mariae* and least in *L. microlepis*, with *Luciolates* occupying an intermediate position in the series.

The fourth Lake Tanganyika endemic, *L. angustifrons* (Fig. 5), is, in most features of its neurocranial profiles, intermediate between the other endemic species and those from outside the lake. Nevertheless, it is clearly differentiated from the latter by

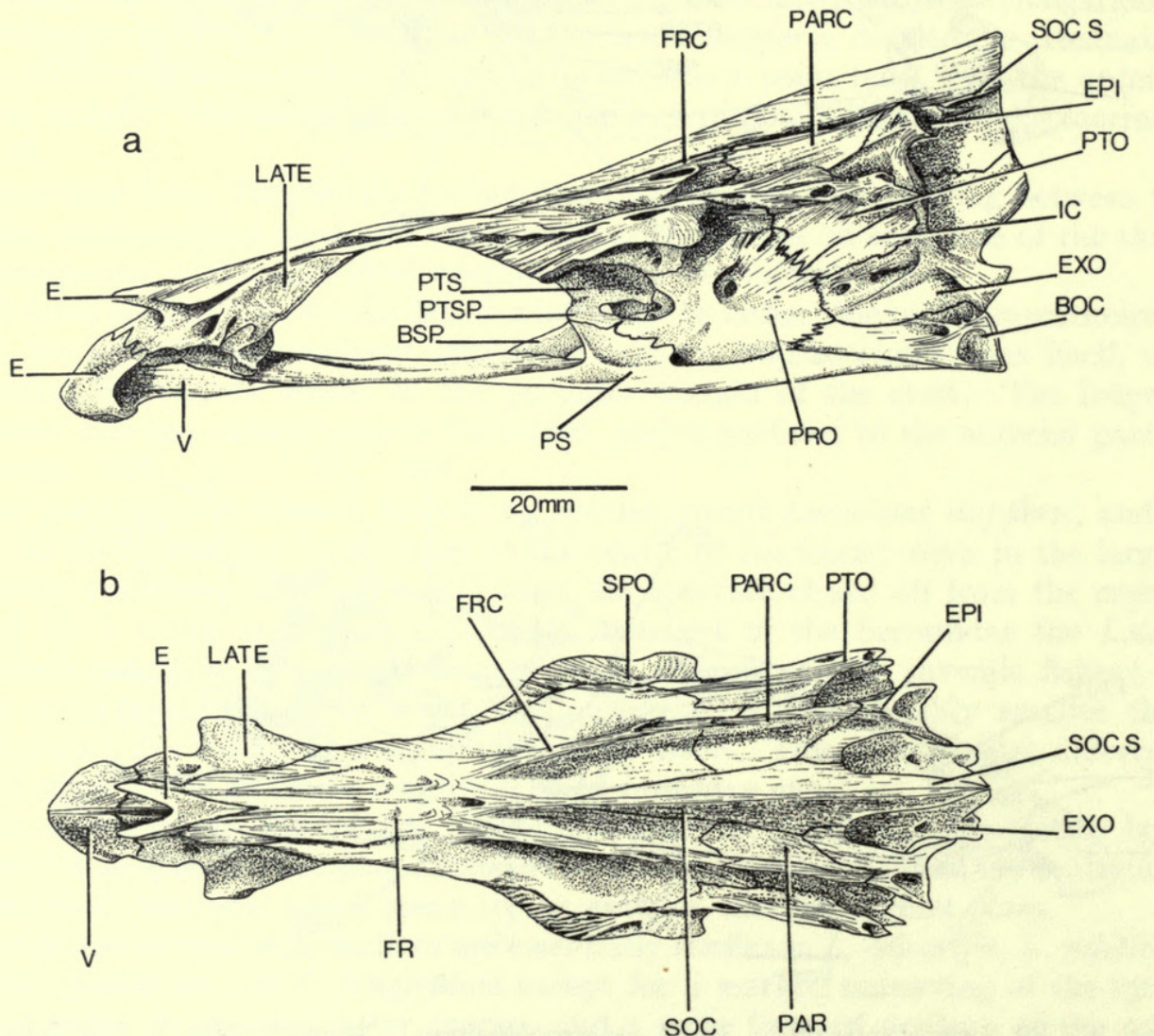


FIG. 5. *Lates angustifrons*. Neurocranium in : (a) left lateral view, (b) dorsal view.

the elongation of its ethmoid region and by the shape of its ethmoid bones, characteristics that unite it with the other endemic species from Lake Tanganyika (see below).

This elongation of the ethmovomerine skull region in all species of *Lates* (and *Luciolates*) from Lake Tanganyika immediately distinguishes the group (see Table 1),

TABLE 1

Relative length of ethmovomerine region in various *Lates* spp., and in *Psammoperca waigiensis*

| Species | Neurocranial ¹ length (mm) | Ethmovomerine ² length (mm) | Ethmovomerine length as % of neurocranial length | |
|-------------------------------|--|---|---|---|
| <i>Lates calcarifer</i> | 103.0 | 25.0 | 24.2% | } Subgenus <i>Lates</i> (see p. 77) |
| <i>L. niloticus</i> | 16.0 | 5.0 | 31.3% | |
| | 76.0 | 21.5 | 28.3% | |
| | 124.0 | 30.5 | 24.8% | |
| | 228.0 | 60.5 | 26.7% | |
| <i>L. macrophthalmus</i> | 32.0 | 8.5 | 26.5% | } Subgenus <i>Luciolates</i> (see p. 71) |
| <i>L. longispinis</i> | 59.5 | 16.5 | 28.7% | |
| <i>L. angustifrons</i> | 120.0 | 43.3 | 36.8% | |
| <i>L. mariae</i> | 26.0 | 10.0 | 38.5% | |
| | 77.5 | 32.0 | 41.3% | |
| <i>L. microlepis</i> | 44.0 | 18.0 | 41.0% | |
| <i>L. stappersi</i> | 71.0 | 31.0 | 43.5% | |
| | 71.0 | 32.5 | 45.8% | |
| | 103.5 | 49.0 | 46.9% | |
| <i>Psammoperca waigiensis</i> | 43.0 | 14.5 | 33.7% | |

¹ Neurocranial length: measured directly from the anterior tip of the vomer to the posterior point on the lower margin of the basioccipital facet for the first vertebra.

² Ethmovomerine length: measured directly from the anterior point of the vomer to that point on the dorsicranium where the lateral ethmoid-prefrontal passes under lateral margin of the frontal.

and argues strongly for their monophyletic origin. The concave posterior face of the lateral ethmoid in *L. angustifrons*, *L. microlepis*, *L. mariae* and *Luciolates stappersi*, as compared with members of the *L. calcarifer*–*L. niloticus* complex, has a distinct posterior slope (cf. Figs 2–4 with 5–8). Furthermore, and most strikingly, the lateral margins of the bone are much wider (or, as it appears in lateral view, much deeper) and have a pronounced downward slope. In the *L. calcarifer*–*L. niloticus* group the posterior margin of the lateral ethmoid is almost vertically aligned, and its lateral margins are narrow and horizontally aligned (cf. Figs 2–4 with 5–8). Once again it is *Luciolates* that shows the most profound modifications with, in this instance, *L. microlepis* showing the least modified condition and *L. angustifrons* and *L. mariae* (in that order) occupying the intermediate places in the series.

There is little interspecific variation in the morphology of the lateral ethmoids of *L. calcarifer*, *L. niloticus*, *L. macrophthalmus* and *L. longispinis* (see Figs 2–4).

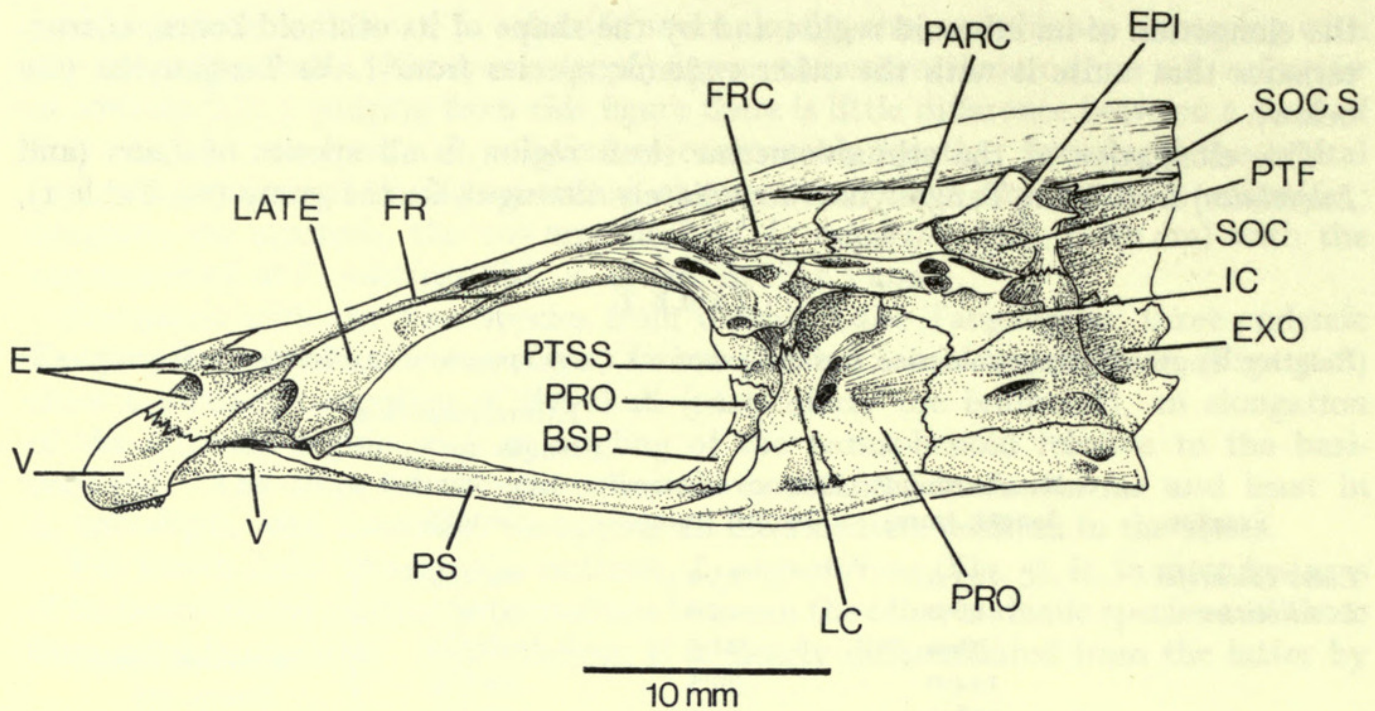


FIG. 6. *Lates microlepis*. Neurocranium in left lateral view.

All *Lates* species, and *Luciolates*, have three facets on each lateral ethmoid; two, ventrally placed, are for articulation with the palatine, and the third (situated dorsolaterally above the posterior palatine facet) for articulation with the first circumorbital bone (lacrimal). The facets are less well defined in the Tanganyika species, and are most poorly differentiated in *Luciolates*.

A noticeable feature of the skull in *L. calcarifer*, *L. niloticus* and, to a slightly lesser degree, in *L. angustifrons* is the way in which the anterior wall of the neurocranium (i.e. the prootic, pterosphenoid and ascending arm of the parasphenoid) are extended forward beyond the level of the lateral commissure (Figs 2, 3 & 5); in *L. calcarifer* and *L. niloticus* the tunnel-like ventral part of this extension surrounds all but the anterior half or more of the basisphenoid. This feature is emphasized when the skulls of these species are compared with those of *L. mariae*, *L. microlepis* and *Luciolates stappersi*, species in which there is only a slight prolongation of the neurocranial wall beyond the level of the lateral commissure (cf. Figs 2, 3 & 5 and 6–8). The situation in *L. macrophthalmus* and *L. longispinis* is virtually intermediate between those in the other two groups. (See Table 2 and Fig. 4.)

Closer examination of the precommissural extension in specimens of *L. calcarifer* (neurocranial length, ncl., 103 mm), *L. niloticus* (ncl., 75 mm and above) and *L. angustifrons* (ncl., 120 mm) reveals the existence of a pterosphenoid pedicle which, through its contact with the parasphenoid anteriorly and the outer lip of a horizontal groove in the prootic, forms a semi-tubular bridge over the oculomotor and profundus nerves and the internal jugular vein (Figs 9 & 10). Rognes (1973) has called a similar structure in labrids an internal jugular bridge, and that name will be used here.

TABLE 2

Precommissural skull proportion in *Lates* and *Psammoperca*

| Species | Neurocranial ¹ length (mm) | Precommissural ² skull length (mm) | Precommissural length as % of neurocranial length |
|--------------------------|--|--|--|
| <i>Lates calcarifer</i> | 103.0 | 25.0 | 24.2% |
| <i>L. niloticus</i> | 76.0 | 10.0 | 13.1% |
| | 124.0 | 22.0 | 17.7% |
| <i>L. longispinis</i> | 59.5 | 6.0 | 10.1% |
| <i>L. macrophthalmus</i> | 32.0 | 3.0 | 9.4% |
| | 74.0 | 10.0 | 13.5% |
| <i>L. angustifrons</i> | 120.0 | 14.0 | 11.7% |
| <i>L. stappersi</i> | 71.0 | 3.5 | 4.9% |
| | 103.5 | 6.0 | 5.8% |
| <i>Psammoperca</i> | | | |
| <i>waigiensis</i> | 43.0 | 2.5 | 5.7% |

¹ See Table 1 (p. 19).² Precommissural skull length: measured directly from the anterior margin of the lateral commissure to the anterior margin of the ascending limb of the parasphenoid.

The relative contributions of the prootic and parasphenoid bones to the internal jugular bridge show marked intraspecific variability, and usually differ on either side (see Fig. 9c-d). The parasphenoid contribution is always the least important, the major part of the ventral wall (and the entire groove) coming from the prootic, and the dorsal and lateral walls from the pterosphenoid pedicle. Except in the small *L. niloticus* skulls examined (see below) there is always some contact between the three bones at the orbital (i.e. front) margin of the bridge. Since the smallest available skulls of *L. calcarifer* and *L. angustifrons* measure 103 mm and 120 mm long respectively, no comment can be made on the interrelationship of these bones in small individuals of those species.

Apparently correlated with the degree of pterosphenoid development and the development of the precommissural braincase is the extent to which the autosphenotic is prolonged anteriorly. The correlation is a positive one in species with an extensive precommissural braincase and a well-developed pedicle (i.e. *L. calcarifer* and *L. niloticus*). The anterior extension of the autosphenotic is least marked in *Luciolates stappersi*, *L. mariae* and *L. microlepis*, and is of intermediate length in *L. angustifrons*, *L. macrophthalmus* and *L. longispinis*.

Before describing and comparing the precommissural crania for all *Lates* and *Luciolates* species, it is necessary to consider the ontogenetic changes involved in the production of an adult *L. niloticus*-type pterosphenoid pedicle and internal jugular bridge.

The smallest *L. niloticus* skulls examined (12 mm long) have no noticeable precommissural extension of the braincase; the parasphenoid does not contact the pterosphenoid and there is no bony bridge over the nerves and blood vessel (Fig. 9a). At the ontogenetic stages represented by those skulls there is also no obvious

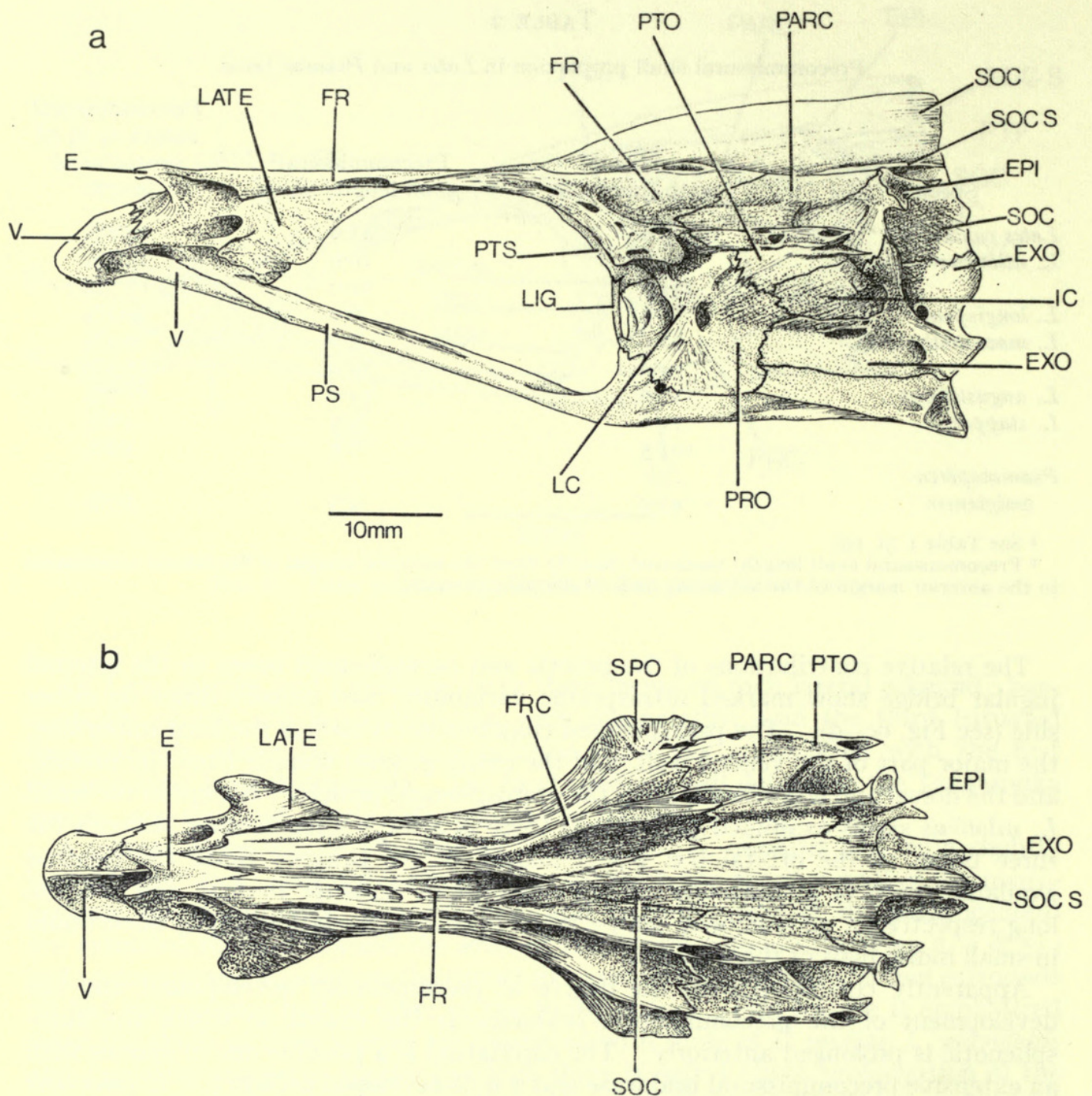


FIG. 7. *Lates mariae*. Neurocranium in : (a) left lateral view, (b) dorsal view.

pterosphenoid pedicle, but a narrow ligament runs from the lower, anterior part of the pterosphenoid to the outer rim of the weakly developed prootic groove lying below the internal jugular vein (Fig. 9a) ; in effect, the ligament occupies the position later taken by the pterosphenoid pedicle arm of the internal jugular bridge. At its dorsal base, the ligament is attached to a small spur of bone on the pterosphenoid, which I would interpret as an incipient pedicle.

In progressively larger skulls (i.e. to a length of 76 mm), there is a gradual development and down-growth of the pterosphenoid pedicle, and of a dorsally directed

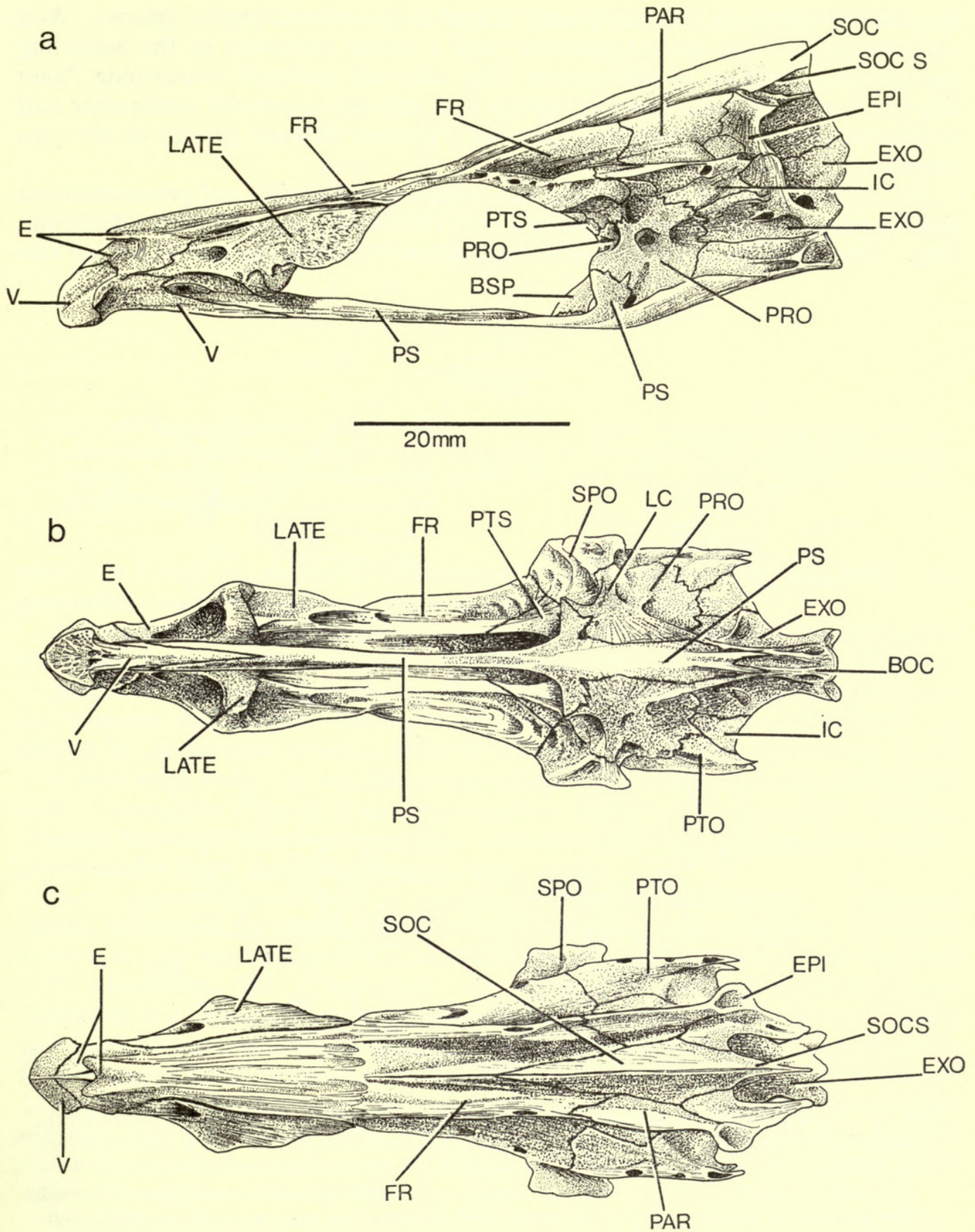


FIG. 8. *Lates stappersi*. Neurocranium in : (a) left lateral view, (b) ventral view, (c) dorsal view. For details on the altered generic placement of this species (previously *Luciolates stappersi*) see p. 50.

spur-like development from the prootic lateral to the internal jugular groove. As a consequence of these growth patterns (and a dorsal extension of the ascending parasphenoid arm) an at first narrow (Fig. 9b), but gradually broadening, bony ridge is formed over the internal jugular vein and the associated oculomotor and profundus nerves. Concurrently, there is a gradual forward growth of the precommissural region of the skull.

A *L. niloticus* skull 76 mm long has the pterosphenoid pedicle and precommissural skull developed to an extent comparable with that in a *L. angustifrons* skull 120 mm long. Growth of the precommissural skull wall in *L. niloticus* continues beyond this

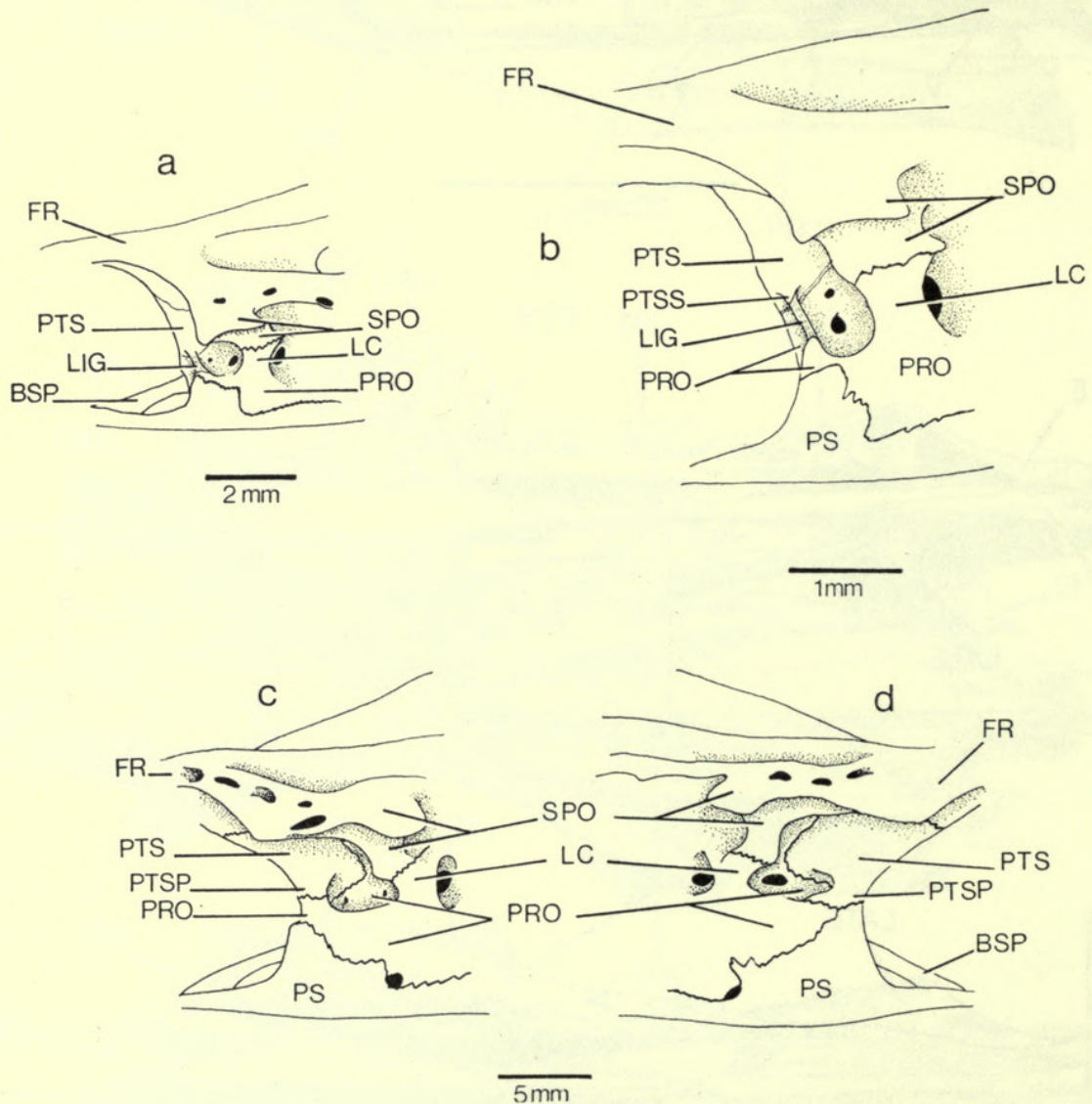


FIG. 9. Outline figures of internal jugular bridge, pterosphenoid pedicle and precommissural skull to show in : (a) & (b) growth changes in *L. niloticus* and in : (c) & (d) variability in the bridge of a single specimen of *L. longispinis*. (a) *Lates niloticus*; left lateral view, neurocranial length 12 mm. Note ligamentous connection between spur of pterosphenoid and process on prootic. (b) *L. niloticus*; left lateral view, neurocranial length 16 mm. Note downgrowth of pterosphenoid spur (= pedicle) to join prootic process. (c) & (d) *L. longispinis*. Left and right sides of skull showing variation in the interrelationships of bones contributing to the internal jugular bridge. Note direct pterosphenoid-parasphenoid contact in (d).

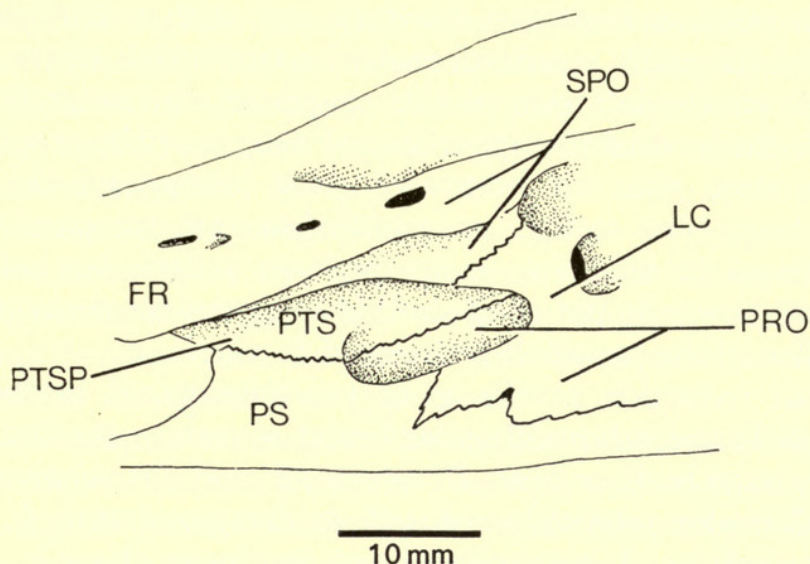


FIG. 10. *Lates calcarifer*. Outline figure to show relative hyperdevelopment of precommissural skull (left lateral view), especially the pterosphenoid pedicle and internal jugular bridge. Compare with Figs 9(c) & (d), 5(a), 2(a). From a skull of 10.3 cm neurocranial length.

point ; in a skull 124 mm long it has attained, however, the overall morphology and proportions seen in the largest skull examined (230 mm long).

Unfortunately no *L. angustifrons* skulls longer than 120 mm could be obtained so it has not been possible to determine the definitive form in that species. However, to judge from the totality of interspecific differences seen in skulls of about the same size it seems unlikely that this region of the neurocranium in *L. angustifrons* ever attains the proportions found in either *L. niloticus* or *L. calcarifer* (see above, p. 21).

As was noted earlier (p. 20), the precommissural skull region in *L. macrophthalmus* and *L. longispinis* is less well developed than in adult *L. calcarifer* and *L. niloticus*. It must, however, be remembered that members of the two former species reach a much smaller adult size (Worthington, 1929, 1932).

In a *L. macrophthalmus* skull 74 mm long (from a fish of 275 mm S.L.) the internal jugular bridge and the pterosphenoid pedicle have about the same degree of development as in a 76 mm long skull of *L. niloticus* (S.L. c. 290 mm) or a 120 mm long skull of *L. angustifrons* (S.L. c. 350 mm) ; the situation is similar in a slightly larger individual of *L. macrophthalmus* (320 mm S.L., neurocranial length 110 mm) Both specimens have a narrow parasphenoidal contribution to the bridge which is otherwise formed mainly from the pterosphenoid pedicle and the prootic spur. The smallest *L. macrophthalmus* skull examined (32.5 mm long, from a fish of 110 mm S.L.) shows a degree of development comparable with that in a *L. niloticus* skull only 16 mm long ; namely, a ligamentous bridge, and the pterosphenoid pedicle manifest only as a small spur of bone (Fig. 9a).

Conditions in *L. longispinis*, as seen in a skull 59 mm long (from a fish c. 250 mm S.L.), are close to those in the 74 mm skull of *L. macrophthalmus*, but the bridge is a little narrower. In a larger skull (70 mm long from a fish 275 mm S.L.) the bridge and pedicle, and the precommissural skull proportions are similar to those in the

76 mm skull of *L. niloticus* described above (p. 24), with a distinct pedicle and, at least on one side of the skull, a parasphenoidal contribution to the internal jugular bridge (Fig. 9d); on the left side of this specimen, the ascending parasphenoid limb fails to reach the level of the upper lateral margin of the prootic (Fig. 9c).

It would seem, then, that the internal jugular bridge and the precommissural skull in both *L. longispinis* and *L. macrophthalmus* are comparable with those in similar-sized skulls of *L. niloticus*, or are perhaps a little less advanced in some individuals. In other words, the adult skull of *L. macrophthalmus* and *L. longispinis* retains at least some of the pre-adult features of *L. niloticus*.

A really marked reduction in the adult precommissural braincase and in the pterospheneid pedicle and internal jugular bridge is seen in the skulls of three Lake Tanganyika taxa, namely *L. mariae*, *L. microlepis* and *Luciolates stappersi*. (This region of the skull is also relatively reduced, as compared with *L. niloticus*, in the fourth Tanganyika species, *L. angustifrons*, see pp. 20–25 above.)

In none of these three species does the parasphenoid contact the pterospheneid, always being separated from that bone by the prootic (Figs 6–8). No trace of a pterospheneid pedicle, even as a low ridge, is detectable in the three *Luciolates stappersi* skulls I have examined (neurocranial lengths 71 (f. 2) and 113 mm), but a low ridge was found in the largest of the three *L. mariae* skulls (26.0, 77.5 and 104.0 mm long).

A similar ridge is developed on the right but not the left pterospheneid of a 44 mm long skull of *L. microlepis*. A larger skull (95 mm) of *L. microlepis*, however, has a well-developed, broad-based but distally narrowed pedicle which reaches almost to the level of the prootic spur (Fig. 6). It is connected to the prootic spur by a short section of what appears to be ossified ligament.

Thus, of these three species, *L. microlepis* is the only one in which the pterospheneid pedicle makes a significant contribution to the internal jugular bridge. Even in the largest skulls of *L. mariae* and *Luciolates stappersi* there is only a ligamentous bridge, a condition directly comparable with that in the smallest specimens of *L. niloticus*, except that in the Tanganyika fishes the ligament appears to be ossified. In other words, the precommissural braincase in large specimens of *L. mariae* and *Luciolates stappersi* (standard lengths 390 and 415 mm respectively) is like that in *L. niloticus* of about 60 mm standard length, while that of a *L. microlepis* 390 mm standard length is comparable with a *L. niloticus* of about 130 mm S.L.

The pterospheneid–prootic ligament found in juvenile *L. niloticus* and adults of Tanganyika taxa described above is readily separated from both its bones of attachment. Thus it seems unlikely that it is truly part of the pterospheneid pedicle. Presumably the ligament is replaced by the pedicle as it grows down to meet the spur from the outer rim of the prootic groove. The large *L. microlepis* specimen noted above represents a late phase in this developmental sequence, the small *L. macrophthalmus* (ncl., 32.5 mm; p. 25) an early phase, and the adult condition in *L. niloticus*, *L. calcarifer* and *L. angustifrons* the terminal state.

An internal jugular bridge is of sporadic and phyletically widespread occurrence amongst living teleosts. Rognes (1973) gives detailed accounts of the bridge in labrine Labridae, and reviews records of its occurrence in other groups. I can

confirm its presence in certain ostariophysans (*Alburnus*; see also Holmgren & Stensiö, 1936, for *Abramis*), certain scorpaeniforms (*Enophrys bison*, *Scorpaena scrofa*, *Trigla hirudo*, see also Allis, 1909; Allen [1905] describes a bridge in *Ophidion* [Hexagrammidae]), and in several percoids (*Epinephelus* species [but not other serranids], *Stizostedion volgensis*, *Perca fluviatilis* [but not, apparently, in *Gymnocephalus*]), and in some sphyraenoids (*Sphyraena* sp.).

In the majority of cases where a bridge is present, it is of the type found in juvenile *L. niloticus*, namely a ligament (generally ossified) joining a reduced pterosphenoid pedicle to a process developed on the prootic (see above, p. 21). Only in *Enophrys bison* is a bridge of the *L. angustifrons* type present.

This list, based on samples taken from the families represented in the dry skeleton collection of the British Museum (Natural History), cannot by any means be considered complete, especially since the bridge is not always preserved in dry skeletons. Nevertheless, it is interesting to find that in none of the beryciform skeletons at my disposal is there any indication of a bridge nor even of the pterosphenoid pedicle (which is usually obvious even if the ligamentous part of the bridge is missing). Neither a bridge nor a pterosphenoid pedicle was noted in any of the Mesozoic beryciforms described by Patterson (1964).

Superficially, *Salmo trutta* has what appears to be an internal jugular bridge, but closer inspection shows that it is formed entirely within the prootic. Thus it would seem to be homologous with the 'prelateral commissure' described by Rognes (1973) in the labrid *Ctenolabrus exoletus* (see Rognes, op. cit., fig. 59).

The pterosphenoid pedicle has a long history in actinopterygian fishes, being well developed in some leptolepids and pholidophorids, in *Amia* and its fossil relatives *Sinamia* and *Ellenes*, and at least partially developed in some palaeoniscids (Patterson, 1975). As Patterson (op. cit., p. 409) observes: '... It is therefore likely that a pterosphenoid pedicle of some sort, or at least the potentiality to develop such a structure is a primitive actinopterygian feature.'

Since the pterosphenoid pedicle is an integral part of the internal jugular bridge (see above) and because this bridge is of widespread occurrence among teleosts, one may conclude that the bridge too is a primitive feature.

The absence or great reduction of the bridge and pedicle in certain *Lates* species can, therefore, be interpreted as an apomorphic feature, at least when individuals of these species attain a size at which the bridge would otherwise be present in related taxa. *Lates macrophthalmus* and *L. longispinis* (both species with reduced bridges) are examples of the situation where maximum adult size is about equal to that in preadult *L. niloticus* and *L. calcarifer*; at that size, specimens of *L. niloticus* (and presumably *L. calcarifer*) have a poorly developed bridge. Thus, it is probably correct to consider *L. macrophthalmus* and *L. longispinis* as plesiomorphic with respect to the bridge character.

Hyopalatine arch and the preoperculum (Figs 11 & 12)

Apart from slight proportional changes in, particularly, the length of the palatine and ectopterygoid bones of the Tanganyika species, there is little interspecific variation in the hyopalatine arch of *Lates* species (see Figs 11 & 12).

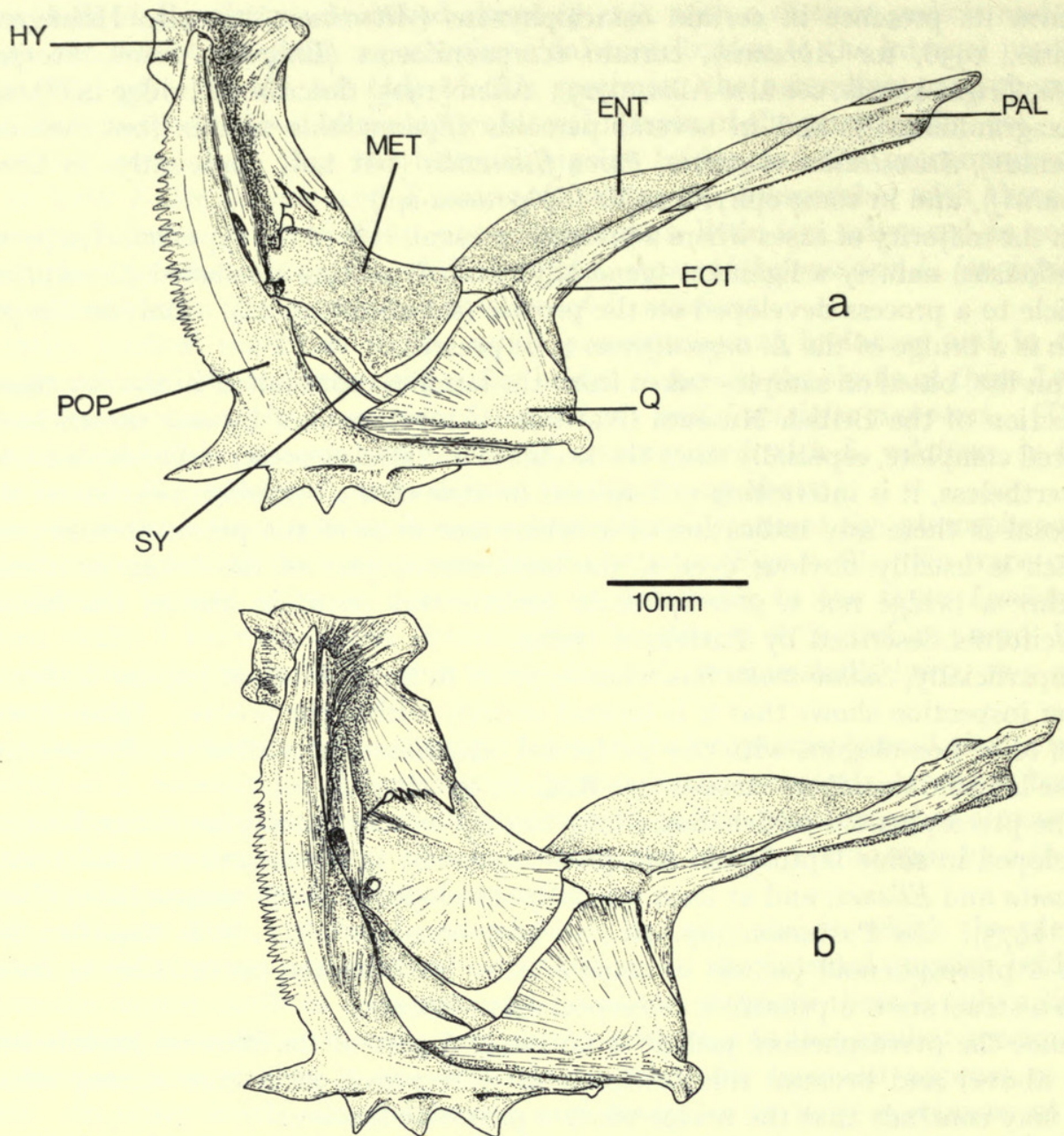


FIG. 11. Hyopalatine arch, right (including preoperculum) in lateral view of (a) *Lates mariae*, (b) *L. niloticus*.

The hyomandibula has two well-defined articulatory facets interconnected by a thin lamina of bone.

The metapterygoid has a strong sutural union with the hyomandibula and with the posterior tip of the expansive endopterygoid. There is no true metapterygoid lamina (*sensu* Katayama, 1956, and Gosline, 1966) but a slight ridge is detectable in the position where a lamina would occur; also, in many species there is a small foramen (or fenestra) in the metapterygoid at the postero-dorsal end of the ridge. I would interpret these structures as the remnants of a greatly reduced metapterygoid lamina.

Fine viliform teeth cover the entire ventral surface of the palatine. A similarly shaped (i.e. elongate ovoid) tooth patch occurs on the medial aspect of the anterior

arm of the ectopterygoid, sometimes extending a short way onto the vertical arm of that bone as well.

The autopalatine is a fairly stout bone. Anteriorly, on its medial face are two well-defined articulatory surfaces for contact with the ethmoid; dorsally there is a weakly demarcated facet for articulation with the lateral ethmoid. A panhandle-like, cartilage-tipped projection from the upper surface of the palatine provides articulation between this bone and the maxilla.

In most details, including the presence of a reduced metapterygoid lamina, the hyopalatine arch of *Luciolates* resembles that of *Lates*, particularly the Lake Tanganyika species of the genus. However, all the bones (especially the endopterygoid) are thinner and the palatine is less robust, with poorly demarcated articulatory facets. The palatine tooth patch is much narrower in *Luciolates*, and there is a great

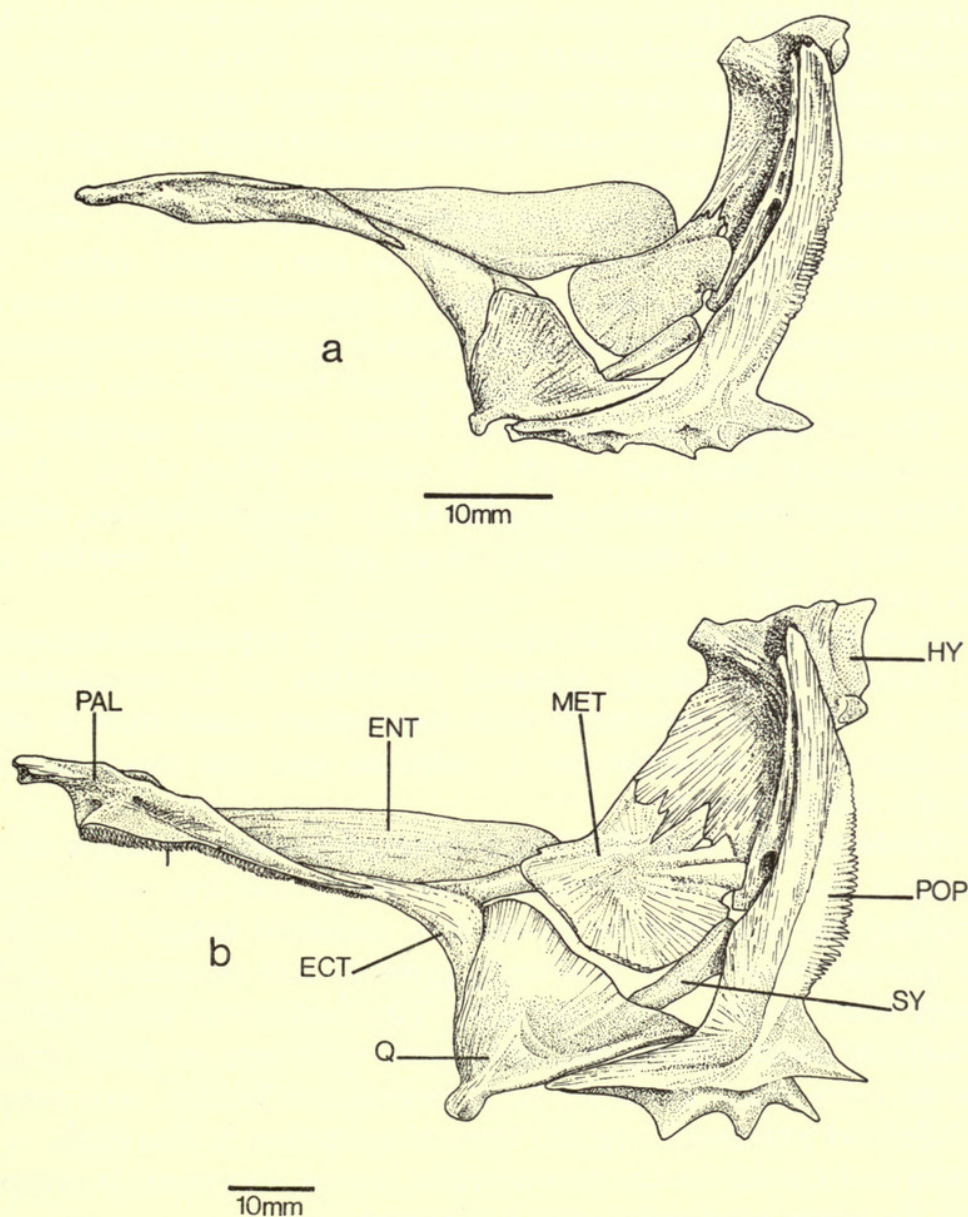


FIG. 12. Hyopalatine arch, left side (including preoperculum) in lateral view of (a) *Lates stappersi*, (b) *L. angustifrons*.

reduction in the area of the ectopterygoid teeth, the tooth-patch being either reduced to a small oval near the ectopterygoid-palatine articulation or it is completely absent. In one of the three skeletons examined the tooth-patch was present on one side only.

Like the hyopalatine arch, the preoperculum in *Lates* shows little interspecific variation, although it does show some intraspecific variability. The entire posterior margin of the vertical limb, except for a short length near its ventral angle, is finely serrate, the individual serrae are slender, sharp-pointed and tall. In very large specimens of *L. niloticus* (> 150 cm S.L.), the serrations are considerably reduced in height, and consequently the posterior margin of the bone is merely irregular (see also Sorbini, 1973).

At the posterior angle between the horizontal and vertical preopercular limbs there is a large, posteriorly directed and triangular spine (Fig. 11); very rarely this spine is subdivided almost to its base, resulting in two narrower but still triangular spines. On the horizontal limb there are generally three triangular spines, each slightly shorter and narrower than the spine at the bone's posterior angle. In larger *L. niloticus* the spines become irregular in outline, relatively shorter, and may have rounded rather than acute points.

Although three preopercular spines are modal for all species but *L. macrophthalmus*, a fourth spine is sometimes developed either on one or both sides. Usually the extra spine is a distinct entity, but sometimes it appears merely to be a subdivision of one of the other spines. *Lates macrophthalmus* is apparently exceptional in having a high proportion of individuals with four spines (seven of the eleven specimens examined). The proportion of four-spined fishes amongst samples of the other species is: *L. calcarifer*, none out of 18; *L. niloticus*, 7 out of 31; *L. longispinis*, 3 out of 6 (a high proportion, approaching that of *L. macrophthalmus*, which may be a related taxon, see p. 13); *L. angustifrons*, none out of 14; *L. mariae*, 4 out of 20; *L. microlepis*, 2 out of 27.

The occurrence of four-spined individuals may be a population feature, hence my reservations about the seemingly unusual condition in *L. macrophthalmus*. All but one of the *L. niloticus* specimens with four spines came from a single sample (incidentally, the largest available for *L. niloticus* and one much larger than was available for any other species).

Luciolates stappersi (Fig. 12a) also has a serrated posterior margin to the vertical preopercular limb, but here the serrations are lower and less well defined (in this respect resembling the condition in 16–20 mm standard length *L. niloticus*). The spine at the preopercular angle is always present and prominent, although it is somewhat finer than in any *Lates* species. The horizontal limb may have three large and relatively short spines, but specimens with two or three groups of very small spines, or even what amounts to a crenellated border, are common. The incidence of bilateral asymmetry in the type of spination is also high.

In both *Lates* and *Luciolates* the preopercular lateral line canal is completely bone enclosed, with its pores confined to the horizontal limb.

Although a serrated or otherwise ornamented vertical preopercular limb is of common occurrence amongst the lower percoids (e.g. in the Serranidae), the presence

of large and discrete spines on the horizontal limb and at its angle is extremely rare (*Percalates* and *Siniperca* [Serranidae] are, as far as I can determine, the only taxa having the same type of preopercular ornamentation as *Lates*). A similar generalization can be made for the lower percomorphs (*sensu* Rosen, 1973; for example, the 'Beryciforms'). Thus, it seems reasonable to conclude that the ventral preopercular ornamentation in *Lates* (and probably other centropomids as well, see below) is a derived condition (see also Rosen, 1973: 469). *Luciolates* too can be included in this generalization, the condition here being interpreted as the secondary simplification of a derived condition mimicking a plesiomorphic one.

Circumorbital bones (Figs 13a-d)

The greater part of the ventral margin to the first circumorbital bone (the lachrymal) is finely serrated in all *Lates* species; only a short anterior part is smooth. In all species the entire margin of the second circumorbital is also serrated.

The infraorbital lateral line canal in *Lates* and in *Luciolates* is enclosed throughout its length, communicating with the exterior through five pores in the lachrymal, one anteriorly on the third circumorbital bone, and through other pores found between successive bones in the series.

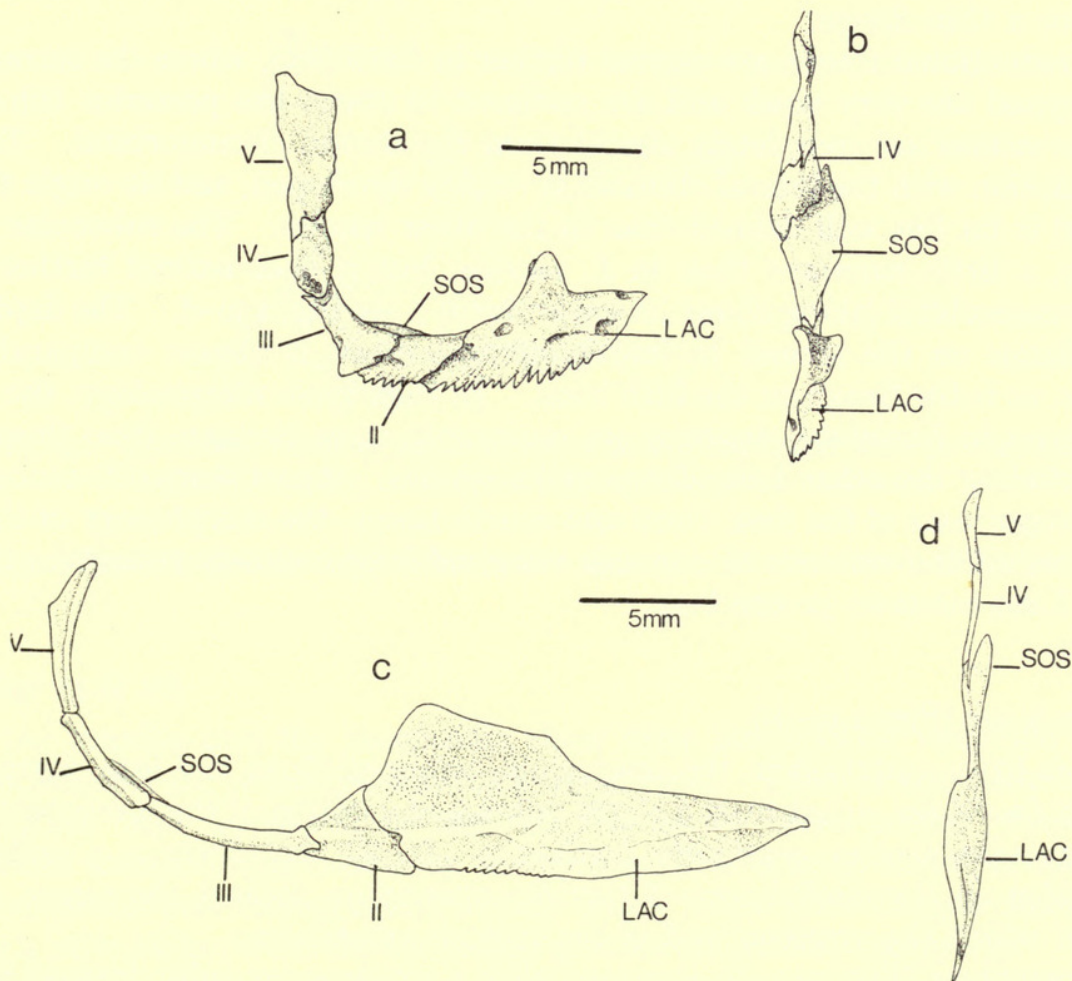


FIG. 13. Circumorbital bones (right side) in : (a) & (b) *Lates niloticus*, and in : (c) & (d) *L. stappersi*; (a) and (c) lateral view, (b) and (d) viewed dorsally and somewhat anteriorly.

All species (including *Luciolates stappersi*) have a well-defined facet developed at about the middle of the upper lachrymal margin ; it articulates with a similar facet on the lateral ethmoid.

There is a general similarity in the shape of the first two circumorbital bones in all *Lates* species, although the three species from Lake Tanganyika (*L. angustifrons*, *L. mariae* and *L. microlepis*) have a slightly more elongate lachrymal. These species (except *L. angustifrons*) also differ from *L. niloticus*, *L. calcarifer*, *L. macrophthalmus* and *L. longispinis* in having a relatively more elongate fifth circumorbital, and in having much narrower bony flanges developed from the ventral contours of the cylindrical canal-bearing portions of the third, fourth and fifth bones.

Greatest departure from the *L. niloticus*–*L. calcarifer* situation is seen in the reduced size of the subocular shelf in the Tanganyika species, again excepting *L. angustifrons* where the shelf is like that in *L. niloticus* and *L. calcarifer*, viz. a thin but broad bony plate that curves upwards from the third circumorbital to lie along the entire length of the fourth bone. In *L. microlepis* the subocular shelf is reduced in width, and just reaches upwards to the level of the articulation between the third and fourth circumorbitals ; in *L. mariae* there is a further and marked reduction in width, and the shelf barely reaches to the level of the articulation between the bones. Both species have the ventral flange on the third and fourth circumorbitals reduced to a thin flange.

These reductional trends are carried further in *Luciolates*, where the serrations on the lachrymal are very weak and are confined to about the posterior third of the bone ; serrations are completely absent from the second circumorbital. The facet for articulation with the lateral ethmoid is weakly developed, and its origin from the lachrymal is far less well defined than in the other species. The subocular shelf is, relatively, a little narrower than in *L. mariae*, but it does extend further up the fourth circumorbital (along about its lower third) ; see Fig. 13c–d. The depth of the ventral flange on the second to fourth circumorbitals is almost comparable with *L. mariae*, as is the flange on the fifth bone. In their gross morphology, the circumorbital bones in *Luciolates stappersi* are noticeably more elongate than those in any *Lates*, including the other Lake Tanganyika species. Apart from differences in the overall proportions of the first, third and fourth bones, the morphology of the entire series in an adult *Luciolates* of 105 mm standard length closely resembles that in a juvenile *Lates niloticus* 32 mm long.

Opercular bones (Figs 14a–b)

There is little variation in the operculum, suboperculum and interoperculum of *Lates* and *Luciolates*, apart from a slight relative elongation of the interoperculum in the Tanganyika species, especially *Luciolates*. In all taxa there is a well-defined, curved ridge on the medial face of the interoperculum against the upper, concave surface of which the proximal end of the epihyal articulates.

The operculum (Fig. 14a–b) is armed with a single stout spine formed from the posterior tip of the near-horizontal strut which runs backwards from the hyomanibular facet of the bone.

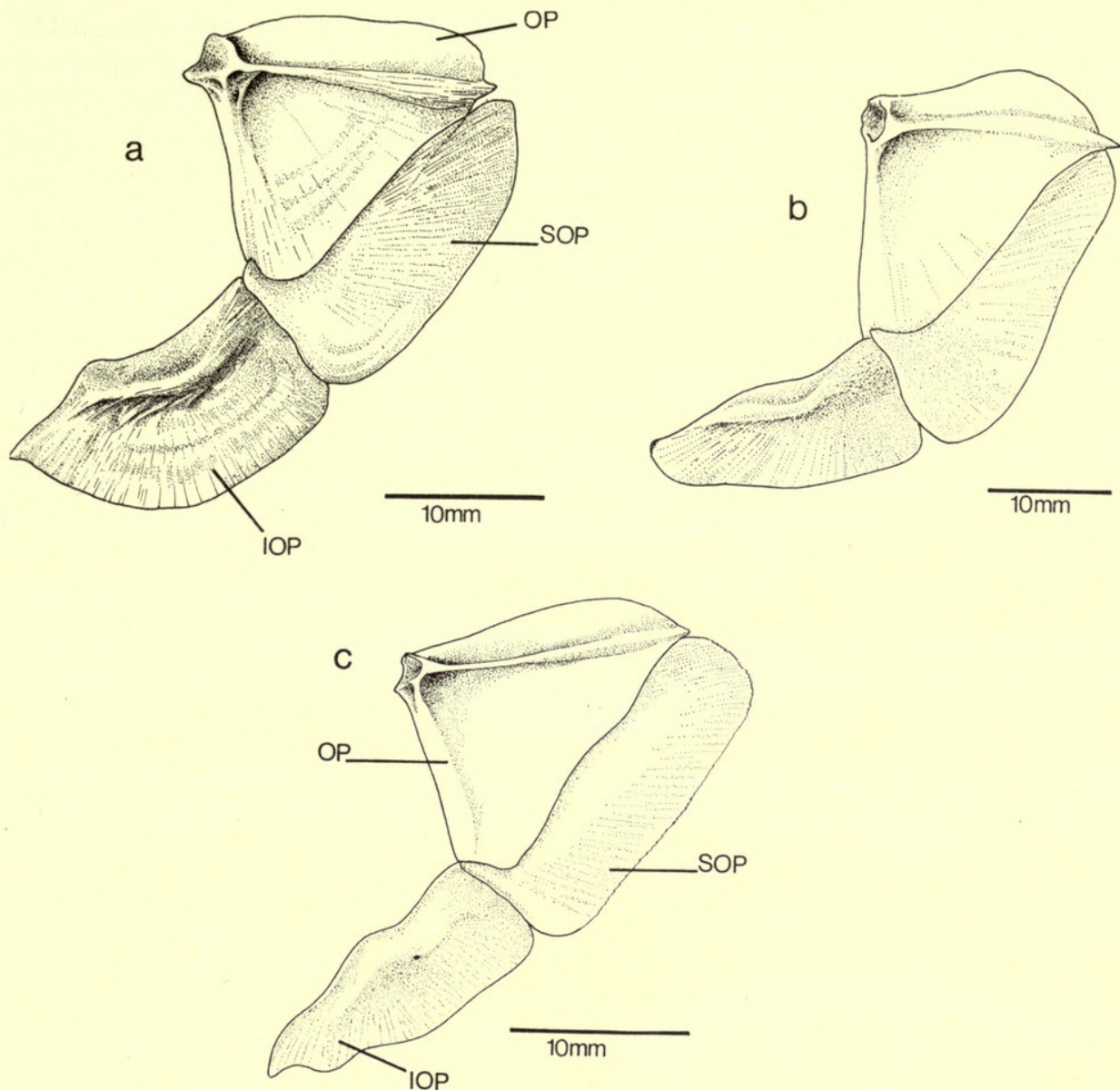


FIG. 14. Opercular series (medial aspect of bones from right side) in : (a) *Lates angustifrons*, (b) *L. stappersi*, (c) *Psammoperca waigiensis*.

A characteristic feature in all taxa is the thinness of the sub- and interopercular bones.

Jaws (Figs 15 & 16)

Both the maxilla and the premaxilla show little interspecific variation amongst *Lates* species, and are of the generalized percoid type. There is also little difference between *Lates* and *Luciolates* in the morphology of these bones. However, in *Lates* species the ascending process of the premaxilla is from 30 to 60 per cent higher than the articular process (apparently being lowest in the Lake Tanganyika species) ; it is only a little higher than the ascending process in *Luciolates stappersi*.

The premaxillary dentition in all *Lates* species is composed of numerous close-set rows of small conical to subconical teeth which form a villiform covering to the complete width of the bone over almost its entire length (Figs 15b-c).

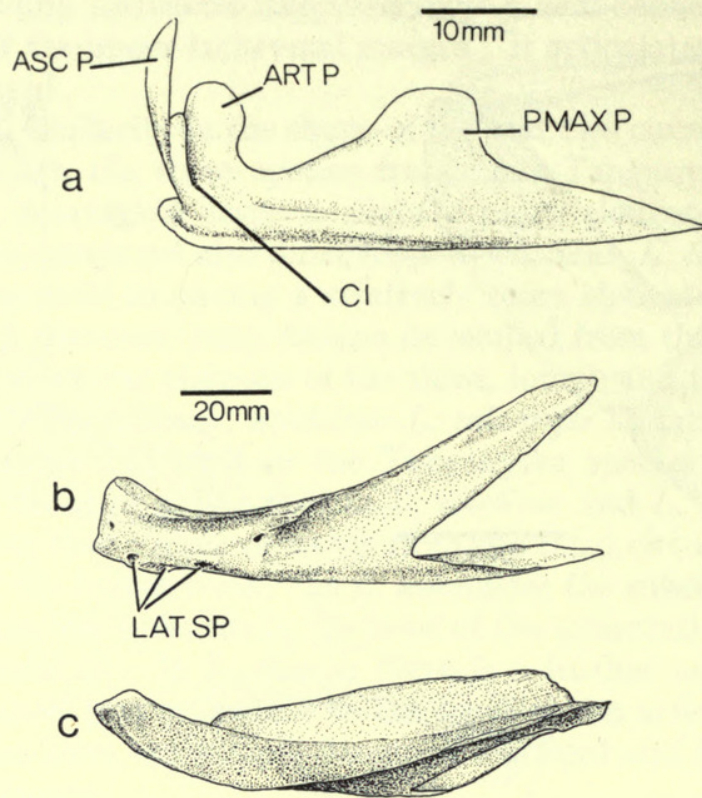


FIG. 15. *Lates niloticus*. (a) Premaxilla (left) lateral view. (b) Dentary (left) lateral view. (c) Dentary (left) occlusal view. (All from Greenwood & Howes, 1975.)

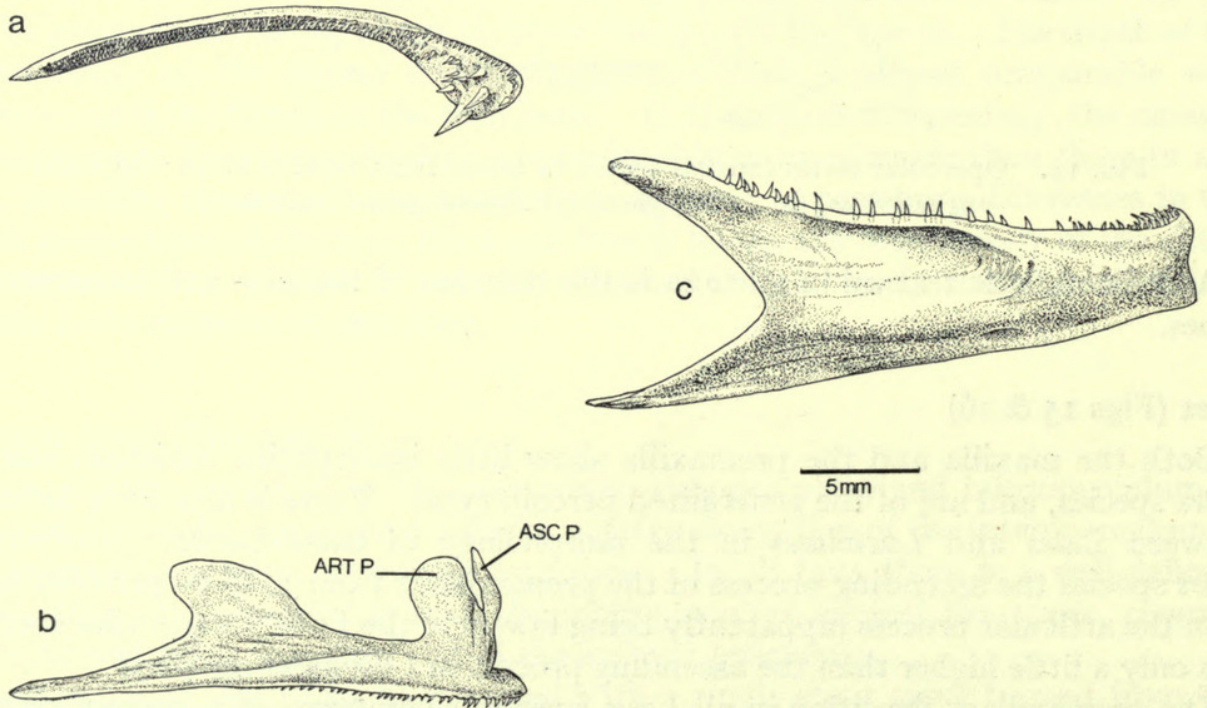


FIG. 16. *Lates stappersi*. (a) Premaxilla (right), occlusal view. (b) Premaxilla (right), lateral view. (c) Dentary (right), lateral view.

Although most premaxillary teeth in *Luciulates stappersi* are like those in *Lates*, the species is noteworthy for the presence of at least one greatly enlarged and two slightly smaller caniniform teeth adjacent to the symphyseal surface of the premaxilla; a few neighbouring teeth may also be somewhat enlarged. In general the larger teeth are linearly arranged, with the largest one situated lingually.

The upper jaw elements in *Lates* and *Luciulates* show no derived characteristics and, of course, both genera retain the supramaxilla. The enlarged median teeth of *Luciulates*, however, would seem to be a derived feature.

Like the upper jaw, the lower jaw elements (dentary, anguloarticular and retro-articular) show little interspecific variation. In *Luciulates* the anguloarticular is relatively shallow, but otherwise has a typical '*Lates*' form.

The dentition of the dentary mirrors that on the premaxilla, except that in *Luciulates* the outermost tooth row is composed of noticeably larger and more clearly caniniform teeth, and there are no enlarged symphyseal teeth.

Branchial skeleton (Figs 17-19)

The branchial skeleton in both *Lates* and *Luciulates* is of a generalized percoid type (see Rosen, 1973), and it shows few interspecific differences, apart from a relative

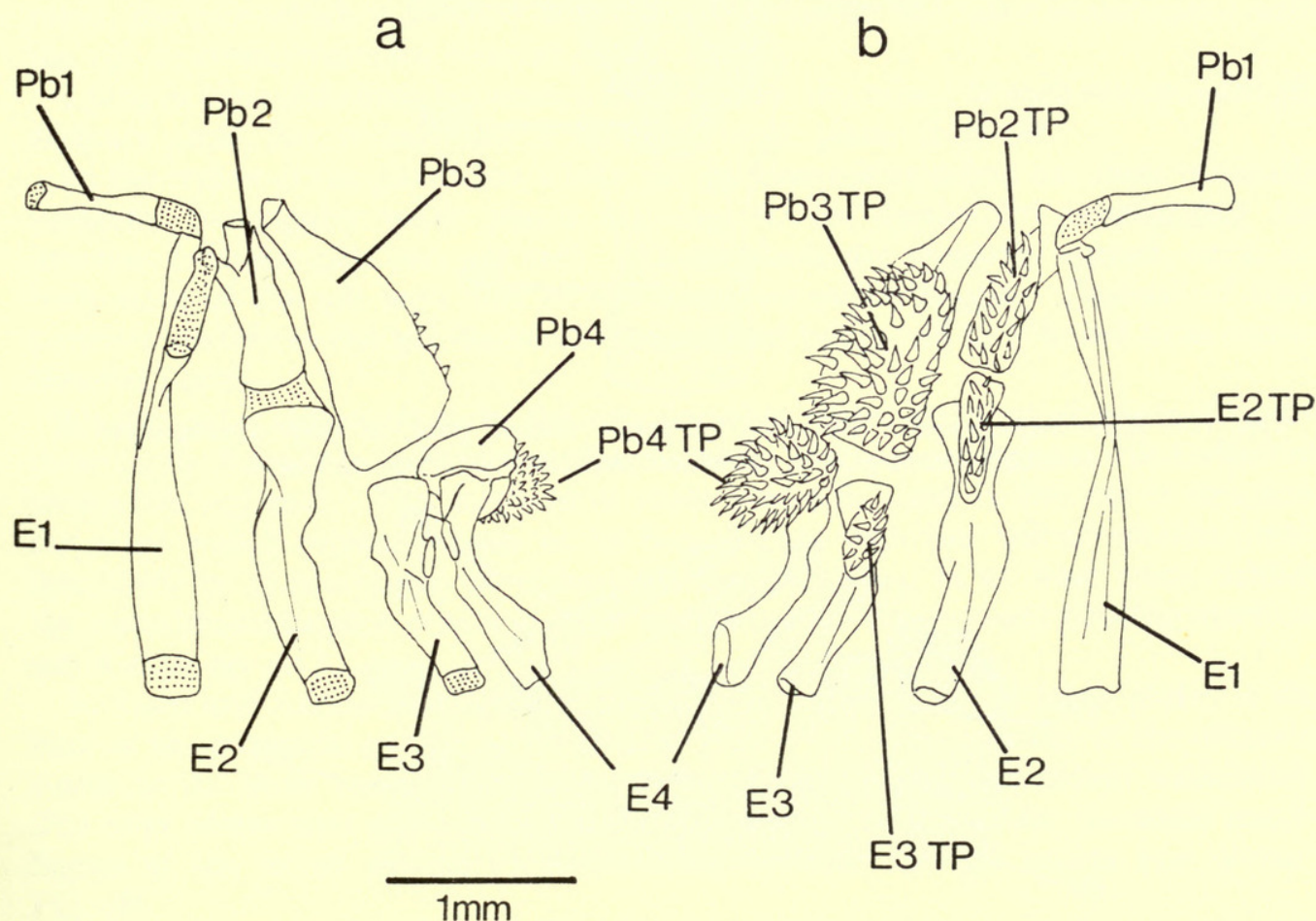


FIG. 17. *Lates niloticus*. Branchial skeleton, dorsal part (drawn from an alizarin preparation, 40 mm S.L.). (a) Dorsal aspect of left side. (b) Ventral aspect (left side) to show upper pharyngeal teeth and tooth plates.

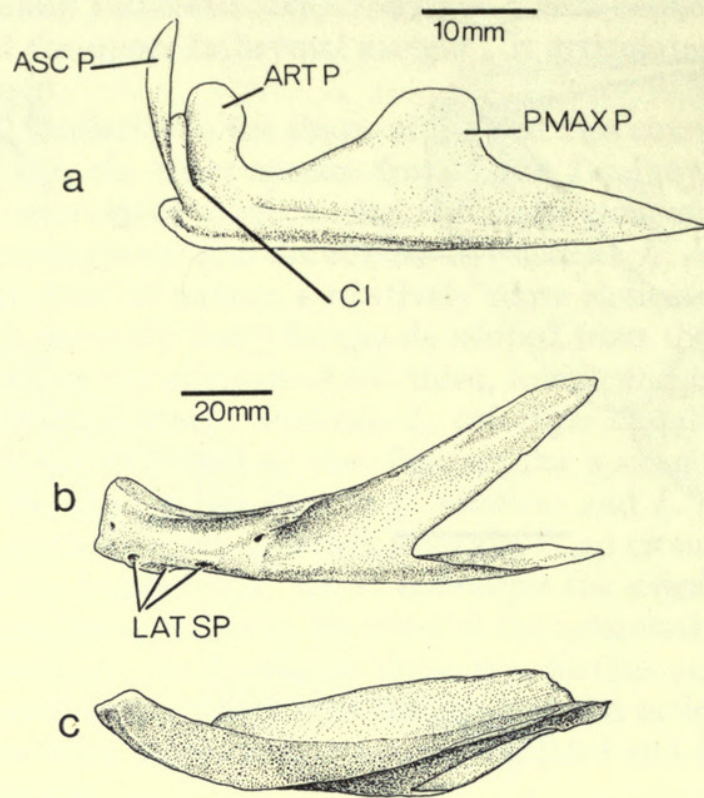


FIG. 15. *Lates niloticus*. (a) Premaxilla (left) lateral view. (b) Dentary (left) lateral view. (c) Dentary (left) occlusal view. (All from Greenwood & Howes, 1975.)

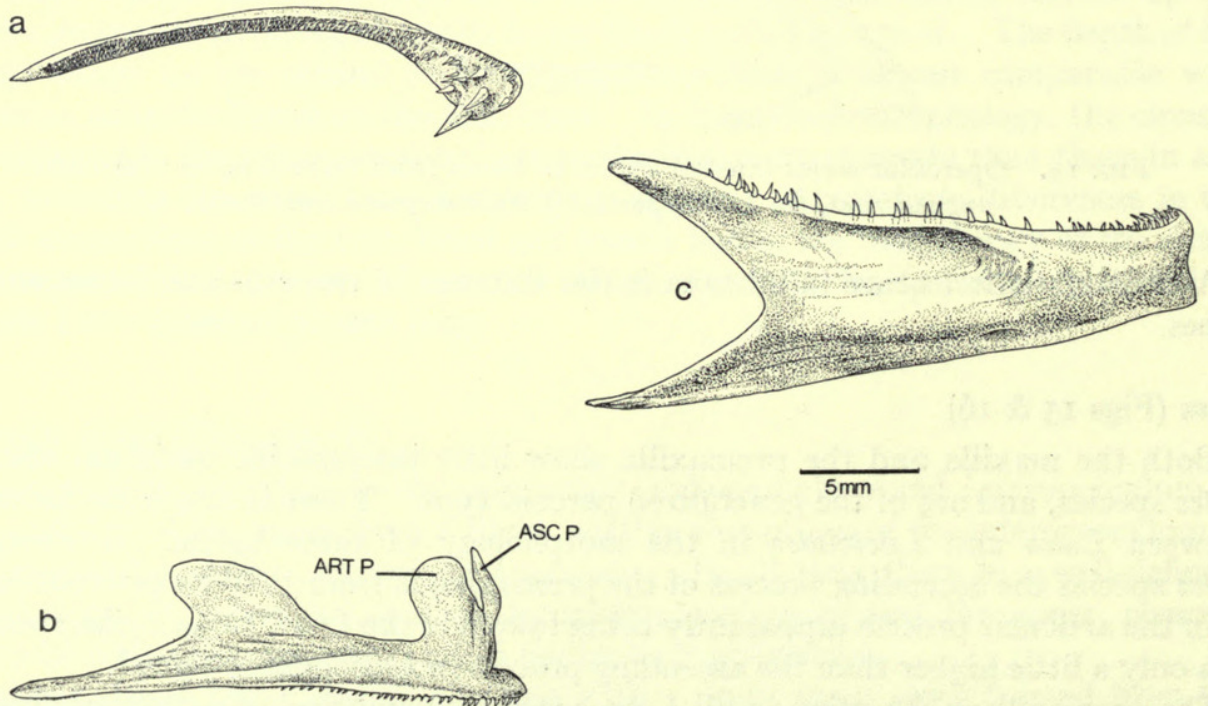


FIG. 16. *Lates stappersi*. (a) Premaxilla (right), occlusal view. (b) Premaxilla (right), lateral view. (c) Dentary (right), lateral view.

Although most premaxillary teeth in *Lucioides stappersi* are like those in *Lates*, the species is noteworthy for the presence of at least one greatly enlarged and two slightly smaller caniniform teeth adjacent to the symphyseal surface of the premaxilla; a few neighbouring teeth may also be somewhat enlarged. In general the larger teeth are linearly arranged, with the largest one situated lingually.

The upper jaw elements in *Lates* and *Lucioides* show no derived characteristics and, of course, both genera retain the supramaxilla. The enlarged median teeth of *Lucioides*, however, would seem to be a derived feature.

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The dentition of the dentary mirrors that on the premaxilla, except that in *Lucioides* the outermost tooth row is composed of noticeably larger and more clearly caniniform teeth, and there are no enlarged symphyseal teeth.

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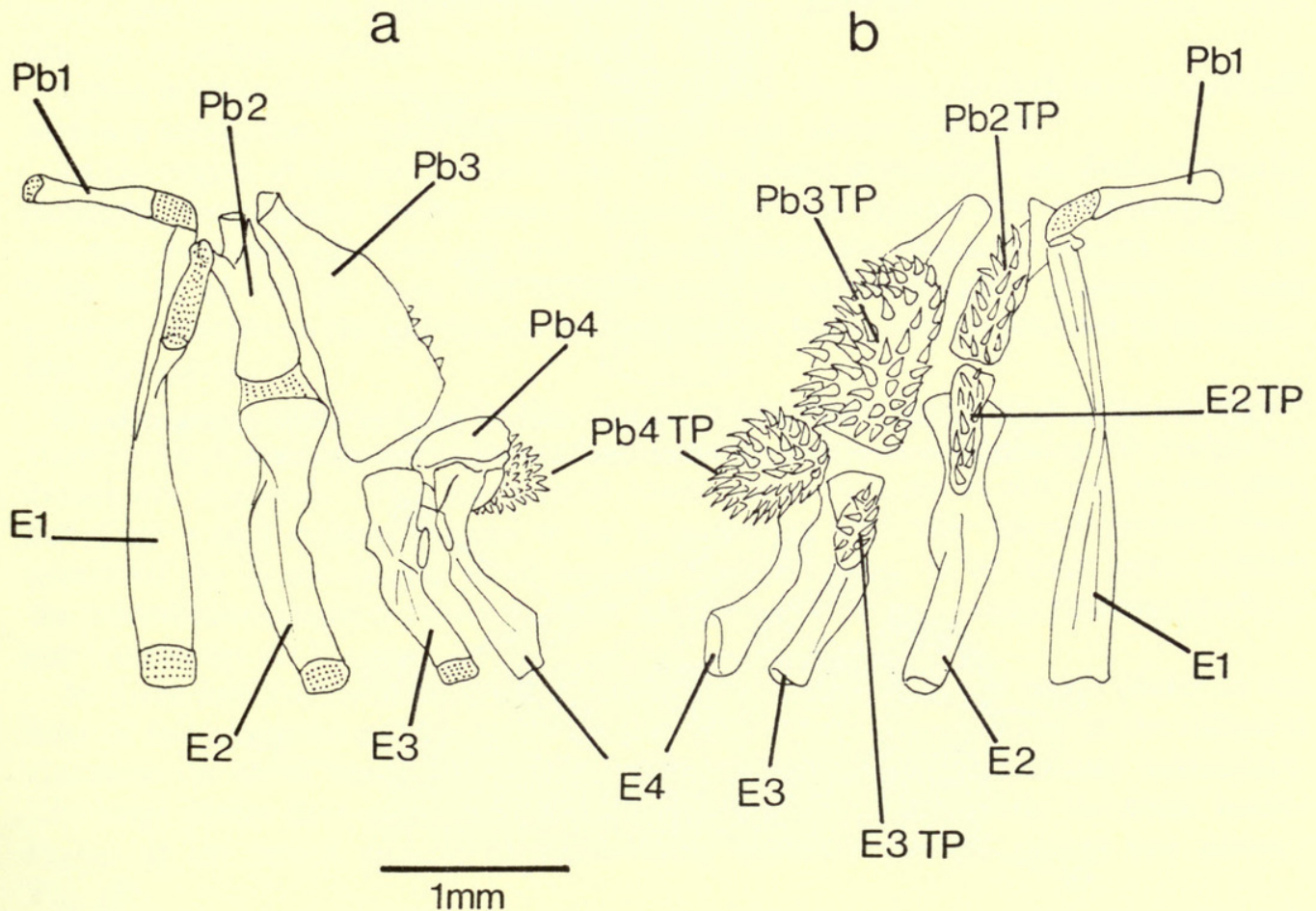


FIG. 17. *Lates niloticus*. Branchial skeleton, dorsal part (drawn from an alizarin preparation, 40 mm S.L.). (a) Dorsal aspect of left side. (b) Ventral aspect (left side) to show upper pharyngeal teeth and tooth plates.

elongate so that it overlaps the joint between the two bones. The plates associated with the third arch are generally the largest of the series, approach one another medially and cover a great deal of the third basibranchial.

In the one available branchial skeleton of *L. angustifrons* the individual plates appear to have fused together on the first two gill arches to form a long tooth plate on each side of the arch. A similar arrangement is seen in the alizarin preparation of a small (96 mm S.L.) *Lucioides stappersi*, but this specimen differs in other respects, especially in having a single, median plate on the third basibranchial and a small plate on each hypobranchial of that arch. The arches dissected from a much larger specimen (270 mm S.L.) have the plates of the third basibranchial narrowly separated medially, a long plate at the base of the second gill arch and a small plate intercalated between it and the basal plate of the first arch. Clearly, at least in this species, there can be quite considerable individual variability in the pattern of tooth plate distribution (see Nelson, 1969 : 500–501, for a description of variation in another percoid, *Pomatomus saltatrix* [Pomatomidae]).

Hyoid arch (Figs 20 & 21)

The hyoid arch in *Lates* and *Lucioides* is of a basal percoid type, with dorsal and ventral hypohyals, a large and complete 'berycoid' foramen and seven branchiostegal rays. There is remarkably little interspecific variability in the shape of this

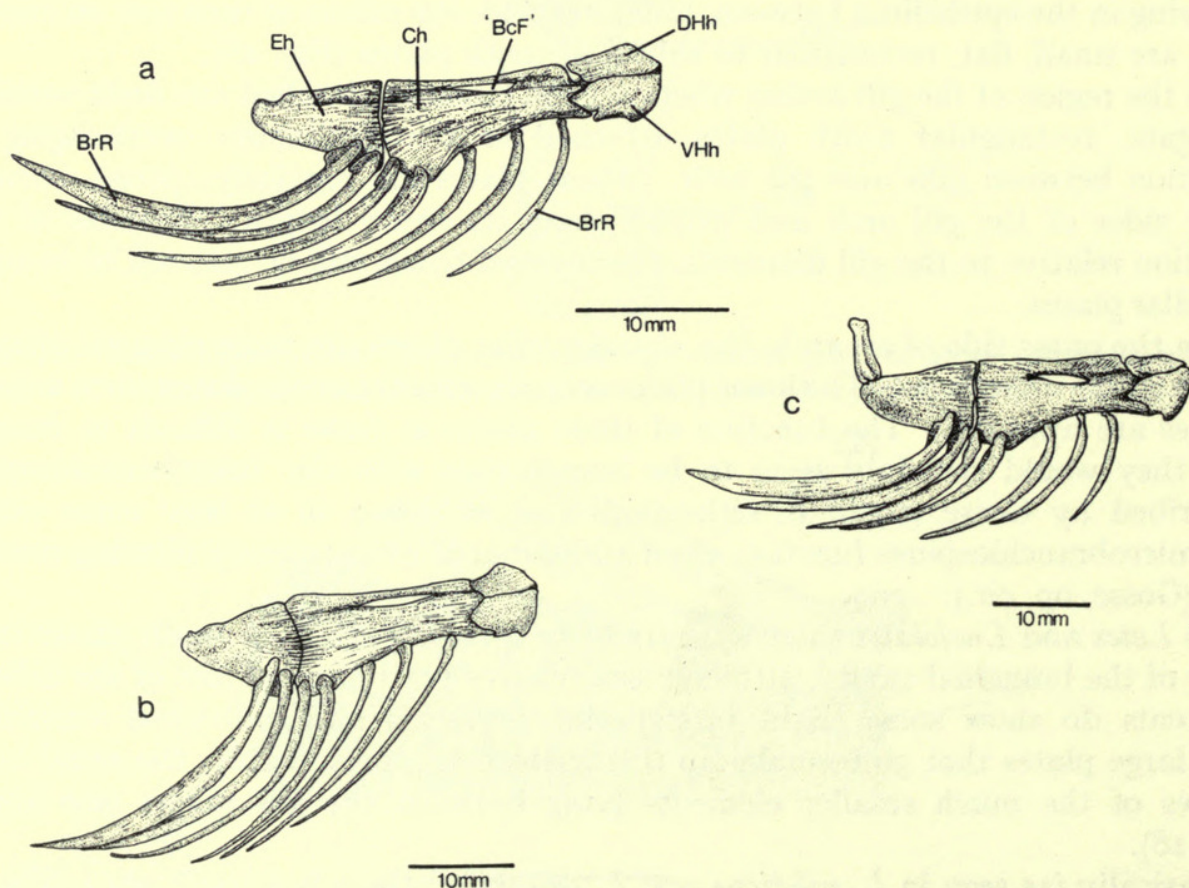


FIG. 20. Hyoid arch and branchiostegal rays (right side), viewed laterally, in :
(a) *Lates stappersi*, (b) *L. mariae*, (c) *L. niloticus*.

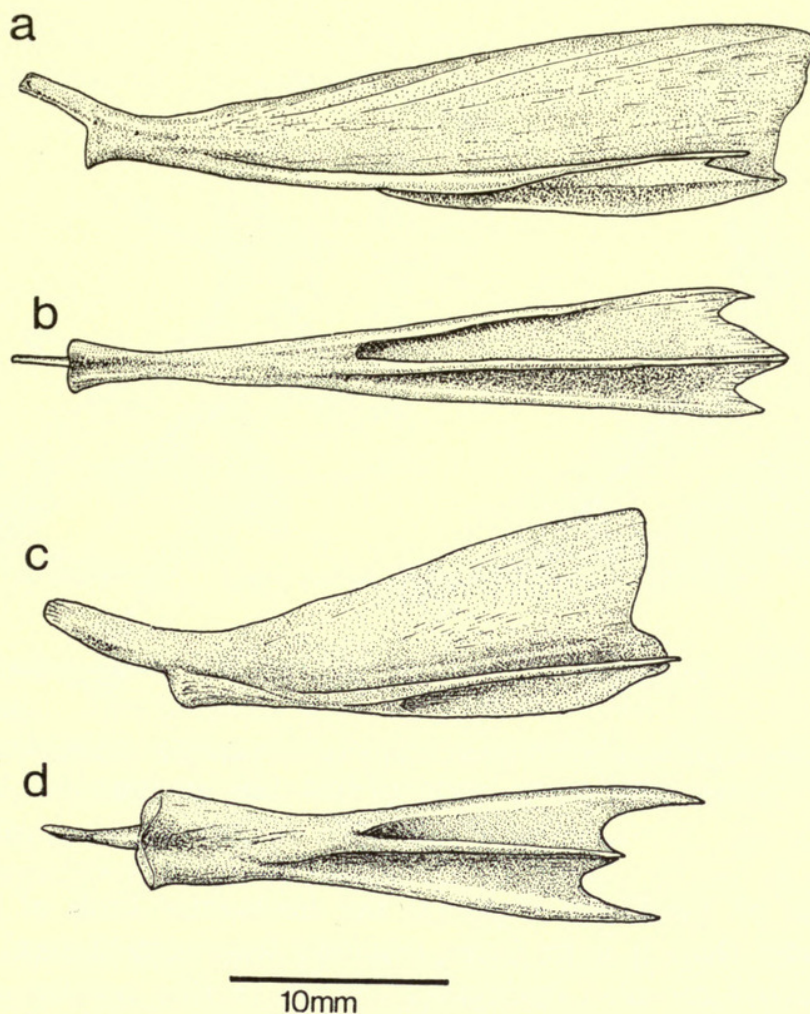


FIG. 21. Urohyal. (a) & (b) *Lates stappersi* (left lateral and ventral views respectively). (c) & (d) *L. angustifrons* (left lateral and ventral views respectively).

arch, without even, as might be expected, clear-cut proportional differences in the arches from species with elongate skulls (i.e. the Tanganyika species).

The first four branchiostegal rays articulate with the ceratohyal, the fifth with either the ceratohyal or at the cerato-epihyal suture, and the last two rays (the stoutest and broadest of the series) articulate with the epihyal. The first three rays contact the ventral face of the ceratohyal, the other four lie on the lateral aspect of the cerato- or epihyal. These latter rays have progressively broader heads, with the dorsal outline of the head on the last two, or occasionally three rays somewhat indented.

The basihyal is an elongate bone, spatulate in dorsal outline, and does not carry a tooth plate.

The urohyal (Fig. 21) is similar in all species, but is markedly more elongate in *Luciolates*, even when it is compared with the urohyal in the *Lates* species of Lake Tanganyika.

Pectoral girdle and associated bones (Fig. 22)

The pectoral girdle shows few interspecific or intergeneric differences, either in its overall proportions or in the shape of its individual bones. Judging from the only

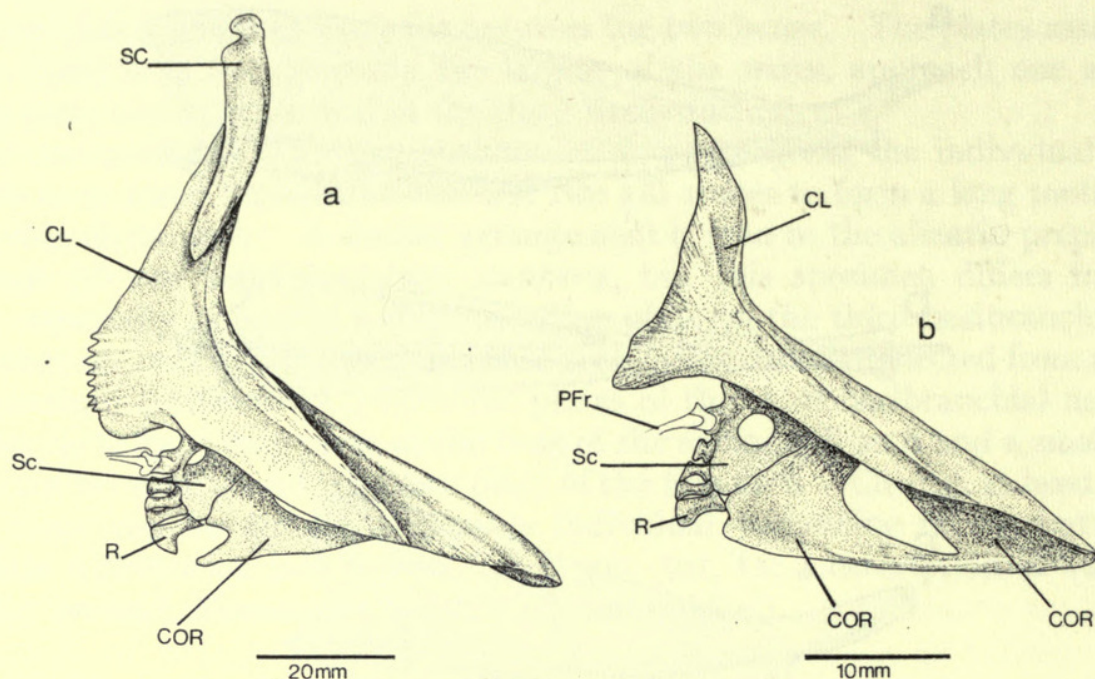


FIG. 22. Pectoral girdle (right half) in : (a) *Lates calcarifer*, (b) *L. stappersi*. (The supracleithrum is removed from this specimen.)

available skeleton of *Luciolates stappersi* the horizontal limb of the cleithrum is somewhat narrower than it is in *Lates*, and has less ventrolateral curvature; the scapula and coracoid are also noticeably deeper in this species and the foramen enclosed between the coracoid and the medioventral margin of the cleithrum is larger (cf. Figs 22a & 22b).

The posterior angle of the cleithrum in both genera is expanded and slightly protracted, and its hind margin is serrated. These serrations are most numerous in *L. calcarifer*, *L. niloticus* and *L. angustifrons* (6–10 serrae, the uppermost often ill-defined), are fewer in *L. macrophthalmus* (5–7) and fewest (3 or 4) in *L. microlepis* and *L. mariae*. Judged on the size range of available material for any one species, the number of serrae is not obviously correlated with the fish's size, and the number may differ on either side of an individual.

In *Luciolates* the cleithral projection can have a smooth posterior border or be ornamented with from one to three weak serrations; as in *Lates* there are lateral discrepancies in the number of serrae.

The three upper radials articulate with the scapula, and the fourth either articulates with the coracoid or partly with the coracoid and partly with the scapula.

The supracleithrum in both *Lates* and *Luciolates* is a slightly curved, dagger-shaped bone showing no interspecific variability in shape or size.

The first postcleithrum is a flat, scale-like bone, the second is elongate and spini-form (Fig. 23). No obvious interspecific or intergeneric differences were detected in either element.

The posttemporal is characterized, in both genera, by a deep and dorsally directed oval pocket formed in the body of the bone immediately lateral to the base of its

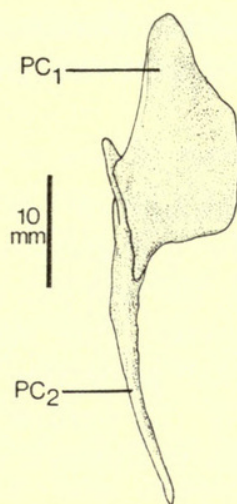


FIG. 23. *Lates calcarifer*. Postcleithra (left).

intercalar limb and a little anterior to the facet for articulation with the supra-cleithrum (Fig. 24). The pocket opens dorsally into the lateral line canal, and its lateral wall bulges slightly outwards; in alizarin preparations of a young *L. niloticus* this wall has a pitted, 'strawberry-skin' appearance similar to that of the auditory bulla in many clupeomorph fishes. The pit is occupied by the distal end of the ligament which runs from the posttemporal to the *tunica externa* of the swimbladder (see p. 47 below).

Posteriorly, the shield-like body of the posttemporal is serrated, the extent and size of the serrations apparently not differing between the various species.

The extrascapula is a small Y-shaped bone, largely occupied by the lateral line sensory canals it carries (i.e. the supratemporal and temporal lines), and shows little

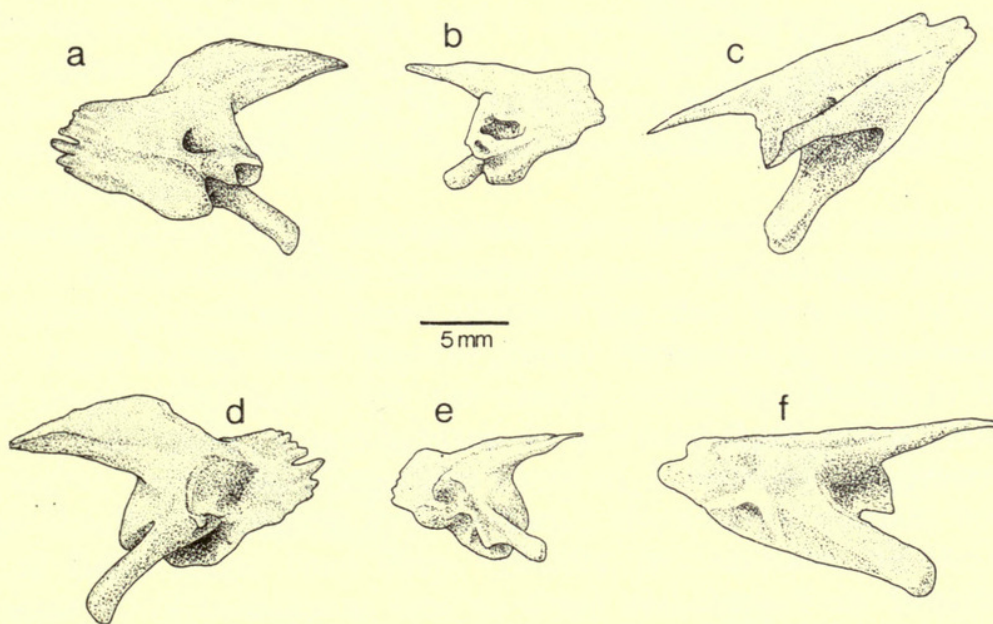


FIG. 24. Posttemporal in : (a) & (d) *Lates niloticus* (right bone), (a) lateral, (d) medial aspect. (b) & (e) *Psammoperca waigiensis* (left bone), (b) lateral, (e) medial aspect. (c) & (f) *Centropomus undecimalis* (left bone), (c) lateral, (f) medial aspect.

interspecific variability. It articulates closely with the posttemporal, the two bones together partially covering the posterior part of the posttemporal fossa.

Vertebral column (Figs 25 & 26)

The total count in all *Lates* species and in *Luciolates stappersi* is 25, viz., 11 abdominal, 13 caudal and the fused first ural and preural centra.

There are nine pairs of pleural ribs, the first pair associated with the third vertebra. On those vertebrae with parapophyses, (the eighth and subsequent abdominals have obvious parapophyses but a small projection is visible on the seventh), the ribs articulate with the posterior face of the parapophysis; at least in *Lates* the rib articulation on the preceding centra is through a shallow facet whose ventral lip is slightly produced laterally.

The parapophyses in *Luciolates* differ from those in *Lates* in being almost vertically aligned, and by having, in all bar the first pair, a horizontal strut joining the parapophyses of each centrum near their distal tips. Also, in this genus the articulatory pit on the first three rib-bearing centra has no ventral lip, but on the fourth rib-bearing centrum (i.e. the sixth abdominal vertebra) the lip is sufficiently produced to resemble a very short parapophysis.

I have been able to check the dorsal ribs in only two species (*L. niloticus* and *Luciolates stappersi*). *Lates niloticus* has epineural ribs associated with the first

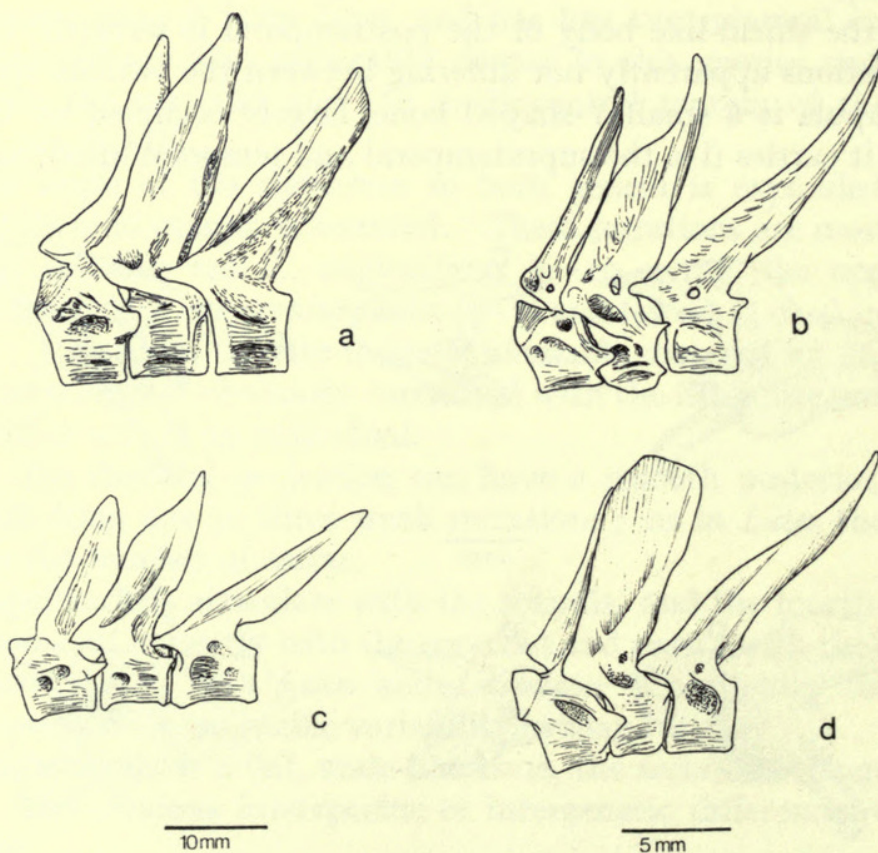


FIG. 25. First three abdominal vertebrae in : (a) *Lates angustifrons*, (b) *Psammoperca waigiensis*, (c) *L. stappersi*, (d) *Centropomus ensiferus*.

two vertebrae, and epipleurals present on the first six pairs of pleural ribs; *Luciolates stappersi* has epineurals as in *Lates*, but the epipleurals apparently are confined to the first three pairs of ribs only.

The first three abdominal vertebrae are the most individually distinctive elements in the entire column (Fig. 25). The second vertebra is characterized by the great expansion anteroposteriorly of its neural spine, which is $2-3\frac{1}{2}$ times broader than the spine of the first vertebra and about twice as broad as the spine of the third vertebra. Not only is the spine expanded but it has a characteristic outline. The anterior and posterior margins run almost parallel to one another for most of the spine's height (rather than converging with one another), and the spine narrows smoothly at a point about three-quarters of its height above the centrum. At this point, the front margin curves backwards to meet the posterior margin which may be almost vertical or, and more generally, it may have a slight posterior curvature. The hind margin of the first neural spine is closely applied to the front of the second spine, but the third neural spine slopes away from the second at a marked angle.

Neither the first nor the third neural spine has parallel margins except basally; the margins slope towards one another over most of their height, giving the spine a narrowly triangular outline.

A variety of skeletons covering a wide size range of individuals (c. 16 to 1000 mm) is available only for *L. niloticus*. These skeletons indicate that the relative antero-posterior expansion of the second neural spine may at first show a positively correlated increase with increasing standard length, but that in very large fishes the spine becomes relatively narrower.

There are quite marked interspecific differences in the length-height proportions of certain centra, particularly those in the abdominal region of the column. In the descriptions that follow the first three abdominal vertebrae are excluded since those are not affected by proportional changes; all measurements are maxima.

In *L. niloticus*, *L. macrophthalmus* and *L. longispinis*, the abdominal and caudal centra are of approximately equal length and depth or are only a little longer than deep (the latter proportions applying especially to caudal vertebrae). *Lates calcarifer* has caudal centra like those in the former species but its abdominal centra are slightly more elongate.

The abdominal centra in *L. angustifrons* have proportions similar to those in *L. calcarifer*, as do the first five or six caudal centra. Beyond that point, however, the caudal centra are noticeably more elongate (i.e. they are about $1\frac{1}{2}$ times longer than deep). *Lates mariae* shows slightly greater elongation of its abdominal centra (c. $1\frac{1}{3}$ times longer than deep), but the caudal centra are similar to those in *L. angustifrons*. This trend is accentuated in *L. microlepis* where, although the abdominal centra have proportions like those of *L. mariae*, the posterior caudal elements are from $1\frac{3}{4}$ to twice as long as deep; the anterior caudals, however, are still about $1\frac{1}{2}$ times longer than deep. Finally, in *Luciolates*, all the centra are clearly elongate (c. $1\frac{3}{4}$ to twice as long as deep) and there is no difference in proportions between the caudal and abdominal elements of the column.

There are three *predorsal bones* in all *Lates* and *Luciolates* (pace Fraser, 1968), the proximal end of the first lying just anterior to the first neural spine, the ends of

the second and third bones lying, respectively, in front of and behind the second neural spine.

Caudal fin skeleton (Fig. 26)

There is but slight interspecific variation in the caudal skeleton of *Lates* (Fig. 26). All species have two epurals, two uroneurals and five hypurals; the first, second and fifth hypurals are autogenous (as is the parhypural and the haemal arch and spine of the third preural centrum). The hypurapophysis is weakly to moderately developed. The neural spine on the second preural vertebra is reduced to a low crest in all species.

The principal caudal fin ray formula for all species is $I, 8 + 7, I$.

Although the caudal skeleton in *Luciolates* is basically similar to that in *Lates*, it differs in having the first to fourth hypurals fused into a single plate except for a narrow proximal gap between the fused first and second, and the fused third and fourth hypurals; the fifth hypural is free and is autogenous basally.

One small specimen (96 mm S.L.) of *Luciolates stappersi*, an alizarin preparation, has a small and free sixth hypural, the fifth hypural in this specimen being fused in with the third and fourth. Unlike the other *Luciolates* examined (by dissection and radiographically) the second and third hypurals in this fish are not apposed over their distal halves but are fused proximally instead.

As in *Lates*, there are $I, 8 + 7, I$ principal caudal rays in *Luciolates*.

The caudal fin margin in adult *L. calcarifer*, *L. niloticus*, *L. macrophthalmus*, *L. longispinis* and *L. angustifrons* is weakly truncate to markedly subtruncate (nearly rounded), in *L. mariae* it is truncate to weakly emarginate, but in *L. microlepis* it is so strongly emarginate as to be almost crescentic. (In juveniles, however,

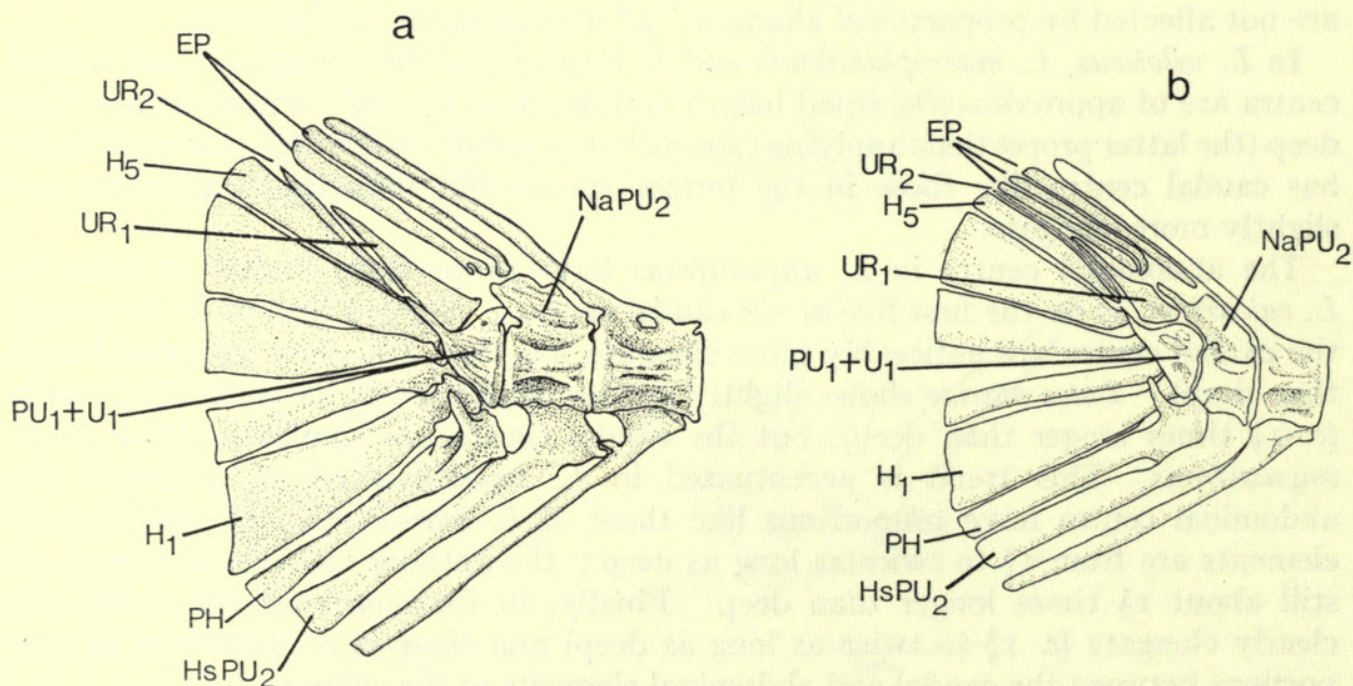


FIG. 26. Caudal fin skeleton in : (a) *Lates niloticus*, (b) *Eolates gracilis* (After Sorbini, 1973).

the margin is distinctly truncate [see Poll, 1953] or weakly subtruncate [see Boulenger, 1915].) A crescentic margin is also developed in *Luciolates stappersi*, and is deepest in fishes over 150 mm standard length.

Dorsal and anal fins

The number of pterygiophores supporting the rays of the dorsal fin (or fins) shows some slight interspecific variation; viz: *L. calcarifer* 18, *L. niloticus* 18 or 19, *L. microlepis* 19 (rarely 20), *L. macrophthalmus* 18 (rarely 19), *L. longispinis* 18 or 19, *L. angustifrons* 19 and *L. mariae* 19. Each of the first eight or nine pterygiophores carries a single spine, and no medial radials are associated with these bones. An examination of the dorsal fin ray supports in alizarin preparations of small (16–20 mm S.L.) *L. niloticus* suggests that the medial radial fuses with the proximal one (the pterygiophore) to form the elongate head of that bone. Distinct medial radials are also absent from those pterygiophores carrying the branched dorsal fin rays.

Luciolates stappersi has 19 dorsal pterygiophores, the first nine of which bear a single spine (again without the interposition of a medial radial). The seventh and eighth pterygiophores have markedly elongate heads, and each carries a short weak spine which is largely embedded in the epaxial body musculature. Superficially, these spines are well separated from each other and from the first and second dorsal fins. The ninth pterygiophore carries a longer and somewhat stouter spine which is the first ray of the second dorsal fin. Unlike *Lates*, the posterior branched rays of the dorsal fin in *Luciolates* do have distinct medial radials, even in the largest individuals examined.

The wide gap between the dorsal fins of *Luciolates* was, and in published accounts of this taxon still is, the principal diagnostic feature for the genus. It is therefore of some importance to reconsider the relative positions of the dorsal fins (or of its two sections where the fin is apparently a single unit, as in *L. niloticus*). As Poll has described (Poll, 1953) and I have been able to confirm, the Lake Tanganyika species of that genus show ontogenetically correlated changes in relative fin position. However, my observations also indicate that the definitive fin positions in these species are reached well before the cessation of obvious growth in body length.

Lates calcarifer (as compared with *L. niloticus*) has a distinctly greater interval between the last and first spines of the two fins than that existing between the penultimate and last spines of the first fin; the gap is bridged by a low membrane. In *L. niloticus* the spacing between these three rays is almost equal, and the inter-connecting membrane appears to be slightly deeper. The condition in *L. macrophthalmus* and *L. longispinis* approaches that in *L. niloticus* but with a slightly greater distance between the spines in *L. macrophthalmus*.

The condition in *L. angustifrons* (the seemingly most generalized of the Tanganyika species) is either comparable with that in *L. calcarifer* or, in some individuals, the inter-fin spacing may be a little greater. Some specimens I have examined (up to 345 mm S.L.) have no membrane connecting the two fins and in a few the 'last' spine of the first dorsal is not connected with the rest of the fin; it is impossible to

tell whether this latter condition is the result of damage. The smallest fish measured (90 mm S.L.) has a distinct but membrane-spanned gap between the fins.

None of the *L. microlepis* examined has a membrane connecting the fins, and in several there is an isolated spine in the gap.

The usual condition in *L. mariae* (except in fishes < 70 mm S.L.) is a distinct gap between the fins, with a single, isolated spine lying at about its midpoint. This species is unusual in having a modal dorsal spine count of nine (eight is the mode in other Tanganyika species, although occasional individuals with nine spines are recorded; see Poll, 1953).

Within the *Lates* species of Lake Tanganyika then, one finds a complete intergradation between a continuous, albeit deeply notched dorsal fin, and two separate fins with an isolated spine interposed. The condition in *Luciolates* differs from the latter state only in the greater width of the gap and the occurrence of two spines within it. *Luciolates* is, however, unusual in having only six spines in the first fin

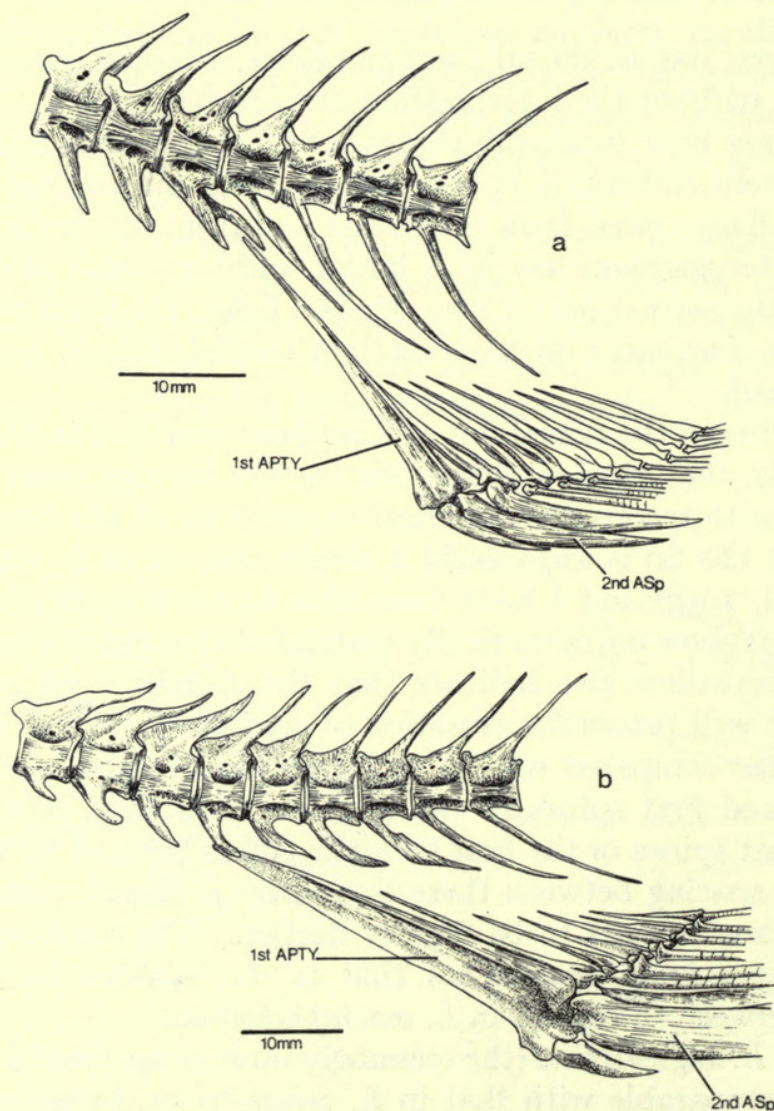


FIG. 27. First anal pterygiophore, and abdominal-caudal vertebral transition, in :
(a) *Lates niloticus*, (b) *Centropomus ensiferus* (drawn from radiograph 1903.5.15:3-5
and dry skeleton 1861.12.12:13).

and one spine with only 9 or 10 branched rays in the second (compared with the usual seven spines and one spine plus 11–13, rarely 10, branched rays in the fins respectively). The two isolated spines in *Luciolates* may therefore represent the detached 'ultimate' and 'first' rays respectively of the ancestral type fin, with what we now consider to be the first spine of the second dorsal fin a neomorphic development from a branched ray. Alternatively, and as would seem more probable, the ancestral species could have had seven spines in the first dorsal fin, an isolated spine between it and the second dorsal, and the latter comprising one spine and 10 branched rays (a condition found in some specimens of *L. mariae*).

The anal fin skeleton is similar in all *Lates* species. There are nine, rarely eight, pterygiophores, the first a large double structure carrying two spines (Fig. 27a); it articulates with the cross-bar on the haemal arch of the first abdominal vertebra. All other anal pterygiophores, except the last, carry a single ray (that on the second a spinous one); the last pterygiophore carries two rays. Medial radials are absent except on the last three or four pterygiophores.

Morphologically the anal fin skeleton of *Luciolates* is like that in *Lates*, although the first pterygiophore is less robust and there are nine others in the series (i.e. a total of 10). A medial radial is present in the last four pterygiophores.

Swimbladder

One outstanding feature of the swimbladder in *Lates* and *Luciolates* is the presence of a tough connective tissue strap running from a point anterodorsally on the *tunica externa* to the posttemporal, which has a well-defined ventrolateral recess for the reception and anchorage of the strap (see above, p. 41). Katayama (1956) does not describe this connection in *L. calcarifer* but I have been able to confirm its presence in that species.

Apart from *Psammoperca* (see p. 60 below), I know of no other percoid species in which a similar swimbladder–posttemporal connection has been described, nor indeed of any connection between those two points. The functional significance of a swimbladder–posttemporal linkage is not readily apparent.

The anterior end of the swimbladder in all *Lates* species and in *Luciolates stappersi* has a deep median indentation which gives that end of the swimbladder a distinctly bilobed appearance.

Baudelot's ligament

This ligament is well defined in *Lates* and *Luciolates*, and originates from a deep pit on the basioccipital. In *L. niloticus* and *Luciolates stappersi* (the two species dissected) little or no epaxial body musculature runs below the ligament medially; laterally, however, there is a broad muscle band passing below and above it to insert partly on the anterolateral aspect of the basioccipital but mainly on the exoccipital. Thus at least the distal half of Baudelot's ligament is embedded in muscle.

The relationship of the ligament to the epaxial musculature seems to combine certain features of both the percichthyid and serranid types described by Gosline (1966), but is more akin to the serranid type.

Lateral line (Fig. 28)

In all *Lates* species the pored lateral line scales of the body continue onto the caudal fin where they extend, or almost extend, to the posterior margin of the fin. Since the posterior margin is generally abraded or damaged it is difficult to tell in the latter cases whether the absence of scales from the immediate marginal area is artefactual or not. Two other rows of pore-bearing scales are present on this fin, one lying above and the other below the median row (from which they are separated by a space usually equal to that between two fin rays). These upper and lower scale rows generally do not quite extend to the posterior fin margin. Because of their small size the scales in these rows are difficult to see in fresh and spirit-preserved specimens unless the fin is allowed to dry out completely.

Superficially there does not seem to be any linkage between the median and the other caudal lateral line scale rows; scales in the latter rows cease to be pored at the base of the fin. Dissection of adult specimens does not reveal any deeper-lying connecting channels.

The presence of a triple lateral line on the caudal fin in *Lates* has not been recorded before, and to the best of my knowledge has not been described in any other percoid species. Since it is clearly a derived condition it is a useful indicator of the monophyletic origin of these species.

The posterior extremity of the lateral line in *Luciolates* is also triradiate, but here the three branches are interconnected by pore-bearing scales (Fig. 28b). The median row extends onto the caudal fin, but the line of pored scales is interrupted by the presence of poreless ones, and it never extends to the margin of the fin. The upper and lower lines do not extend for more than one or two scales beyond the limits of the body scales. However, in a few specimens an occasional pored scale is found some distance onto the fin membrane and in the same line as a basal branch.

Although the condition of the caudal lateral line in *Luciolates* does differ from that in *Lates* it is still a triradiate one and the two taxa can reasonably be thought to

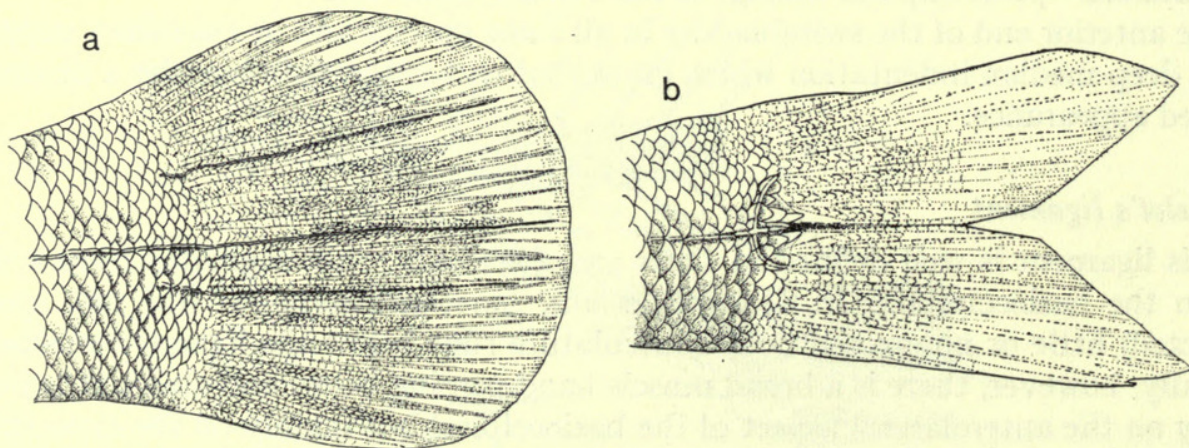


FIG. 28. Caudal fin, showing: (a) lateral line pore scales in three rows (drawn from *Lates niloticus*, but typical for all species except *L. stappersi*), (b) *L. stappersi* showing 'trident' arrangement of lateral line pore scales at body-caudal fin junction; note that pores do not continue onto membrane of fin.

share a derived character. It is difficult to tell from the evidence available whether the *Luciolates* condition should be considered a further derivative – albeit a reductional one – of the *Lates* type, or whether it represents an early stage in the evolution of the *Lates* type.

THE INTERRELATIONSHIPS OF SPECIES WITHIN THE GENUS *LATES*,
AND THE TAXONOMIC STATUS OF *LUCIOLATES* BLGR.

An analysis of the osteological and other anatomical features described in the previous sections shows that all seven *Lates* species share two derived characters, viz. (i) three rows of pored lateral line scales on the caudal fin and (ii) the ventral (i.e. horizontal) arm of the preoperculum has three or more large serrae.

There are three other derived characters (the swimbladder–posttemporal ligament, the anterior extension of the supraoccipital, and the presence of two epurals in the caudal fin skeleton), but as these are shared with *Psammoperca* (see below, p. 61) they are of no value in establishing the monophyletic origin of the genus *Lates* on the basis of synapomorph characters occurring within its constituent species. Since, however, the first two apomorph features noted above do not occur in any other members of the Centropomidae except *Lates* species, they argue strongly for the monophyly of the genus.

It is possible to subdivide the genus *Lates* by grouping together three species sharing one clear-cut apomorphy and at least four apomorph trends. Such a subdivision would bring together *L. angustifrons*, *L. mariae* and *L. microlepis*, species with an elongate ethmovomerine region in which the posterior face of the lateral ethmoid slopes backwards at a pronounced angle and the dorsolateral aspects of that bone slope sharply downwards; this characteristic appearance of the snout region is clearly seen in Figs 5, 6 & 7. The apomorph trends shared by these species are an elongation of the caudal and posterior abdominal vertebrae (most marked in *L. mariae* and *L. microlepis*; see p. 43), a division of the dorsal fin into two separate parts (reduced interconnecting membrane in *L. microlepis*, actual separation of the fins in *L. mariae*; see p. 45), reduction of the pterosphenoid pedicle and internal jugular bridge (slight reduction in *L. angustifrons*, progressively greater reduction in *L. microlepis* and *L. mariae*; see pp. 20–27) and, lastly, an elongation and narrowing of the entire skull (a trend not necessarily correlated with the former which is also manifest in species with broad skulls, e.g. *L. macrophthalmus*; see pp. 17–19). Finally, and no doubt of significance, it may be noted that the three species are all endemic to Lake Tanganyika.

In view of these characteristics, especially the changes in lateral ethmoid morphology, it would seem phyletically proper to recognize the species as more closely related to one another than to any other *Lates* species still extant. This topic will be taken up again later (p. 51).

It is difficult to establish any well-founded scheme of interrelationships for the remaining species, *L. calcarifer*, *L. niloticus*, *L. macrophthalmus* and *L. longispinis*. Part of this difficulty stems from the problematical relationships of *L. longispinis* and *L. macrophthalmus*, as was discussed above, p. 13. These two species alone in the

group show and share definite apomorph characters* (enlarged eyes and long dorsal fin spines ; for a discussion of the reduced pterospheoid pedicle see p. 25). All four species otherwise exhibit only the synapomorph features of the genus, and are distinguished from each other by slight meristic and morphometric differences.

The taxonomic status of *Luciolates* has never been reviewed critically since Boulenger (1914) first differentiated the genus from *Lates* on the grounds of its having '... corps plus allongé, nageoires dorsales largement séparées l'une de l'autre, et ventrales insérées en arrière de la base des pectorals'.

It will be recalled (p. 47) that the condition of the dorsal fin in *Luciolates* represents a slight exaggeration of that existing in *L. mariae*. In turn, the *L. mariae* fin condition is a development of that in *L. microlepis* which is a further slight deviation from the condition found in the basic *L. calcarifer*-*L. niloticus* type. In other words, the apparently characteristic dorsal fin of *Luciolates* is in fact linked by intermediates with that of the most generalized *Lates* species.

Amongst the various *Lates* species similar intermediate character states can be found for most of the features which, at first sight, might seem to distinguish *Luciolates* from a generalized *Lates* species. As examples of these 'distinguishing' features one can cite the relative elongation of the vertebral centra, the protraction of the snout (especially the ethmovermerine skull region) and the general elongation and narrowing of the neurocranium. But, all are features shared with the *Lates* species of Lake Tanganyika, especially the peculiarly shaped ethmoid (cf. Figs 8, with 5-7). Even the supposedly distinctive position of the pelvic fins in *Luciolates* is closely approached by *L. mariae*.

There are, of course, certain characters in which *Luciolates* does differ trenchantly from all *Lates* species, and these features must be given particular attention.

No *Lates* species has enlarged caniniform teeth such as occur, in small numbers, near the symphysis of the upper jaw in *Luciolates* (see p. 35), none shows such a high degree of hypural fusion (see p. 44), and *Luciolates* is unique in having the three caudal extensions of the lateral line restricted to the proximal part of the fin and visibly interconnected with each other.

One may, I think, rate the dentition and fused hypural plates of *Luciolates* as derived characters. The condition of the lateral line may be primitive or it could be a secondary reduction of the *Lates* type (i.e. a derived character), although the interconnection of the lines might argue against such a conclusion. But, even if all these character states are derived ones, they are autapomorphies ; on the basis of synapomorphies *Luciolates* still has as its nearest relatives the three *Lates* species of Lake Tanganyika. Furthermore, *Luciolates* shares with these species one apomorph character (the morphology of the lateral ethmoid) which distinguishes the group as a whole from all other African species of *Lates*, as well as from the Indo-Pacific marine species *L. calcarifer*.

For these reasons I propose that *Luciolates* should be united with its nearest relatives in the genus *Lates*. At the same time I propose placing the Lake Tanganyika

* On the evidence currently available, *L. macrophthalmus* (from Lake Albert) and *L. longispinis* (from Lake Rudolf) could either be sister taxa derived from a common ancestor (itself a sister species of *L. niloticus*) or each could have been derived locally, in late Pleistocene times, from the population of *L. niloticus* then inhabiting these lake basins.

Lates species, that is *L. angustifrons*, *L. microlepis*, *L. mariae* and now *Lates stappersi* in one subgenus (for which the name *Luciolates* Blgr. is available), separate from *L. calcarifer*, *L. niloticus*, *L. macrophthalmus* and *L. longispinis* which species comprise the subgenus *Lates*. Definitions and synonymies for these taxa are given on pp. 77-78.

Interrelationships within the subgenus *Luciolates* may be delimited on the basis of vertebral morphometry, the division of the dorsal fin, the morphology of the lateral ethmoid, and on neurocranial anatomy and morphology (see relevant sections on pp. 14-45).

Lates angustifrons is clearly the plesiomorph sister species of all others in the subgenus. *Lates mariae* and *L. microlepis* show generally similar degrees of specialization in all the characters noted above, and can thus be considered sister species; since in some features (e.g. the lateral ethmoid) *L. microlepis* is less specialized than *L. mariae* it can be considered the plesiomorph member of the pair.

The greatest level of specialization is seen in *Lates stappersi* which is therefore ranked as the apomorph sister species of *L. mariae* and *L. microlepis* combined (see Fig. 37).

The difficulties of ranking species within the nominate subgenus have been discussed above (see pp. 49-50). Indeed, it is not even possible to show that this subgenus is monophyletic since its 'diagnostic' features are those plesiomorphic for the genus as a whole.

A REVIEW OF THE GENUS *PSAMMOPERCA* RICHARDSON

Introduction

There are no published accounts of the osteology and anatomy of *Psammoperca*. A brief outline of the osteology of *P. waigiensis* (Cuv.) is given here, together with some notes on various aspects of the soft anatomy in this species, particularly those features which have some bearing on the phyletic relationship of the taxon.

Fishes of the genus *Psammoperca* (Richardson, 1844) occur in coastal waters from the Bay of Bengal, the Indo-Australian archipelago, northern Australia, the Philippines and the China Sea. To a considerable extent, this distribution overlaps that of *Lates calcarifer* (see above, p. 12; also Fig. 36, and Weber & de Beaufort, 1929). Two nominal species, *P. waigiensis* (Cuv.) and *P. macroptera* Günth. are recognized, the latter restricted to Australia and known only from the holotype. The material I have examined is entirely of *P. waigiensis*, but the individual variability represented in these samples certainly indicates that *P. macroptera* should be considered a synonym. The question could be solved if large samples from the type locality and other regions of Australia were examined.

Superficially, *P. waigiensis* is much like *L. calcarifer* (Fig. 1), but is distinguished by its widely separated nostrils, smooth lower border to the preoperculum and to the lachrymal, and by the more extensive squamation of the dorsal and anal fins.

Osteology and anatomy of *Psammoperca waigiensis**Neurocranium* (Figs 29a-b)

The proportions and general appearance of the neurocranium closely resemble those of *Lates macrophthalmus* (cf. Figs 29 & 4b); that is to say, a member of the subgenus *Lates* in which there is a reduction in the length of the precommissural neurocranium without elongation of the ethmoid skull region.

The ethmovomerine region is exactly like that in members of the subgenus *Lates*; the posterior wall of the lateral ethmoid is slightly concave and rises steeply to meet

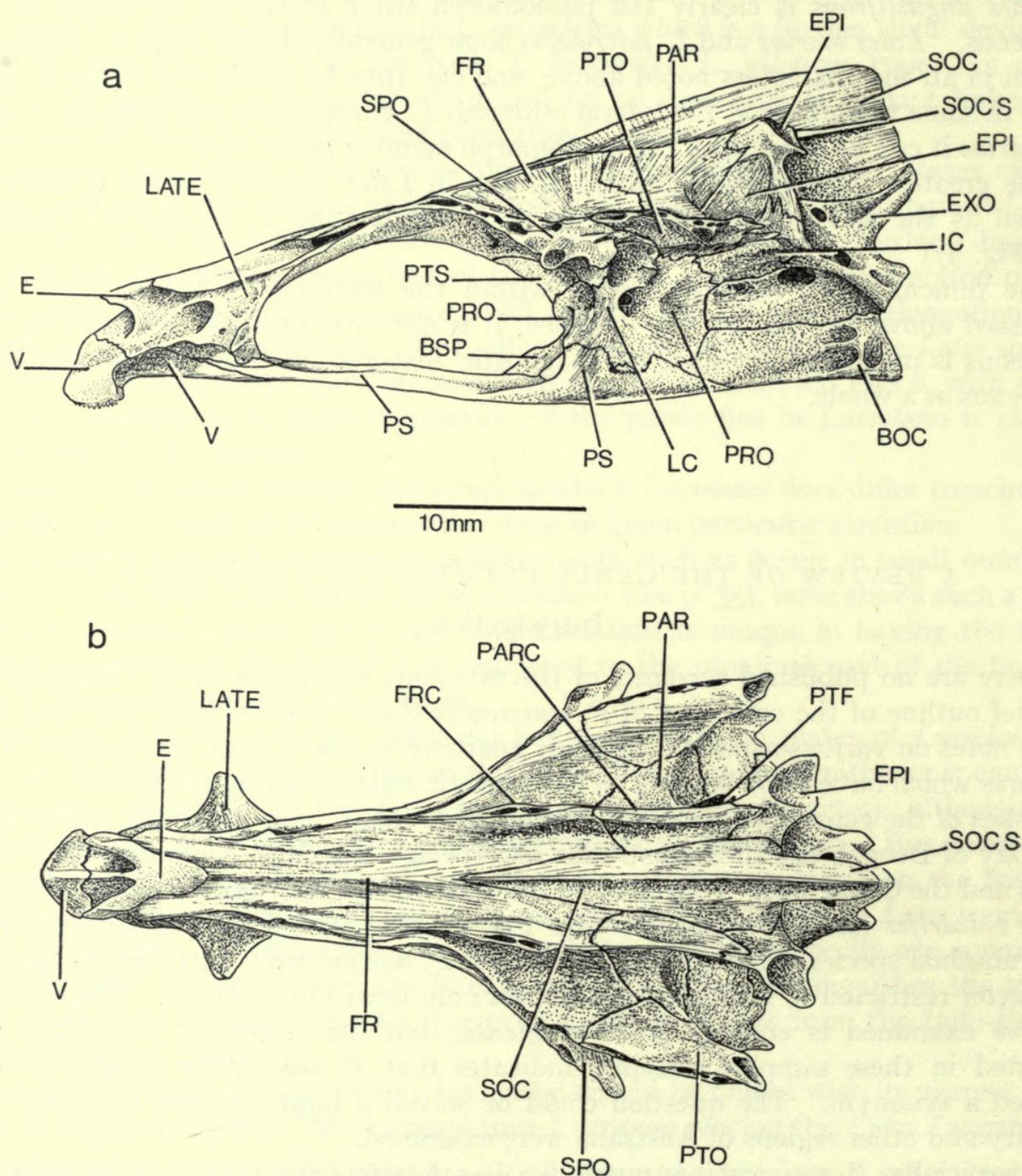


FIG. 29. *Psammoperca waigiensis*. Neurocranium in : (a) left lateral view, (b) dorsal view.

the frontal, and there are two palatine and one lachrymal articulatory facets on this face. A slight intergeneric difference lies in the strongly concave posterior margin of the vomer, which gives the tooth patch in *Psammoperca* a distinct arrowhead outline in ventral view.

The precommissural region (see p. 20) of the braincase in *Psammoperca* differs in certain details from that in *L. macrophthalmus*. The pterosphenoid is about the same relative size and the ascending limb of the parasphenoid meets the prootic to create a generally similar appearance for this region of the skull. However, in *Psammoperca* there is no trace of a pterosphenoid pedicle and there is no bridge, not even a ligamentous one, across the internal jugular vein and its associated nerves (see pp. 20–26 above). In this respect the skull of *Psammoperca* resembles, most closely, that of *Lates (Luciolates) stappersi*.

The otic skull region in *Psammoperca* is like that in *Lates (Lates) macrophthalmus* as far as the relative sizes and relationships of the constituent bones are concerned, but the posterior half of the prootic is noticeably inflated and is thinner in *Psammoperca*.

The posttemporal fossa, like that in all extant *Lates* species, is large and deep, and does not have a complete bony floor. The exoccipital facets meet medially.

The autosphenotic does not extend far into the orbit medially or dorsolaterally; again the resemblance is more to *L. macrophthalmus* than to other members of the subgenus *Lates*, and there is some resemblance to species of the subgenus *Luciolates*.

The dorsocranium is, in all respects save one, like that in *L. macrophthalmus*, with the supraoccipital extending forwards to separate the frontals, high frontoparietal crests, deep excavations between these crests and the supraoccipital, and a clearly demarcated lateral shelf on the supraoccipital where the crest extends posteriorly beyond the epioccipitals. The one difference I can detect is the absence of a bone-enclosed supraorbital transverse commissure in *Psammoperca*. The cephalic lateral line system in other respects, however, is like that in *Lates*.

The parasphenoid resembles closely that in *Lates* but is more sharply angled upwards from the level of the ascending limb; in this respect *Psammoperca* resembles species of the subgenus *Luciolates*.

Hyopalatine arch and the preoperculum (Fig. 30)

Again, it is only in certain details that the hyopalatine arch of *Psammoperca* differs from that arch in *Lates*.

Psammoperca has no tooth patch on the ectopterygoid, and the dermopalatine tooth patch is very narrow. According to Weber & de Beaufort (1929), ectopterygoid teeth are present in *P. waigiensis* but I have been unable to detect any on the specimens I have examined. Ectopterygoid teeth are absent in some specimens of *Lates (Luciolates) stappersi*, and it is interesting to recall that the dermopalatine tooth patch is narrowed to an extent comparable with that in *Psammoperca*. The palatine in *P. waigiensis* has a distinct dorsal ridge on the autopalatine immediately in front of the facet for articulation with the lateral ethmoid. This ridge is absent in all members of the subgenus *Luciolates* and is but weakly developed in species of the nominate subgenus.

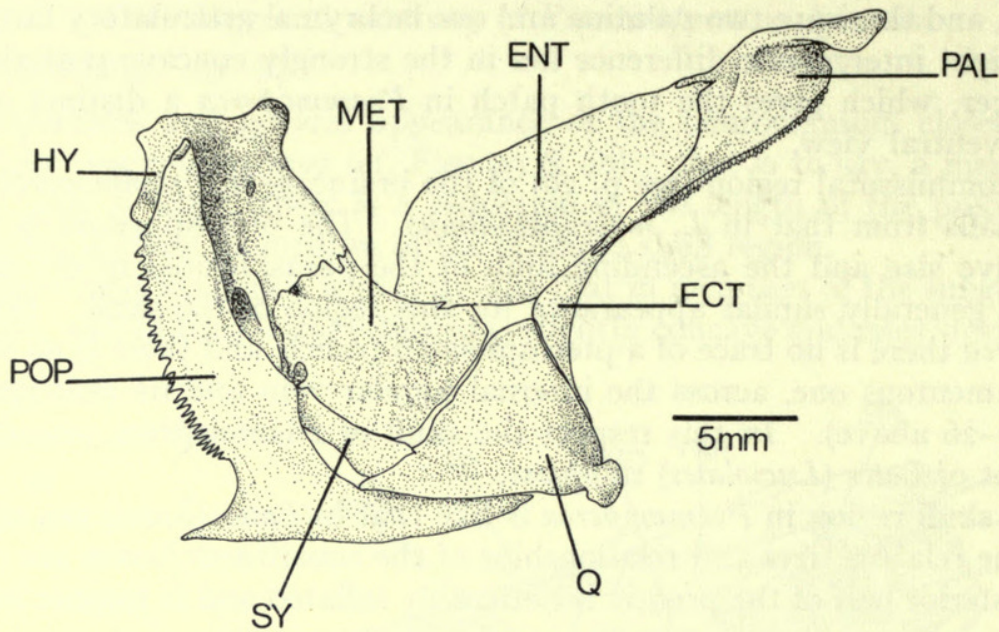


FIG. 30. *Psammoperca waigiensis*. Hyopalatine arch, including preoperculum (right side), viewed laterally.

As in *Lates*, the vertical limb of the preoperculum has a finely serrated posterior border, and the mandibular-preopercular sensory canal is bone enclosed (but opening through three ventrally directed and elongate pores on the horizontal arm). The margin of the ventral limb, however, is entirely smooth except for a stout, posteriorly directed spine at the angle between the vertical and horizontal limbs (Fig. 30). A similar spine is, of course, present in all *Lates* species but *Psammoperca* lacks the three or four stout and ventrally orientated spines on the horizontal limb. *Lates* (*Luciolates*) *stappersi*, it will be recalled (p. 30), often shows some reduction in the size of these spines, but in no individual are they entirely wanting.

Circumorbital bones (Fig. 31)

The five circumorbital bones are very similar to those in *Lates*; the relative elongation of the lachrymal and of the fifth circumorbital in *Psammoperca* is more like that seen in members of the subgenus *Luciolates*.

The lateral line canal is bone enclosed but opens to the exterior through five pores on the lachrymal, a pore between each articulation of the individual bones, and a ventral pore on the third circumorbital bone.

The suborbital shelf (on the third bone) is well developed to an extent almost equalling that found in members of the subgenus *Lates*; it extends dorsally to about the upper end of the fourth circumorbital bone.

The most marked difference between the circumorbital series in *Psammoperca* and *Lates* lies in the completely smooth ventral margin to the lachrymal and second circumorbital bones. These bones are strongly serrated in all *Lates* species, except *L. stappersi*, but even in that species some definite trace of the serrations does remain on the posterior part of the lachrymal (see p. 32 and Fig. 13c-d).

Opercular series (Fig. 14c)

The operculum of *Psammoperca*, like that in *Lates*, is armed with a single stout spine developed at the posterior end of the stay running from the articular facet for the hyomandibular boss. Indeed, the entire opercular series is like that of *Lates*, the relatively elongate interoperculum having the proportions of that bone in *L. (Luciolates) mariae*, *L. (Luciolates) microlepis* and *L. (Luciolates) stappersi* rather than that in other species of the genus. As in *Lates*, the sub- and interopercular bones of *Psammoperca* are thin.

Jaws (Figs 32a-c)

The maxilla, supramaxilla and premaxilla are, except for the coarser teeth on the latter bone, identical with those elements in species of the subgenus *Lates*.

The bones of the lower jaw (dentary, anguloarticular and retroarticular) are also like their counterparts in members of that subgenus; again, the teeth are stouter than in *Lates*.

Branchial skeleton

In its basic morphology and in the details of its upper pharyngeal dentition the gill arch skeleton of *Psammoperca* is identical with that of *Lates niloticus* (see p. 35). The only difference I can detect from the one *Psammoperca* skeleton studied is that the regularly arranged, small, rectangular tooth plates lying laterally on the gill arch above the filaments (the supralamellar plates, see p. 37) are restricted to the outer side of the first four gill arches (in *Lates* plates are present on both aspects of an arch).

This reduction in tooth plates should be considered as a derived condition since a marked reduction or even the complete loss of free dermal tooth plates is a feature of the more specialized percomorph groups.

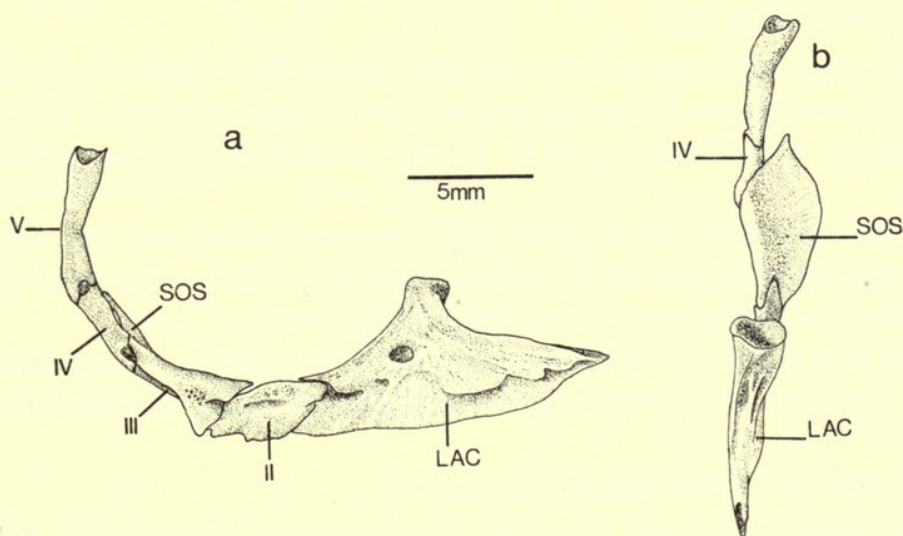


FIG. 31. *Psammoperca waigiensis*. Circumorbital bones (right) in: (a) lateral view, (b) viewed dorsally and somewhat anteriorly.

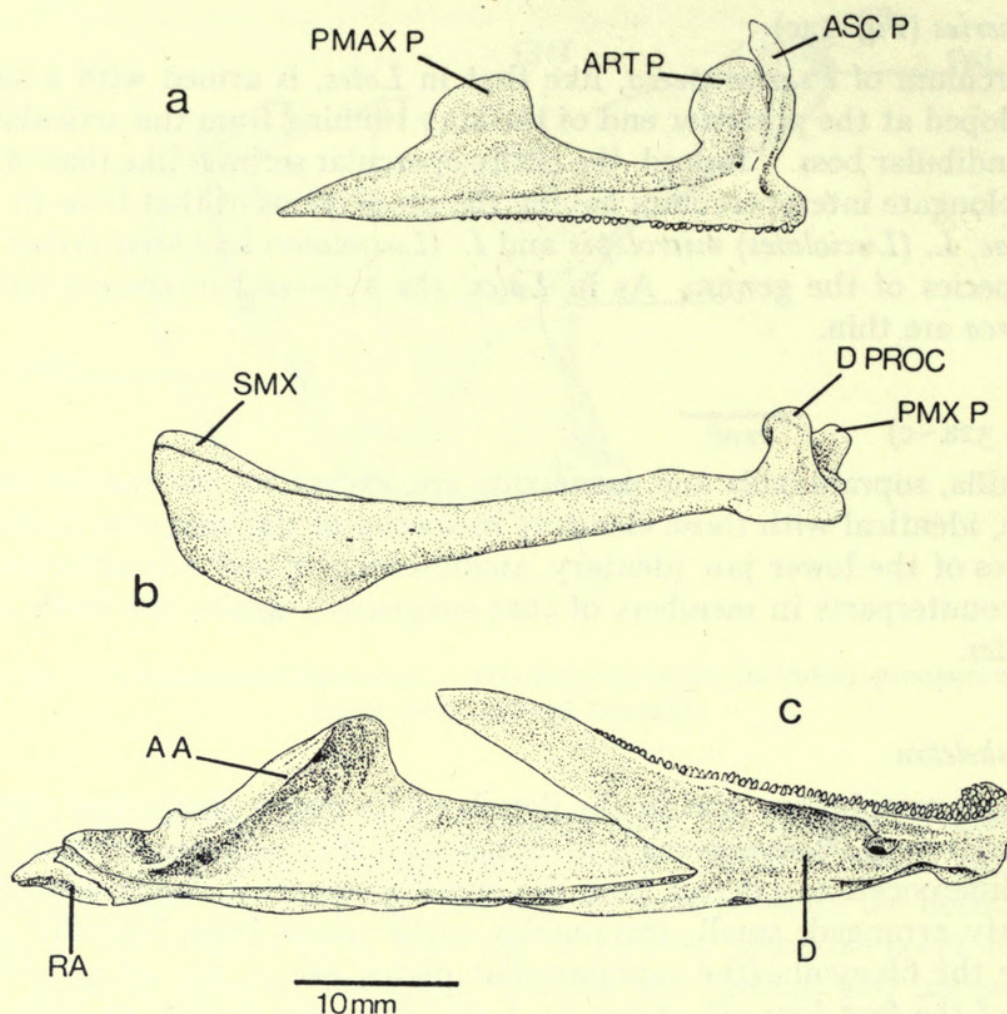


FIG. 32. *Psammoperca waigiensis*. (a) Premaxilla (right) in lateral view. (b) Maxilla (right) in a slightly oblique dorsal view to show supramaxilla. (c) Dentary (right), with anguloarticular and retroarticular, in lateral view.

Hyoid arch skeleton (Fig. 33)

The only marked difference between the hyoid skeletons of *Psammoperca* and *Lates* (especially members of the subgenus *Lates*) is the presence in the former of a moderately large, ovoid tooth-patch firmly attached to the broadly spatulate basihyal.

Psammoperca has seven branchiostegals, the posterior two of which articulate laterally with the epihyal, the next two with the ventrolateral face of the ceratohyal, and the first three with the ventral margin of that bone.

The presence of a basihyal tooth plate must be considered a plesiomorph character for the genus, the only living member of the Centropomidae in which it has persisted.

Pectoral girdle and associated bones (Fig. 34)

The one obvious difference between the pectoral girdles (i.e. supracleithrum, cleithrum, scapula and coracoid) of *Psammoperca* and *Lates* is the absence of serrations on the posterolateral angle of the cleithrum. In all other respects the girdles

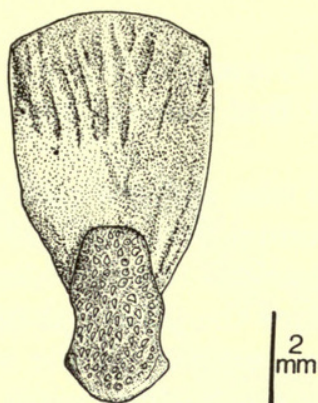


FIG. 33. *Psammoperca waigiensis*. Dorsal view of basihyal, showing tooth plate.

in the two genera are similar, but with a greater resemblance in overall proportions between the girdle of *Psammoperca* and that in the subgenus *Lates*.

Although in *Psammoperca* there are no serrations at the posterior cleithral angle, the bone in that region is drawn out into a short but well-demarcated spine.

As in *Lates*, the three upper fin radials articulate with the scapula, and the lowest with the coracoid.

There are two postcleithra, but in *Psammoperca* the upper member of the pair is less expansive than in *Lates*.

The posttemporal and extrascapula are similar in both genera, the posttemporal in *Psammoperca* even having the same kind of pit for the reception of the swimbladder ligament (see p. 41), but it does lack serrations on its hind margin.

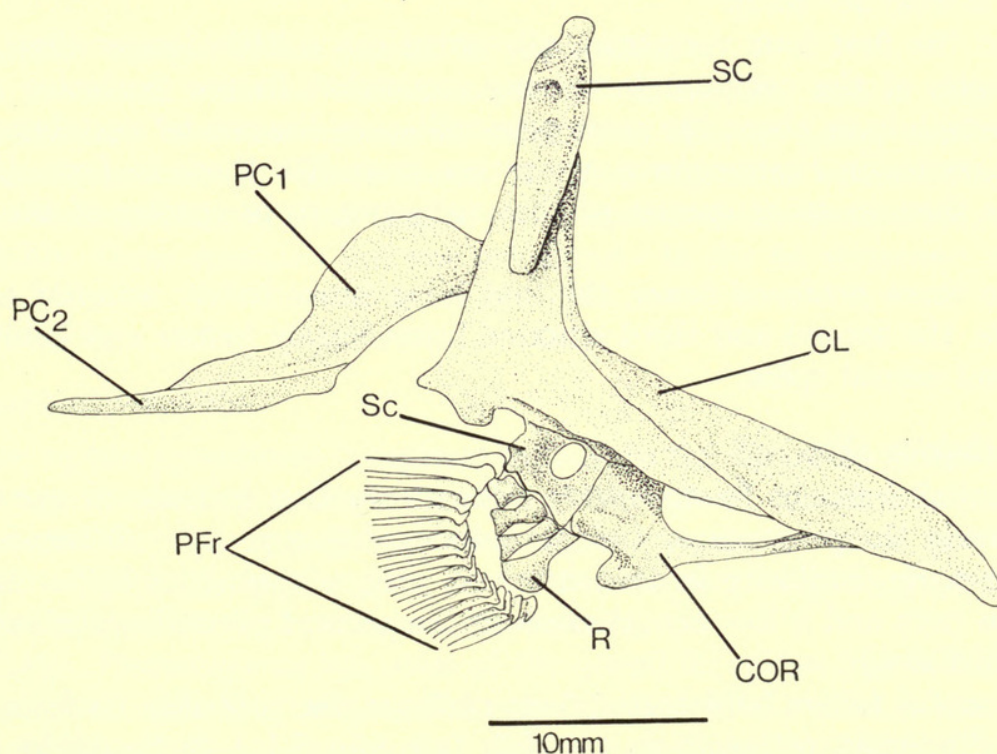


FIG. 34. *Psammoperca waigiensis*. Pectoral girdle (right half) with supracleithrum *in situ* and post-cleithra displaced posterodorsally. Lateral view.

Vertebral column

The total vertebral count in *P. waigiensis* is 25, comprising 11 abdominal vertebrae, 13 caudal, and the fused first preural and ural elements of the caudal fin skeleton.

There are nine pairs of pleural ribs, the first pair carried on the third vertebra, the last pair on the eleventh abdominal vertebra; this latter pair of ribs, instead of sloping gently backwards parallel with the preceding pair (as in *Lates*), runs almost horizontally and generally overlaps the proximal tip of the first anal pterygiophore.

The first definite parapophyses appear on the seventh vertebra, and are but a little shorter than those on the succeeding centra, although there is a slight and posteriorly progressive elongation of these processes. Anterior to the seventh vertebra, the ribs articulate with a shallow pit on the centrum. Where parapophyses are present, the rib articulates with the posterior face of the process.

In all these features, except for the better developed first and second parapophyses, and the angling of the last pair of ribs, *Psammoperca* is like *Lates* (see p. 42).

Epineural ribs are present on the first three vertebrae, and epipleural ribs on at least the first four pleural ribs. (These data were obtained from radiographs.)

The first three vertebrae are shown in Fig. 25b; their close resemblance to those in *Lates* is obvious (cf. Fig. 25a). One slight difference is in the development of a low median ridge on the ventral face of the second centrum of *Psammoperca*.

As in *Lates*, the neural spine of the second vertebra is much broader than the spine of the first and third centra, has its anterior and posterior margins parallel over much of their lengths, and tapers rather abruptly to form a slightly hooked tip. The angle between the posterior face of the second spine and the anterior face of the third spine is from 20° to 25° .

Except in the first four vertebrae, all centra are a little longer than deep, the relative length of the centrum increasing somewhat in the posterior abdominal vertebrae, which have about the same proportions as the caudal vertebrae. In this respect the centra in *Psammoperca* are rather more like those in *Lates* (*Luciolates*) *angustifrons* than in other species of that subgenus or in species of the nominate subgenus.

There are three *predorsal bones*, the first lying immediately anterior to the first neural spine, the second and third situated immediately before and behind the tip of the second neural spine.

Caudal fin skeleton (Fig. 35)

The caudal skeleton in *Psammoperca* differs from that in *Lates* in one important respect, namely the presence of a single uroneural (see p. 44). Otherwise there is great intergeneric similarity in this structure (viz. 2 epurals, 5 hypurals, 1, 8+7, 1 principal fin rays and a low neural crest on the second preural vertebra [lower, in fact, than in *Lates*]).

There is, as far as can be detected from radiographs, probably no fusion between any of the hypurals, although in one fish (240 mm S.L.) of the eight examined, hypurals 3 and 4 are so closely apposed as to appear fused. The first and fifth hypurals are autogenous, the others are fused to the underlying vertebral support.

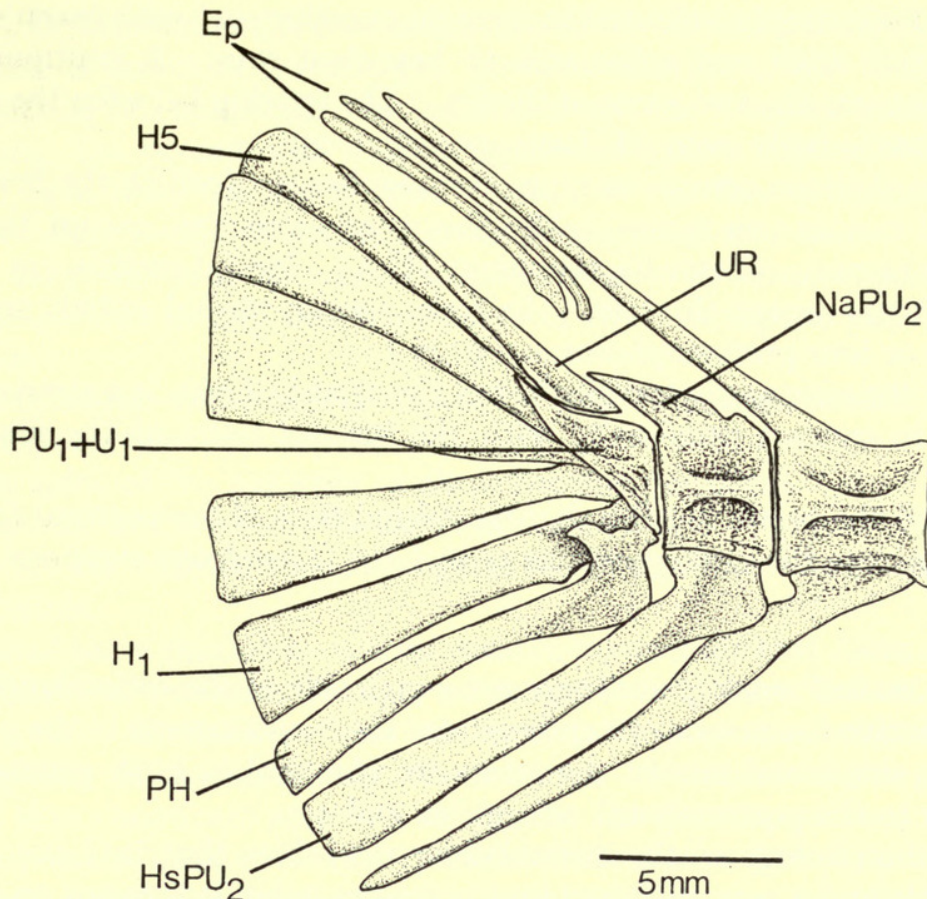


FIG. 35. *Psammoperca waigiensis*. Caudal fin skeleton (drawn from specimen 1872.9.2:10-11).

The posterior margin of the caudal fin is rounded.

A single uroneural must be considered a derived feature, and in this respect the caudal fin skeleton in *Psammoperca* is, relative to that in *Lates*, more specialized. Indeed, since there are in *Psammoperca* two and not three epurals the caudal fin skeleton is more specialized than that in any member of the Serranidae (where there are, invariably, three epurals – but one uroneural – in the fin skeleton; see Gosline, 1966).

Dorsal, anal and pelvic fins

There are 19 pterygiophores (proximal radials) in the dorsal fin skeleton, each one except the last supporting a single fin ray. Although an occasional member of the subgenus *Lates* may have 19 pterygiophores (see p. 45), the usual number in that taxon is 18. Nineteen, however, is the modal number of pterygiophores (20 the unusual one) in species of the subgenus *Luciolates*.

Unlike *Lates*, *Psammoperca* has some of the dorsal fin spines (the fifth through the eighth) associated with discrete medial radials; a medial radial is also associated with the last branched ray in this fin. *Lates* (*Luciolates*) *stappersi* alone amongst the *Lates* species has medial radials (associated with the posterior four or five branched rays).

The dorsal fin is deeply indented to form an anterior part with seven spines, and a posterior portion with one spine and 12 branched rays. A continuous but low membrane connects the two parts of the fin. The spacing between the spines of the two fin divisions is fairly even (cf. *Lates* species, p. 45).

The anal fin skeleton comprises nine pterygiophores, of which the first is a double structure and carries two spines. All other pterygiophores, except the last, carry a single spine or ray. (Total fin ray count III,8.) Medial radials are absent from all pterygiophores except the last. (In *Lates* species medial radials are present on the last three or four pterygiophores, see p. 47.)

The first of the nine anal pterygiophores, like that in *Lates*, is a stout and elongate bone and is in contact proximally with the haemal spine of the first abdominal vertebra.

The origin of the pelvic fins lies slightly behind that of the pectoral fins; in other words the fins have the same positions as in *Lates* (*Luciolates*) *stappersi*.

Swimbladder

As in *Lates*, so in *Psammoperca* there is on each side of the swimbladder anteriorly a tough connective tissue strap extending from the *tunica externa* to the posttemporal. The position, shape and size of the strap are identical in both genera (as are the modifications to the posttemporal, see pp. 41 and 47).

The gross morphology of the swimbladder resembles that in *Lates*. The *tunica externa* is thick, and a pair of short blunt processes extends forward on either side of a median invagination of the swimbladder. *Psammoperca* does differ, however, in having a narrow posterior diverticulum extending outside the visceral cavity. In a single specimen dissected, this caudal swimbladder prolongation lay on the left side of the first anal pterygiophore; it is embedded in the body musculature of that region and does not penetrate into the haemal arches of any caudal vertebrae.

Baudelot's ligament

The ligament is well developed and its relationships with the body musculature in the cervical region are like those described for *Lates niloticus* on p. 47; that is, it closely approximates to the serranid type described by Gosline (1966).

Lateral line

Unlike *Lates* there is only one series of pore-bearing scales on the caudal fin of *Psammoperca*. These small scales are an uninterrupted continuation of the body lateral line scales; they extend almost to the posterior margin of the caudal fin. In one of the nine specimens available, a few widely separated pore scales were found on the fin membrane between a pair of rays on the lower part of the fin.

THE RELATIONSHIPS OF *PSAMMOPERCA*

The close overall resemblance between *Psammoperca* and *Lates* has long been recognized (Regan, 1913), and has even resulted in a false record of *Psammoperca* for the Japanese fauna (see Katayama, 1956).

A detailed examination of the characters shared by the two taxa shows that many must be ranked as primitive features (i.e. symplesiomorphies) and therefore of little value in estimating relationships. Included amongst the symplesiomorphies are the vertebral count, the presence of a single opercular spine, similarities in gill arch anatomy and dentition, the single spine carried on the first pterygiophore of the dorsal fin, and many details in syncranial morphology and anatomy.

There are, however, four derived characters shared by *Psammoperca* and *Lates* which are not present in any other members of the Centropomidae. These synapomorphies are :

- (i) A swimbladder-posttemporal ligament (and correlated modifications to the posttemporal bone) ; see p. 60.
- (ii) A large spine at the posterior angle of the preoperculum.
- (iii) Two epurals in the caudal fin skeleton ; see p. 58.
- (iv) An anteriorly extended supraoccipital which separates the posterior parts of the frontals.

On the basis of these characters it is reasonable to conclude that *Lates* and *Psammoperca* are members of the same lineage, a lineage distinct from that of *Centropomus* (see below, p. 62). To indicate this relationship I propose placing *Psammoperca* and *Lates* together in one subfamily, the Latinae. Members of the genus *Centropomus* would thus constitute a second subfamily, the Centropominae, which can be readily defined on the basis of several specialized characters (see p. 67 below).

Psammoperca waigiensis (and, where these features can be checked, also *P. macroptera* ; see p. 51 above) differs from all or most species of the genus *Lates* in at least 14 features. In the list that follows, the condition of these features in *Lates* is given in parentheses.

1. A single series of lateral line scales on the caudal fin. (Three series.)
2. A single uroneural. (Two uroneurals.)
3. Some spine-bearing dorsal fin pterygiophores with a median radial. (None.)
4. No tooth patch on the ectopterygoid. (Present, but reduced in *L. stappersi*.)
5. No spines on the ventral (horizontal) limb of the preoperculum. (Three or four spines.)
6. Ventral margin of the first infraorbital bone (lachrymal) smooth. (Serrated, strongly so in most species.)
7. No pterosphenoid pedicle or internal jugular bridge. (Pterosphenoid pedicle present in all species except *L. stappersi* and *L. mariae* ; internal jugular bridge present in all species, even if reduced to a ligament.)
8. Transverse commissure of supraorbital lateral line system absent or poorly developed. (Present and well developed.)
9. Dermal tooth patch fused with basihyal. (Absent.)
10. Supralamellar tooth plates (p. 37) present only on the outer side of each gill arch. (Present on both sides.)
11. Posterior margin of the posttemporal smooth. (Serrated.)
12. A single short spine at the posterior angle of the cleithrum. (One large and two smaller spines.)
13. Posterior extravisceral extension of the swimbladder. (None.)
14. Second dorsal and anal fin entirely covered by small but densely arranged scales. (Squamation restricted to about the proximal two-thirds of the fin.)

In some of these characters (e.g. 1, 3, 5 and 9) *Psammoperca* is more primitive than any *Lates* species ; in others (2, 4, 7, 10 and 13) it shows derived characters. The

status of characters 6, 11, 12 and 14 is at present indeterminable. (See discussion on pp. 30–32.)

It is on the basis of the unique derived characters (i.e. autapomorphies) found in each of the two taxa that I would maintain them as distinct genera, the implication being that *Psammoperca* split off from the common latine lineage before the evolution of a serrated preoperculum and the tripartite lateral line extension onto the caudal fin. The derived characters seen in *Psammoperca* (especially the loss of a pterosphenoid pedicle, the presence of a single uroneural, the loss of certain branchial arch tooth plates, and the loss of ectopterygoid teeth) must have evolved after this split occurred. In these features *Psammoperca* is certainly more 'advanced' than is *Lates*.

It is interesting to note that a reduction and ultimate loss of the pterosphenoid pedicle is seen in certain *Lates* species of the subgenus *Luciolates* (see pp. 20–27), and that *Lates* (*Luciolates*) *stappersi* also shows a considerable reduction in, and occasionally the loss of, ectopterygoid teeth. Furthermore, this species also shows a marked weakening of the serrations on the lachrymal. Similar parallel trends in all three characters are found amongst the species of *Centropomus* (see below) thus suggesting that this is the manifestation of a potentiality possessed by the common ancestor of all living centropomids.

THE RELATIONSHIPS OF *CENTROPOMUS* WITH THE LATINAE

Fraser (1968) has given a good account of the osteology of five species of *Centropomus* but he was unable, through lack of published information, to compare fully these species with members of the genera *Lates* and *Psammoperca*. He did, however, list a number of differences between *Lates* and *Centropomus* and these will be commented upon below.

In my comparison of *Centropomus* and the Latinae I have drawn on Fraser's (op. cit.) information and supplemented it from dissection, radiographs and dry skeletons of *C. parallelus* Poey, *C. pectinatus* Poey, *C. armatus** Gill, *C. unionensis** Bocourt, *C. robalito** Jordan & Gilbert, *C. nigrescens** Günther, *C. ensiferus* Poey and *C. undecimalis* (Bloch); species not described by Fraser (op. cit.) are marked with an asterisk.

The *neurocranium* in all *Centropomus* species is narrow and elongate, with a pronounced relative lengthening of the ethmovomerine region. In these respects it resembles the neurocranium of *Lates* (*Luciolates*) *mariae* and *L.* (*Luciolates*) *stappersi*, but it does differ in having only a gently angled parasphenoid (or even a straight one; cf. *C. pectinatus*, text-fig. 4, and *C. undecimalis*, text-fig. 5, in Fraser (1968), with Figs 7 & 8 above), and in having the postotic region of the skull relatively longer.

Within the *Centropomus* species I have examined, there is a trend of neurocranial elongation which closely parallels that found in members of the *Lates* subgenus *Luciolates*.

Another parallelism with *Lates* is seen in the reduction of the pterosphenoid pedicle and internal jugular bridge.

The pedicle and bridge are best developed in *C. ensiferus* (see text-fig. 6 in Fraser, 1968) where the condition of the bridge is like that in *L.* (*Luciolates*) *angustifrons*

(see p. 24 and Fig. 5a). A noticeable difference, however, is that, in *C. ensiferus*, there is no ascending arm of the parasphenoid and the bridge is formed by contact between the pterosphenoid and prootic. (The prootic in all *Centropomus* contributes to the posteroventral margin of the orbit; in *Lates* this rarely happens because part of the ascending parasphenoid arm usually rises in front of the prootic. This tongue of parasphenoid is, however, very narrow in the more specialized species of the subgenus *Luciolates*.)

In all other *Centropomus* species I have examined or which are figured by Fraser (1968), excepting *C. undecimalis*, the pterosphenoid pedicle is either reduced (e.g. *C. pectinatus*) or is greatly reduced to a small bony knob (that is, to conditions comparable with those in very small *L. (Lates) niloticus* or those in adult *L. (Luciolates) microlepis*; see p. 26). In *C. undecimalis* there is no trace of a pterosphenoid pedicle; in other words a situation directly comparable with that in *L. (Luciolates) stappersi* and in *Psammoperca waigiensis*.

Correlated with this reduction in the pedicle, the internal jugular bridge is reduced from a narrow bony strut in *C. ensiferus* to a ligament in the other species (except *C. undecimalis*), again paralleling exactly the trend seen in *Lates* (pp. 21–26). In *C. undecimalis* even the ligament has disappeared (at least in the specimen of 175 mm S.L. I dissected); this, it will be recalled, is the condition also found in *Psammoperca* (p. 53).

Probably as a correlate of the lengthening ethmoid-vomerine skull region, the shaft of the vomer in all *Centropomus* species is much broader anteriorly and has a closer sutural union with the lateral ethmoid than it does in any latine species. In other details, however, this region of the skull is generally similar in both *Centropomus* and the Latinae.

The otic region in *Centropomus* is bullate, more markedly so in some species than in others, but always more inflated than in any *Lates* species and rather more so than in *Psammoperca*.

An outstanding inter-subfamilial difference is found in the lateral line system of the dorsicranium. In *Lates* and in *Psammoperca* all three major canals are bone enclosed. In *Centropomus* the canals are in the form of laterally orientated open gutters, with only the posterior part of the supraorbital line completely tubular. The frontal cross-commissure is also open (with the gutter directed medially), as is the entire length of the frontoparietal branch (whose gutter is directed laterally).

Fraser (1968) has corrected Regan's (1913) erroneous observation that parietal crests are absent in *Centropomus*, but as compared with *Psammoperca* and *Lates*, the parietal crests, and their counterparts on the frontals, are low and very poorly defined, and do not extend to the posterior margin of each parietal (often being confined to the anterior half of that bone).

The supraoccipital in *Centropomus* does not extend so far anteriorly as it does in *Lates* and *Psammoperca*, its tip barely separating the frontals and only reaching a level with a vertical through the middle or the posterior third of the prootic.

There are few noteworthy differences in the *hyopalatine* arches of *Centropomus* and the Latinae. As Fraser (1968) noted (*pace* Regan, 1913), ectopterygoid teeth are present in *Centropomus*. From Fraser's drawing (op. cit., text-fig. 11) one gains

the impression that a metapterygoid lamina is present in at least some *Centropomus* species, but I cannot confirm this from the dry skeletons I have examined.

There are several inter-subfamilial differences in the morphology of the *preoperculum*. First, the lateral line canal in *Centropomus* is an open gutter, the opening orientated posteriorly on the vertical limb of the bone and ventrally on its horizontal limb. It is the upper rim of this gutter that has been described as a 'ridge' on the preoperculum in *Centropomus* species (see Fraser, 1968). In the Latinae, where the canal is bone enclosed and tubular no 'ridge' is, of course, detectable.

A second and pronounced difference is in the ornamentation of the preoperculum, a difference most obvious when *Centropomus* is compared with *Lates*. In *Centropomus*, as in *Lates* and *Psammoperca*, the posterior margin of the vertical limb is serrated (less regularly so in *Centropomus*), but the horizontal limb in that genus has a number of low, rather irregular serrations that are enlarged posteriorly at the angle of the bone. In no *Centropomus* species is there any indication of the three (or four) large triangular spines that characterize all *Lates* species; likewise, no *Centropomus* has the completely smooth horizontal preopercular arm of *Psammoperca*. Also, unlike both *Lates* and *Psammoperca*, there is no single, stout spine at the posterior angle between the two preopercular arms; instead, in *Centropomus* there are a variable number of spines, all of which are somewhat larger than those preceding and succeeding them on the arms of the bone, but none is as large nor as distinctive as the single spine of the latines.

The *operculum* in *Centropomus* lacks a spine at its posterodorsal angle (see p. 55) but otherwise the opercular series shows no marked departure from its counterpart in the Latinae.

The open lateral line gutters of the *circumorbital bones*, the reduced serration of the ventral lachrymal border, and the relatively short fourth and fifth circumorbitals are the most obvious inter-subfamilial differences noted in this region of the skull. Apparently the subocular shelf in *Centropomus* is like that in *Psammoperca* and members of the latine subgenus *Lates*, but I have been unable to check this point in all *Centropomus* species, and in particular those with narrower and more elongate heads.

Apart from some slight proportional differences, the major feature differentiating *jaw* elements in the two subfamilies is the much shorter ascending process of the premaxilla in *Centropomus*. In the Latinae the ascending process is at least one and a half times the height of the maxillary process (see p. 34) but in *Centropomus* the two processes are of equal height (cf. text-fig. 12 in Fraser, 1968, with Figs 15, 16 & 32 above).

The basic *gill arch* morphology and dentition are similar in *Centropomus* and the Latinae, although the tooth plates associated with the basibranchials are slightly more elongate in at least some members of the Centropominae. The supralamellar tooth plates in most *Centropomus* species which I have dissected (*C. ensiferus*, *C. parallelus*, *C. pectinatus*, *C. undecimalis* and *C. armatus*) show a unique arrangement not found in any member of the Latinae. The plates are present only on the outer aspect of the second to fourth gill arches, and are fused, in pairs, with the bases of

the gill rakers on that aspect of the arch ; occasionally a single plate may occur between a pair of gill rakers. An exception is provided by a small (160 mm S.L.) specimen of *C. parallelus* in which the plates are serially arranged like those in *Psammoperca*.

A slightly larger fish (220 mm S.L.) shows a condition intermediate between that in the smaller specimen and that of the other species (and specimens of *C. parallelus*) I examined. Possibly this change in plate arrangement is a growth phenomenon.

All *Centropomus* species have 24 *vertebrae* (including the fused first ural and preural centra), comprising 9 abdominal and 15 caudal elements. (Fraser, 1968, gives a count of 10 + 14, indicating that we differ in our interpretation of which vertebra constitutes the first caudal element ; I identify it as that vertebra with which the first anal pterygiophore articulates.) All members of the Latinae, in contrast, have 25 vertebrae (11 abdominal and 14 caudal elements).

There are seven or eight pairs of pleural ribs in centropomines (nine in the Latinae), the number apparently showing some intraspecific variability. The first rib articulates directly with the third vertebra. Definite parapophyses are developed on the seventh abdominal centrum but a low process occurs on the sixth vertebra. Anterior to these centra the ribs articulate as in the Latinae, that is, with a pit in the centrum. Also as in the Latinae, the ribs articulate with the posterior face of the parapophysis when these are present.

As far as I can tell from radiographs, the shape and proportions of the centra in all *Centropomus* species are like those in *Lates calcarifer*. That is, posterior to the third vertebra all the centra are slightly longer than deep, with little difference in proportion between abdominal and caudal elements. Apart from the neural spine on the second vertebra the first three vertebrae are like their counterparts in latine fishes. The second vertebra, however, has a very greatly expanded neural spine (see Fig. 25d) into the anterior face of which the entire posterior margin of the first neural spine is fitted. Fraser (1968) has shown that the proportions of the second neural spine change with age in at least some species of *Centropomus* ; the spine in young fishes resembles that in adult *Lates* and *Psammoperca* (see Fraser, op. cit., text-fig. 14, and pp. 454-5 ; and cf. Figs 25a-c above).

All *Centropomus* species have three *predorsal bones*, the first situated above the tip of the first neural spine, the second at about the middle of the expanded second spine, and the third lying immediately behind that spine. Fraser (1968) states that there are only two predorsals in *Lates*, but this is not so (see p. 43 above) ; there are, in fact, no intergeneric differences in this feature.

A distinct gap separates the two *dorsal fins* in all *Centropomus* species ; the size of the gap, however, shows some specific variation. Unlike those Latinae with separate dorsals (members of the subgenus *Luciolates* ; see p. 45), the centropomines have no isolated spines between the fins. The head of the seventh pterygiophore is drawn out posteriorly so that it effectively underlies the gap between the fins ; the spine which this pterygiophore carries thus becomes the first (and only) spine of the second dorsal fin.

There are 16 or 17 dorsal pterygiophores in *Centropomus* (cf. 18 or 19, rarely 20 in the Latinae), none of which, as far as I can determine, has a separate medial

radial (see p. 45). The first dorsal pterygiophore, unlike that of the latines, carries two spines; except for the last dorsal and first anal pterygiophores, all the others carry a single spine or ray.

The dorsal fin ray counts in *Centropomus* are VII or VIII and I,8 or 9 (cf. VI–VIII and I,10–13 in all Latinae except *Lates* (*Luciolates*) *stappersi* which has VI+I+I and I,9 or 10). Thus in the centropomines there has been not only a trend towards separation of the dorsal fins (a trend also apparent in the latines, see p. 46 above) but also a reductional trend in the number of dorsal fin rays, particularly the branched rays. Interestingly, if the two independent and much reduced fin spines are 'removed' from the fin formula of *Lates* (*Luciolates*) *stappersi*, the result – save for an extra branched ray – is the formula of a *Centropomus* (i.e. VI+I+I and I,10 → VI and I,10).

A most characteristic feature of all *Centropomus*, and one not even approached by any member of the Latinae, is the very strong and long first *anal pterygiophore* (see Fig. 27b); in many species there is also hypertrophy of the second anal spine. Despite the length of this pterygiophore it extends only a little further distally (i.e. towards the vertebral column) than does its counterpart in the Latinae. The greater length of the bone in *Centropomus* is accommodated by the bone sloping obliquely backwards so that the articulation for the spines lies in a vertical below about the seventh rather than the second or third abdominal vertebra as is the case in *Lates* (Fig. 27a) and *Psammoperca*.

The *caudal fin skeleton* in *Centropomus* differs from that in the Latinae in either one (*Lates*) or two (*Psammoperca*) characters and is of a more primitive kind. Primitive features in *Centropomus* are the three epurals (two in Latinae) and the two uroneurals. *Lates* also has two uroneurals but only one is present in *Psammoperca* (the fin skeleton in that genus being the most evolved within the Centropomidae).

All *Centropomus* species have a deeply forked caudal fin whereas in the Latinae the fin is usually rounded or truncate, although it is weakly forked in some species of the *Lates* subgenus *Luciolates*. Like the Latinae, the caudal fin formula of the Centropominae is I,8+7,I.

The *pectoral girdle* and fin skeleton are basically alike in the Centropominae and Latinae except for slight differences in the postcleithral elements.

The *posttemporal* in *Centropomus* lacks the cavity and associated bullation that characterize this bone in *Lates* and *Psammoperca*, a consequence of there being no swimbladder–posttemporal ligament in *Centropomus* (see below). Otherwise the posttemporal is similar in both subfamilies. The extrascapula in *Centropomus* is also basically like that in the Latinae, but it is characterized by having the lateral line canals situated in open gutters and not enclosed in bony tubes (see p. 41 above).

In those *Centropomus* species which I have been able to dissect, the anterior end of the *swimbladder* has no medial invagination (see p. 60 above). However, in some species there are a pair of short horns arising from the dorsolateral aspect of the bladder and extending part way towards the skull; in none could I find any direct connection between the skull and the horns, and neither could I find any trace of a swimbladder–posttemporal ligament such as occurs in all members of the Latinae. The development of the swimbladder horns seems to be restricted to certain species.

When present these appendages may be short, simple and anteriorly directed, or, as in *C. undecimalis*, they may be elongate and curved backwards to lie laterally along the swimbladder (see Meek & Hildebrand, 1925). This latter condition is reminiscent of that found in certain species of Sciaenidae (a family in which there is also an extension of the lateral line onto and reaching the margin of the caudal fin; the possibility of there being some phyletic relationship between sciaenids and centropomids is under review).

Baudelot's ligament is present in *Centropomus* and is moderately well developed. The relationships between this ligament and the body muscles are like those in the Latinae (see p. 60 above), with little or no muscle passing medially below the ligament, but with a broad band passing underneath it laterally to insert on the basioccipital and exoccipital.

A single extension of the body *lateral line* scale series onto the caudal fin is found in all species of *Centropomus* (there are three extensions in *Lates* but only one in *Psammoperca*). In *Centropomus*, as in the Latinae, the caudal extension of the lateral line is continuous to the margin of the fin or almost so.

When all these characters are taken into account, it is clear that the Centropominae (i.e. *Centropomus* species) differ from the Latinae (*Lates* and *Psammoperca* species) in a number of features. Some of these differences involve the retention of characters primitive for the family whilst others represent the development of unique specializations shared only by *Centropomus* species. In the former (i.e. plesiomorph) category may be listed the caudal fin skeleton, the short supraoccipital bone, the single lateral line extension onto the caudal fin, and the absence of a swimbladder-posttemporal ligament. The autapomorphic features of the Centropominae are more numerous and include the open cephalic lateral line canals, the separation of the dorsal fin, the hypertrophy of the first anal pterygiophore (and at least relative hypertrophy of the second anal spine), the absence of medial radials throughout the dorsal and anal fins, the development of a curved and posteriorly protracted head on the seventh pterygiophore of the dorsal fin (see p. 65), the development in most species of anterior horns on the swimbladder, the incorporation of the supralamellar tooth plates into the gill rakers, and the elongation of the skull, especially its ethmovomerine region (with which feature may be correlated changes in the shape of the ethmoid and vomer).

There are other differences, like the absence of an opercular spine, the forked caudal fin, and the markedly reduced squamation of the dorsal, caudal and anal fins, whose apo- or plesiomorph status is uncertain.

On the basis of those characters that are clearly synapomorphic the *Centropomus* species can be recognized as a monophyletic group and one which, although sharing a common ancestry with the Latinae, is clearly distinct from that lineage. It is for this reason that I propose giving the *Centropomus* species-group coordinate ranking (as the subfamily Centropominae) with the Latinae (see also above p. 61; and p. 75 below for diagnoses).

When the mosaics of apo- and plesiomorph characters within the two subfamilies are compared it becomes impossible to decide which taxon should be considered the plesiomorph sister group of the other. However, it does seem that what we are now

observing is the product of vicariant differentiation from a once widespread basic centropomid taxon, a differentiation that produced the Centropominae in America, and the Latinae in Asia and the Mediterranean region (including Africa), leaving each group with its own association of primitive and derived features.

Fraser (1968) noted certain shared characters amongst the various species of *Centropomus*, and from their pattern of occurrence concluded that three phyletic lineages are represented amongst the living species. Unfortunately, Fraser does not give a really critical analysis of the characters on which his phylogeny is constructed and it is thus impossible to test the supposed interrelationships of the three lineages he hypothesizes. In particular it would seem that his monotypic lineage comprising *C. pectinatus* is more likely a member of the *C. ensiferus* – *C. robalito* lineage, and not, as is expressed in Fraser's diagram, one distinct from the other two lineages and occupying an equal phyletic relationship with both of them (see Fraser, 1968, text-fig. 9).

Although Fraser's analysis is not documented in terms of synapomorph and symplesiomorph characters it obviously shows that similar trends can be found within the Centropominae and the Latinae. This aspect is particularly well demonstrated in the neurocranial morphology and in the reduction of the pterosphenoid pedicle and internal jugular bridge. There is also inter-subfamilial similarity in the trend towards greater separation of the two parts of the dorsal fin. In this trend the Latinae appear not to have evolved much beyond the early phases, whereas the centropomines have carried the trend further and no longer preserve traces of its earlier stages within their numbers.

FOSSIL CENTROPOMIDAE

Apart from identifications based solely on otoliths,* all species of fossil centropomids so far discovered are currently referred either to *Lates* or to *Eolates* Sorbini (see Sorbini, 1973), that is, to the subfamily Latinae.

The time range of these fossil taxa extends from the Eocene to the Holocene, and their geographical range from the Paris Basin, through Austria, Portugal, northern Italy and Croatia to Egypt, the Sahara and eastern Africa (Sorbini, 1973; Greenwood, 1974; Greenwood & Howes, 1975).

With the exception of some material from Europe (Sorbini, 1973) the majority of fossils are from Africa and are in the form of disarticulated and damaged bones. The problems of specific (or, indeed, generic) identification when dealing with material of this nature need not be stressed. In most instances the fossil bones have been compared with their counterparts in *Lates calcarifer* and *L. niloticus*. If the fossils are from Africa, and the bones are not noticeably different from their counterparts in *L. niloticus* the material was either referred to that species or, and probably more accurately since diagnostic features are rarely preserved, merely to *Lates* sp.

* *Psammoperca sheppeyensis* Frost 1934, *Centropomus superpendens* Frost, 1934 and *C. excavatus* Stinton, 1966, all from the London Clay (Eocene), are species described from otoliths only. Since so little is known about otolith morphology in living centropomids and because no skeletal material is available for the species, these records can at present contribute little to our understanding of centropomid phylogeny and biogeography.

When obvious morphological differences could be detected the remains have been taken to represent different species (e.g. *L. fajumensis* Weiler, 1929 ; *L. karungae* Greenwood, 1951 ; *L. rhachirhinchus* Greenwood & Howes, 1975).

Because these species are based on fragmentary, disarticulated bones it is impossible to determine their phyletic relationships with each other or with the extant species of Latinae (see discussions on *L. rhachirhinchus* in Greenwood & Howes, 1975). About all that can be said with any certainty is that latine centropomids had, by late Miocene times, a distribution that included Egypt, Tunisia and eastern Africa (Lakes Victoria and Albert regions) and that at least one species, *L. rhachirhinchus*, showed several derived characters even when compared with extant species of that genus (Greenwood & Howes, 1975). All these remarks are, of course, based on the assumption that the taxa are correctly placed in the genus *Lates* ; in no case is it possible to check on the autapomorph characters used here to define the genus (see p. 77), the generic identity being based on an overall similarity between the fossil bones and their counterparts in extant *Lates* species.

The situation is little better for the three European species in which the entire skeleton is preserved, viz. *L. partschii* Heckel, 1855 (Miocene, Vienna Basin) ; *L. croaticus* Kramberger, 1902 (Miocene, Croatia) and *L. macropterus* Bassani, 1899 (Oligocene of Vicenza).

I have not been able to examine any material of *L. croaticus*, and the only published description and figures of this species are inadequate for critical interpretation, although Kramberger (1902) does give a vertebral count of 27, that is two more vertebrae than in any other member of the Latinae for which the count is available. The status and relationships of this nominal species must therefore remain *incertae sedis*.

Sorbini (1973) has re-examined *L. macropterus*, but was unable to draw any definite conclusions about its relationships. Again it is impossible to check on any diagnostic characters of phyletic importance.

Lates partschii (Miocene of Vienna) has been thoroughly redescribed by Sorbini (1973), who also published a photograph of the holotype, and a close-up picture of its caudal skeleton. But once again certain critical details are either not preserved, are obscured, or are damaged. For instance, there seems to be only a single and median row of lateral line scales on the caudal fin but one cannot be certain that dorsal and ventral scale rows were not present. There are certainly only two epurals in the caudal fin skeleton, and there are, apparently, two uroneurals, both features which are characteristic of *Lates* (see pp. 44 and 77). From this and other circumstantial evidence given in Sorbini's account, it seems likely that *partschii* can be placed in *Lates*, but it is impossible to determine its relationships with any extant species of that genus.

Fortunately, many important features are preserved in the extensive material of *Eolates* that is available for study (Sorbini, 1973 ; personal observations on specimens in the collections of the British Museum (Natural History))*.

* Two nominal species are recognized, *Eolates gracilis* (Agassiz) 1833, and *E. macrurus* (Agassiz) 1833. According to Sorbini (1973), *E. macrurus* may yet prove to be a synonym of *E. gracilis*. For this reason, and because the osteology of *E. gracilis* is much better known, only that species is taken into account in the discussions that follow.

Eolates gracilis is distinguished from all *Lates* species by at least one character complex (the caudal fin skeleton), and probably by two other characters as well (the absence of upper and lower lateral line scale rows on the caudal fin, and the disposition of the branchiostegal rays).

I have examined eight specimens of *E. gracilis* (from the BMNH collections) in which the caudal fin is well preserved. In all, the median lateral line scale row is clearly developed and it is also possible to see other scales, often still in their rows, on other parts of the fin. None of these other scales is perforated and I am confident that only one lateral line scale row (the median one) is preserved. My colleague, Dr K. Banister, has recently examined *E. gracilis* holotype in the Paris Museum and reports that only a median row can be detected in this specimen as well.

The caudal fin skeleton in *E. gracilis* (Fig. 26b) shows a well-developed neural spine on the second preural centrum (spine greatly reduced in *Lates*), three epurals (two in *Lates*) and two uroneurals (two uroneurals also present in *Lates*). In other words, the caudal fin skeleton is of a more primitive type than that in *Lates*. (It will be recalled that *Centropomus* also has three epurals, but the second preural arch and spine are reduced and resemble those in *Lates*.)

A possible third intergeneric difference concerns the number and disposition of the branchiostegal rays, but this requires confirmation since it is based on data available from only one of the *E. gracilis* specimens examined by Sorbini (1973). In the sole specimen from which a branchiostegal ray count could be made Sorbini (op. cit.) records, with some uncertainty, a total of eight rays (seven in *Lates* and other centropomids). Judging from the photograph of this specimen (Sorbini, 1973, Plate IV, fig. 1), I should doubt that the fragment at the anterior end of the ceratohyal is indeed part of a branchiostegal ray.

There is, however, no doubt that in this specimen all the branchiostegal rays are associated with the ceratohyal. According to McAllister (1968) this condition is not found in any living percoid fish; there is always at least a half articulation between a ray and the epihyal. The rays in the *E. gracilis* specimen are in no way disarranged, and the posterior one is well forward of the epi-ceratohyal junction. Clearly no decision can be made on the validity of this apparent intergeneric difference (or its apparent uniqueness amongst percoids) until further specimens can be examined.

Like the preoperculum in *Lates* this bone in *Eolates* has three large ventral spines on its horizontal limb, and an enlarged spine at the posterior angle of the bone. Also as in *Lates*, there is a single, large spine on the posterodorsal margin of the operculum in *Eolates*. Ornamentation of the cleithrum and on the first infraorbital bone (lachrymal) is similar in *Eolates* and *Lates*, but the phylogenetic importance of these latter characters is probably not great.

Regrettably, little detailed information can be obtained about the morphology of the neurocranium in *Eolates*. Sorbini (1973) gives no description of the posterior orbital region of the skull, presumably because in his material, as in that of the BMNH, this area of the head is either crushed or obscured by other bones overlying it. Thus it is impossible to determine what type of pterosphenoid pedicle and internal jugular bridge is present.

The ethmoid region is generally well preserved, and resembles that found in members of the subgenus *Lates* (see p. 19 above).

In a few *E. gracilis* specimens the posttemporal is well preserved; it seems to show the slightly bullate outer surface that, in living centropomids, is associated with the insertion point of a swimbladder-posttemporal ligament (see p. 41 above), a derived feature characterizing members of the subfamily Latinae (see above, p. 66).

In brief, *Eolates* (as represented by *E. gracilis*) is clearly a member of the subfamily Latinae and shares at least one derived character (the ventral preopercular spines) with the genus *Lates* (see p. 31). *Eolates* differs from *Lates* in having only one series of lateral line scales on the caudal fin (presumed in this context to be a primitive feature, see p. 48 above), and in having a caudal fin skeleton that is primitive in relation to this skeleton in *Lates* (see above, p. 66). A third intergeneric difference is in the less deeply indented dorsal fin of *Eolates*, a feature with which may be correlated the equal spacing between the 'last' (i.e. shortest) spine of the anterior part of the fin and the longer 'first' spine of the fin's posterior half. This character too should be considered a plesiomorph one because a deeply divided fin is a basal condition in the centropomid trend leading towards completely separate first and second dorsal fins (see above, pp. 46 and 65).

All the features discussed so far indicate that *Eolates* should be considered more primitive than *Lates*. In phyletic terms it should be ranked as the plesiomorph sister group of that taxon. The relationship of *Eolates* within the subfamily Latinae is, therefore, best indicated by uniting *Eolates* with *Lates* in a single tribe (Latini, new tribe) which would then become the sister taxon of the tribe containing only the genus *Psammoperca* (tribe Psammopercini nov.).

Sorbini (1973) also recognizes the affinity of *Lates* and *Eolates*, but he would regard the relationship as an ancestor-descendant one (op. cit.: 41) rather than that of recent shared common ancestry as is proposed here.

Sorbini's claim that '... The living marine species *L. calcarifer* presents the greatest relationship to fossil Tertiary species, which lived in a similar habitat' (Sorbini, 1973: 41) certainly cannot be substantiated by the meristic and morphological data available from these fossils. For example, as interspecific similarities between *L. calcarifer* and *E. gracilis* Sorbini lists (op. cit.: 36) '... disposizione delle vertebre, n. raggi branchiostegi, habitat...'. The habitat is similar, but what importance can be attached to this feature in a family with several euryhaline species? The arrangement of the vertebrae in *Eolates* is like that in several *Lates* species, while the reference to the number of branchiostegal rays is, I presume, a *lapsus* for 'spine branchiali'. *Eolates* has either seven or eight branchiostegal rays (there are seven in all other centropomids; see above, p. 70), but nine gill rakers (the same number as *L. calcarifer*). However, a low gill raker count (8–12) is common to several *Lates* species, and is apparently the primitive state for the family as a whole.

BIOGEOGRAPHY

The contemporary world distribution of the Centropomidae (Fig. 36) strongly suggests a Tethyan distribution for the common ancestor of its two subfamilies, the

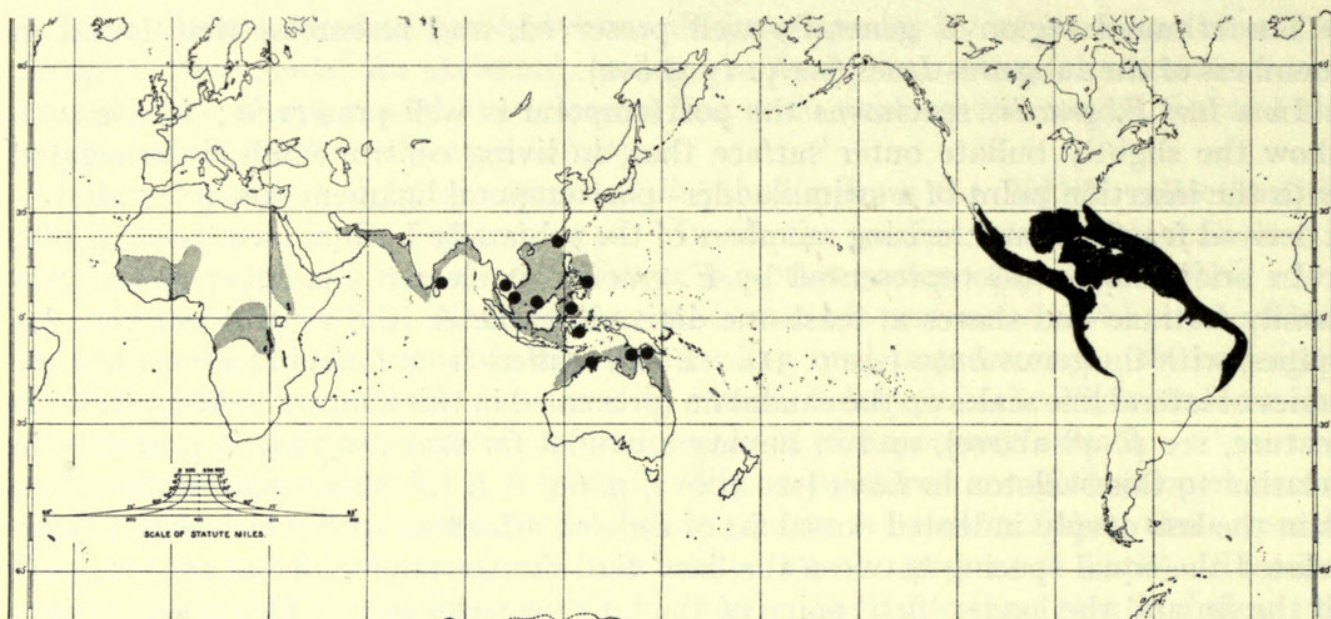


FIG. 36. World distribution of extant species of Centropomidae. Stippled areas : *Lates* species (outside Africa = *L. calcarifer*). Black spots : *Psammoperca* species (probably only one, *P. waigiensis*). Black area ; *Centropomus* species.

Centropominae (America) and the Latinae (Mediterranean, African freshwaters and Asia).

The Centropominae, on this hypothesis, have evolved in the tropical New World, probably in estuarine and marine habitats, and the Latinae principally in African freshwater habitats. There is, however, a major dichotomy in the Latinae, between the tribes Latini and Psammopercini, which must have taken place before the Latini invaded Africa.

As evidenced by various European fossil species (see above, pp. 68–71, and Sorbini, 1973) and by the wide dispersal of *Lates calcarifer* (see p. 12), the Latini were and still are successful coastal fishes. The greater diversification of the tribe in African freshwaters can probably be attributed to the greater opportunities for speciation provided by the developing tropical lakes and river systems of later Tertiary and Quaternary Africa. (For a summary of these historical factors see Beadle, 1974.) It will be recalled that there are seven extant and at least three extinct *Lates* species in Africa, compared with the single extant (*L. calcarifer*) and three extinct marine or estuarine species (see above, p. 69 ; also Sorbini, 1973 ; Greenwood, 1974 ; Greenwood & Howes, 1975).

There are, of course, at least nine species of *Centropomus* (Centropominae) all of which are essentially marine species (although some freely enter freshwater ; Meek & Hildebrand, 1925). Trans-isthmian isolation could account for four of these species (Fraser, 1968) but there still remain the other five species to contrast with the single marine *Lates* species (*L. calcarifer*) of the Indo-Pacific region. The causal factors involved in this aspect of *Centropomus* speciation are not apparent.

It is interesting to compare the morphological radiation undergone by the Centropominae and Latinae, and to notice the marked parallelism apparent in the two

groups. For example, in both subfamilies there are trends of specialization leading to the reduction and loss of the pterosphene pedicle and internal jugular bridge (p. 63), to elongation of the skull through differential lengthening of the ethmoid region (p. 62), to an increase in the number of gill rakers on the first gill arch, to a reduction in the number of supralamellar tooth plates (p. 64), and towards the division and then separation of a primitively continuous dorsal fin (see p. 66). So similar are all the features involved in any one of these trends that one can eliminate any possibility of convergence. The similarities must reflect shared genotypic factors stemming from common ancestry.

The absence of *Lates* (or some related latine fish) from the present-day Mediterranean Sea may, as Sorbini (1973:40) suggests, be due to climatic changes adversely affecting the one or more species that were present in the Mediterranean basin during parts of the Tertiary (Sorbini, op. cit., especially text-fig. 10). Increasing salinity in the developing Mediterranean may also have had its effect on local populations.

During the Eocene and Miocene, species of *Lates* were also present in Africa (Sorbini, 1973; Greenwood, 1974). The Eocene fishes from the Fayum in Egypt may have been estuarine and marine (Weiler, 1929), as may have been the Miocene species from Tunisia (Greenwood, 1973). However, Miocene records of *Lates* from the equatorial regions of Lake Victoria (Greenwood, 1951) and Lake Albert (Greenwood & Howes, 1975) show that some latine species had adjusted fully to freshwater environments, and that enough time had elapsed since the first invasion for latine species to have reached areas some 3750 km inland from the Mediterranean coast.

Like all other fossil Latinae from Africa, the Miocene species are referred to *Lates* solely on the overall similarity between the preserved fossil bones and their counterparts in extant *Lates* species. Such critical features as the nature of the lateral line scales on the caudal fin and the morphology of the posttemporal bone are unknown for any one of them. One Miocene species, *L. karungae* Greenwood, 1951, from Rusinga Island, Lake Victoria, is represented by only a few vertebrae; the specific diagnostic features for this taxon relate to the morphology of the third vertebra (Greenwood, 1951). The other taxon, *L. rhachirhynchus*, from the Lake Albert-Lake Edward region of Zaire is better represented by numerous skeletal parts (Greenwood & Howes, 1975). It differs from all other *Lates* species in several features, many of which can be considered as derived, and one of which (vertebral proportions) is shared with certain members of the endemic subgenus *Luciolates* from Lake Tanganyika (see p. 43 above, and Greenwood & Howes, op. cit.). Even though it is impossible to identify specifically the *Lates* remains from the Miocene and Pliocene deposits in North Africa and Egypt, *L. rhachirhynchus* is morphologically quite distinct from those taxa.

Thus, one may conclude from this situation either that more than one taxon invaded Africa or that, by Miocene times, the population of *Lates* in the Lake Albert-Lake Edward region had undergone marked morphological differentiation, presumably in isolation from its parental stock. The same arguments could be applied to *L. karungae* although in this instance there is less evidence for the extent to which the morphological differentiation had progressed.

Sorbini (1973) postulated certain time sequences and migration routes to explain the present-day distribution of *Lates* species in Africa. Basically the problem Sorbini sets out to explain is the widespread occurrence of one species, *L. niloticus*, in the Nile, Niger, Zaire, and Senegal river systems, and in Lakes Rudolf, Albert and Chad, in contrast to the occurrence of four endemic species (one supposedly a distinct genus) in Lake Tanganyika. He notes the former occurrence of *Lates* in other lakes (Edward and Victoria) but is not concerned with the factors that led to these local extinctions, and neither does he take into account the endemic species that coexist with *L. niloticus* in Lakes Rudolf and Albert.

There are two basic tenets in Sorbini's hypothesis, first that the various invasions he postulates originated in Egypt, and second that fossils identified as *L. niloticus* are indeed representatives of that species. As I have discussed above the latter assumption is not necessarily acceptable, and neither can I find any *a priori* grounds for postulating repeated and temporally extended invasions from a single area (in this argument, Egypt).

That a species of *Lates* had reached the regions of Lake Victoria and Lake Albert–Lake Edward by Miocene times is not disputed (see above), and Sorbini's argument for the contemporaneous presence of a *Lates* species in the Lake Tanganyika basin is also acceptable. Why, then, should *Lates* not have occurred in other Miocene rivers and water bodies, environmental conditions, of course, permitting such colonization? To the best of my knowledge there is no evidence to show that suitable conditions were confined to the regions from which Miocene fossils have been recovered. Thus I find it difficult to understand why, in order to explain the present distribution of *L. niloticus*, Sorbini should postulate two invasions, each following different routes, but both originating from Egypt during the Pliocene and continuing through the Pleistocene. Presumably a major reason for putting forward this hypothesis is the fact the fossils identified as *L. niloticus* are first recorded from the Pliocene of Egypt, thereby implying the origin of that species in Egypt at a later date than the one at which another species (*L. karungae*) was already present in the Lake Victoria area (and, had he known it, a second species *L. rhachirhinchus* was present in the area of Lake Albert–Lake Edward; Greenwood & Howes, 1975).

In view of the known distribution for Miocene *Lates* and because of the uncertainties associated with the specific identification of most fossil *Lates* remains, a simpler hypothesis can be made, viz. :

At some stage prior to the late Eocene a species of *Lates* invaded Africa, possibly through more than one entry point, but almost certainly from the north. In the course of time this species gradually dispersed through the various river systems with some isolated populations evolving into distinct species now extinct (e.g. *L. rhachirhinchus* and *L. karungae*, possibly also *L. fajumensis*), and others or their descendants (like the endemic species of Lake Tanganyika) still surviving. A little modified descendant of the original invader, the species now recognized as *L. niloticus*, continued to spread (by such means as river capture or lake extension) until it came to have its present distribution. The *L. niloticus*-like fossils of Pleistocene times (Greenwood, 1959, 1974; Sorbini, 1973) stand witness to a much wider area

for the distribution of *Lates* and even probably for the species *L. niloticus* (but of that point we must remain uncertain).

It is unnecessary here to discuss the history of *L. niloticus* in lakes such as Rudolf and Albert which may, at some time in their histories, have dried out completely, and which have had complex relationships with the River Nile and other lakes (see discussions in Greenwood, 1959, 1974; also Beadle, 1974). There is still, however, the problem of the endemic *Lates* species in the two lakes, *L. longispinis* in Lake Rudolf and *L. macrophthalmus* in Lake Albert. In brief, on morphological criteria (p. 12) these species are apparently more closely related to one another than either is to *L. niloticus*, the species from which each was supposed to have been derived at some time during the Pleistocene (Worthington, 1932; Holden, 1967). On the evidence currently available it is impossible to determine whether *L. longispinis* and *L. macrophthalmus* do in fact represent survivors of a distinct lineage or if, as Worthington (1932) postulated, they are offshoots of earlier *L. niloticus* populations that once inhabited the two lakes (see discussions on pp. 13 and 14).

DIAGNOSES FOR THE CENTROPOMIDAE, ITS SUBFAMILIES,
GENERA AND SUBGENERA

CENTROPOMIDAE Poey, 1868

Poey, F., 1868, *Repertorio Fisico-Natural de Cuba*, 5, no. 2: 280. (See also Gill, T., 1883, *Proc. U.S. natn. Mus.*, 5: 484-485).

TYPE GENUS: *Centropomus* Lacépède, 1802.

DIAGNOSIS. Percoid fishes, some attaining a large size (up to 2 m), with the neural spine of the second vertebra markedly expanded in an anteroposterior

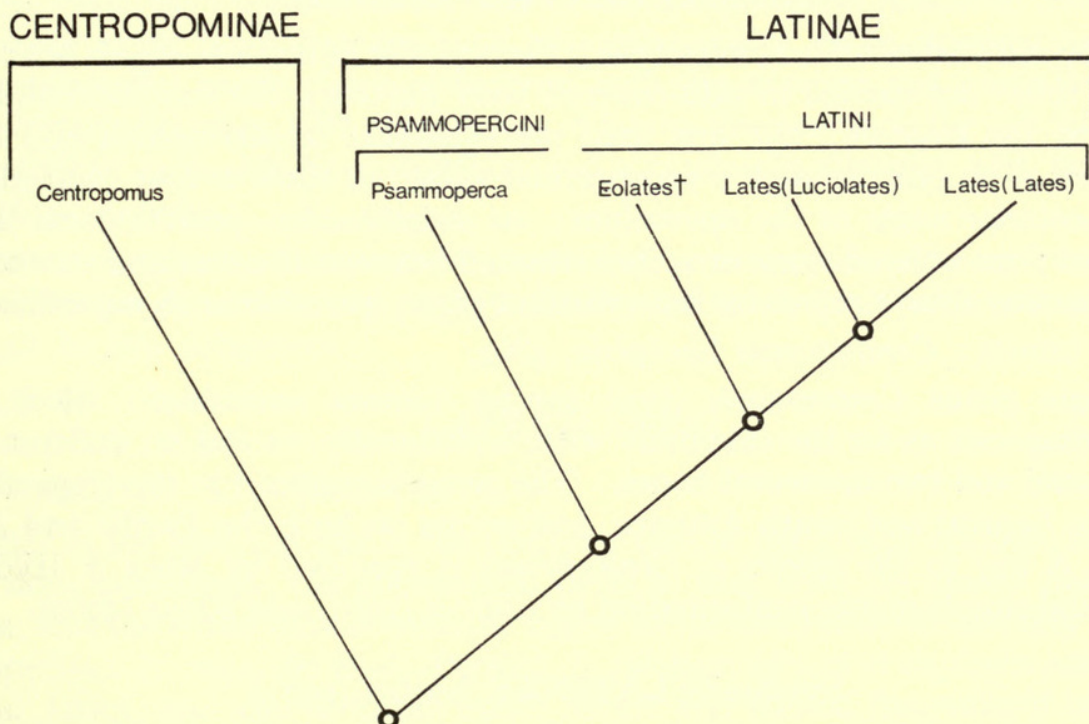


FIG. 37. Cladogram to illustrate phyletic relationships within the Centropomidae.

direction, and the pored scales of the body lateral line continued onto the caudal fin, reaching the posterior margin of that fin in all but one species. Twenty-four or 25 vertebrae (including the fused first ural and preural centra of the caudal skeleton); pleural ribs associated with parapophyses except on the first three to five rib-bearing vertebrae (the first two vertebrae of the column are without ribs); 3 predorsal bones. Dorsal fin either deeply divided, the first part entirely spinous (7 or 8 spines), the second of one spine and 8–11 branched rays, or the two parts of the fin separated by a distinct gap; anal fin with 3 spinous and 6–9 branched rays; caudal fin with 17 principal rays, its posterior margin rounded, truncate or forked. Scales ctenoid, small to moderate in size, dorsally not extending forward on to the head beyond the level of the midpoint of the eye (usually only to the level of the posterior margin of the orbit) but present on the cheek and operculum; scaly sheath at the base of the anal and soft dorsal fins, but squamation extending onto all fin membranes (including that of the caudal). No scales on the maxilla; a small supramaxilla present. Teeth on the premaxilla, dentary, vomer, palatine and, in most species, the ectopterygoid; teeth absent, except in *Psammoperca*, from the glossohyal. Jaw teeth generally small, viliform or conical, and arranged in several rows. Pterosphonoid pedicle and internal jugular bridge present in all but three or four species, although variously developed; frontoparietal crests present. Seven branchiostegal rays. Pseudobranch present. About 20 extant species from marine, estuarine and freshwater habitats in the tropical New World (Atlantic and Pacific coasts), tropical Africa (predominantly fresh- or brackish water species), and from Indo-Pacific coastal waters. Six extinct species (some from Europe), the earliest being from the Eocene of Monte Bolca.

Subfamily **CENTROPOMINAE**

Centropomid fishes with 24 vertebrae; the cephalic lateral line canals not enclosed in bony tubes but carried in skin-covered bony gutters; the supraoccipital barely separating the frontals; the first anal pterygiophore hypertrophied and inclined backwards at an oblique angle; no opercular spine but three or four enlarged spines at the posterior angle of the operculum; no swimbladder—posttemporal ligament developed; no isolated spine or spines situated between the first and second dorsal fins (these fins always separated by a distinct gap); pseudobranch superficial.

TYPE GENUS: *Centropomus* Lacépède, 1802.

A single genus *Centropomus* (type species *Sciaena undecimalis* Bloch, 1792), generic diagnosis as for the subfamily with, additionally, caudal fin skeleton having three epural and two uroneural bones. The genus is confined to the tropical waters of North, Central and South America, and occurs on both the Pacific and Atlantic coasts. A key to the species of *Centropomus* is provided by Meek & Hildebrand (1925), and supplementary information by Chávez (1961) and Rivas (1962).

Subfamily **LATINAE** Jordan (1923)

Centropomid fishes with 25 vertebrae; the cephalic lateral line enclosed in bony tubes; the supraoccipital extending far forward between the frontals; the first

anal pterygiophore not hypertrophied, and inclined backwards at only a slight angle ; a single well-developed opercular spine and a single, enlarged spine at the posterior angle of the preoperculum ; a stout ligament connecting the swimbladder with the posttemporal (which is itself modified to receive the ligament) ; dorsal fin deeply indented or separated into two fins (between which there are one or two isolated spines) ; pseudobranch covered.

TYPE GENUS : *Lates* Cuvier & Valenciennes, 1828.

Three genera, two extant and one extinct.

The two extant genera are :

***PSAMMOPERCA* Richardson, 1844**

TYPE SPECIES : *Labrax waigiensis* C. & V., 1828.

Latine fishes with : a smooth horizontal limb to the preoperculum, a basihyoid tooth plate, supralamellar tooth plates present on the outer face of the first four gill arches only ; with a single series of lateral line scales on the caudal fin, with the nostrils of each side widely separated, and a caudal fin skeleton in which there are two epural bones and a single uroneural.

Probably only one species, *P. waigiensis* (a second nominal species *P. macroptera* Günther, 1859, is almost certainly a synonym), widely distributed in the coastal waters of the Indo-Pacific.

***LATES* C. & V., 1828**

TYPE SPECIES : *Perca nilotica*, L., 1758.

Latine fishes with the horizontal limb of the preoperculum produced into three or four (rarely more) large, flattened and triangular spines, no basihyoid tooth plate but supralamellar tooth plates present on both the anterior and posterior faces of the first four gill arches, with three series of lateral line scales on the caudal fin, with the nostrils of each side close together, and a caudal fin skeleton with two epurals and two uroneurals.

Eight extant species (seven of which are African and confined to freshwaters, and one marine or estuarine and widely distributed in Indo-Pacific coastal waters) arranged in two subgenera :

LATES (LATES)

TYPE SPECIES : *L. niloticus* (L.).

Species of the genus in which the posterior face of the lateral ethmoid has only a slight slope posteriorly, the dorsolateral parts of that bone are almost horizontally aligned, and the entire ethmovomerine region of the skull is not noticeably elongate. Four species : *L. calcarifer* (Indo-Pacific), *L. niloticus* (rivers of northern and western tropical Africa, and also in Lakes Chad, Albert and Rudolf [introduced into Lakes Victoria and Kioga]), *L. macrophthalmus* (Lake Albert only) and *L. longispinis* (Lake Rudolf only).

LATES (LUCIOLATES)

TYPE SPECIES : *Luciolates stappersi* Boulenger, 1914.

Species of *Lates* having a characteristically shaped and elongate ethmovomerine skull region in which the posterior face of the lateral ethmoid slopes backwards at a pronounced angle, and the dorsolateral aspects of that bone are directed ventrally at a steep angle. Four species, all endemic to Lake Tanganyika : *L. angustifrons*, *L. microlepis*, *L. mariae* and *L. stappersi*.

The single extinct genus is :

EOLATES Sorbini, 1970

TYPE SPECIES : *Lates gracilis* Agassiz, 1883.

See Sorbini, 1973, for full description, synonymies, etc.

Eolates, with one species (*E. gracilis*) and possibly a second, *E. macrurus* (Ag.), 1833, is known only from the lower Eocene deposits of Monte Bolca, northern Italy.

Eolates differs from *Lates* in the structure of its caudal fin skeleton (three epurals ; a well-developed neural spine on the second preural vertebrae), in having only a single series of lateral line scales (the median one) on the caudal fin, and in having a less deeply indented dorsal fin (see p. 70 above).

The phyletic relationships of *Eolates* within the Latinae are discussed on p. 71, where it is suggested that *Lates* and *Eolates* are sister taxa and should be placed in the Tribe Latini nov., the sister group of the Tribe Psammoperkini nov. (a taxon containing only the genus *Psammoperca*).

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