Evolution of the premaxillary in the primitive fossil actinopterygians

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Poplin C. & Lund R. 1997. — Evolution of the premaxillary in the primitive fossil actinopterygians. *Geodiversitas* 19 (3) : 557-565.

ABSTRACT

The different conditions of the premaxillary in primitive actinopterygians are individualized, or fused to adjacent bones. Their dental field can also be divided and fused to neighbouring bones, the premaxillaries may be separated across the midline, or, finally, they have disappeared. This separation and absence can result in a rostral notch observed in rhadinichthyids, and presumed in other groups such as the redfieldiiformes. It can be suggested that the plesiomorphous gnathostome dermal skeletal condition is micromeric, that the primitive actinopterygian larval snout condition derived from that condition was mesomeric, and that heterochronic changes during early actinopterygian evolution gave rise during development (1) of mesomeric adult primitive actinopterygians through neoteny, (2) of macromeric adult primitive actinopterygians through fusions of bones, (3) to the condition of actinopterygians lacking a premaxillary through its loss. The neopterygian condition may have arisen through paedomorphosis from either mesomeric primitive fossil actinopterygians, or directly by heterochrony from the larval primitive condition.

KEY WORDS
Vertebrata,
Actinopterygii,
comparative anatomy,
evolutionary trend,
premaxillary,
dermal snout.

RÉSUMÉ

Les différentes dispositions du prémaxillaire chez les actinoptérygiens primitifs sont : différencié ou fusionné à des os adjacents, le territoire dentaire peut être divisé et fusionné à des os voisins, les deux prémaxillaires être séparés sans contact l'un avec l'autre, enfin le prémaxillaire peut avoir disparu. Cette séparation ou cette absence se traduisent le plus souvent par une lacune osseuse rostrale observée chez des rhadinichthyidés et supposée dans plusieurs autres groupes dont les redfieldiiformes. Il est suggéré que la disposition plésiomorphe du squelette dermique des gnathostomes est micromérique, que la disposition larvaire du museau des actinoptérygiens dérivée de cette disposition plésiomorphe était mésomérique et que les changements hétérochroniques au début de l'évolution des actinoptérygiens ont donné pendant le développement, (1) par néoténie, des actinoptérygiens primitifs adultes mésomériques, (2) par des fusions osseuses, des actinoptérygiens primitifs adultes macromériques, (3) par disparition, des formes dépourvues de prémaxillaire. Les néoptérygiens seraient issus par pédomorphose, soit des actinoptérygiens primitifs fossiles mésomériques, soit directement, par hétérochronie de la disposition primitive larvaire.

MOTS CLÉS
Vertebrata,
Actinopterygii,
anatomie comparée,
tendance évolutive,
prémaxillaire,
museau dermique.

INTRODUCTION

The snout in teleostome fishes is a region of the dermal skull concentrating elements sensitive to adaptations and evolution, as it bears teeth, narial openings and the anteriormost part of the lateral sensory system. The variations of its anatomy have been often dealt with in the past (Westoll 1937; Pehrson 1947, 1958; Gardiner 1963; Wenz 1967; Pearson & Westoll 1972; Patterson 1975; Pearson 1982; Schaeffer 1984; Long 1988). More recently the evolutionary implications of some of its bony units in lower actinopterygians were discussed (Poplin & Lund 1995). In the present work, analysis is focussed on the area of the premaxillary among the dermal bones of the snout which underwent the most numerous modifications of any area of skull bones. Therefore, it is potentially one of the most significant complexes of bones and lateral line canals for phylogenetic purposes in lower actinopterygians. Because of difficulties in observation and preservation in fossil fishes, accurate descriptions and reconstructions of the snout are rather rare so that we refer here to the best known taxa, even if reappraisials of them should be eventually desirable.

THE DIFFERENT STATES OF THE PREMAXILLARY IN LOWER ACTINOPTERYGIANS

In order to avoid confusion owing to the many bone nomenclatures used by authors, which somehow darkened the understanding of the dermal snout evolution in the past, the "premaxillary" is defined here as the most anterior paired upper anamestic toothbearing bone of the rim of the mouth. When it is fused to other bony territories, compound names are used (Poplin & Lund 1995). As a whole, the five following states of the premaxillary have been observed among primitive actinopterygians.

1. Individualized typical premaxillae are rather rare in lower fossil actinopterygians: for instance, in Lower Carboniferous, fishes from Bear Gulch (Montana, USA), the Triassic *Pteronisculus* (Nielsen 1942), *Perleidus* (Fig. 1A; Lehman 1952). According to Hutchinson (1978), it is also present in monophyletic lineages such as the Triassic Brookvaliidae and Schizurichthyidae. In recent forms, separate premaxillaries are present in larval *Polypterus* (Fig. 1B; Pehrson 1947, 1958) and in all the neopterygians, where they may even be larger than the maxillae (Fig. 1C).

2. More often, in lower fossil actinopterygians, the premaxillary is fused with adjacent bones resulting in compound bony units such as "rostro-premaxillo-antorbitals", "rostro-premaxillaries" and "antorbito-premaxillaries" (Fig. 1D, E; Poplin & Lund 1995). In adult *Polypterus* the

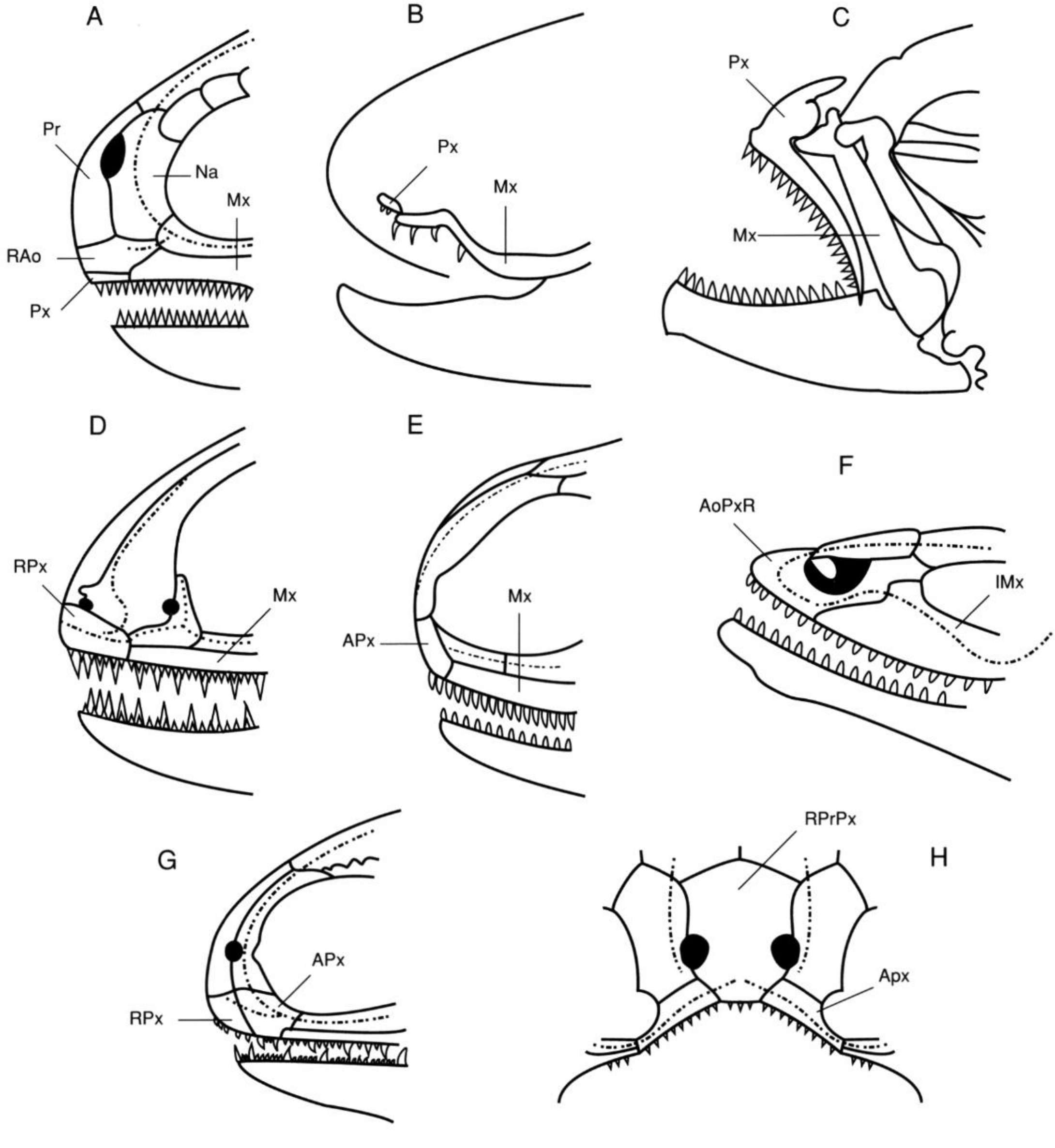

FIG. 1. — Dermal snouts: **A**-**G**, left lateral view; **H**, front view. **A**, *Perleidus piveteaui* (after Lehman 1952, fig. 86); **B**, *Polypterus*, 9.6 mm larva (after Pehrson 1958, fig. 8); **C**, *Pomatomus saltatrix* (after Gregory 1933, fig. 177); **D**, *Birgeria groenlandica* (after Nielsen 1949, fig. 69); **E**, *Moythomasia nitida* (after Jessen 1968, fig. 1); **F**, *Polypterus* adult (after Daget 1958, fig. 1791); **G**, *Watsonichthys pectinatus* (after Gardiner 1963, fig. 1); **H**, *Howqualepis rostridens* (after Long 1988, fig. 14B). **APx**, antorbito-premaxillary; **AoPxR**, antorbito-premaxillo-rostral; **IMx**, infraorbito-maxillary; **Mx**, maxillary; **Na**, nasal; **Px**, premaxillary; **Pr**, postrostral; **RAo**, rostro-antorbital; **RPx**, rostro-premaxillary; **RPrPx**, rostro-postrostro-premaxillary.

premaxillary is fused to the lateral rostral and to the antorbital (Fig. 1F; Pehrson 1947, 1958; Lehman 1958: 2092).

3. The territory of the premaxillary dental field may also be divided into two units that are fused to neighbouring bones (Moy-Thomas 1934; Ten Cate 1985). This is the case for instance in *Watsonichthys pectinatus* (Fig. 1G) which shows an antorbito-premaxillary together with a rostro-premaxillary. The Devonian *Moythomasia durgaringa* and *Howqualepis rostridens* (*cf.* Gardiner 1984; Long 1988) are more complex and questionable cases (Fig. 1H); their anterior marginal teeth are borne by three bones: paired antorbito-premaxillaries (= Gardiner's and Long's "premaxillaries") and a median rostro-postrostro-premaxillary (= "dentigerous rostro-postrostral"). According to our interpretation, the territories of the right and left premaxillaries (or their dental fields) are divided into four units: the median ones are fused to the single rostro-postrostral and the lateral ones are fused to the paired antorbitals (Poplin & Lund 1995).

4. In some cases, such as in some Bear Gulch taxa, both premaxillaries are so weak and so loose that they are not in contact with each other. This situation results in a small median rostral notch quite like that described below.

5. The last state of the premaxillary is encountered in a number of primitive fossil actinopterygians: its disappearance revealed by the complete absence of the characteristic features of its territory, *i.e.* anamestic and presence of anterior marginal teeth (Poplin & Lund 1995).

Such a lack has been sometimes observed, or suspected, in the past. Westoll (1937) and later Heyler (1969) noticed that the Aeduellidae have no premaxillaries. The Redfieldiiformes gave rise to a small disagreement on this respect between Hutchinson (1973, 1978) and Schaeffer (1967, 1984): the former thinks that the lack of a premaxillary characterizes only the family Redfieldiidae, and the latter claims that it is a feature of the whole order. More recently the absence of this bone has been directly observed in Lower Carboniferous paleoniscoids from Bear Gulch (Montana, USA; Poplin & Lund 1995).

The absence of the premaxillary results either in the anterior development of the maxillaries which then meet each other above the mouth (e.g. *Aeduella*, Fig. 2C), or in the snout skeleton having a median notch above the mandibular symphysis. Such a notch is observed in Lower Carboniferous rhadinichthyids (Fig. 2A, B) like those from Montana (Poplin & Lund 1995) and Scotland (Moy-Thomas & Dyne 1938). We suspect the presence of this notch in many other paleoniscoid forms which lack the characteristic features of the premaxillary and show, in side view, a typically protruding snout above the aperture of the mouth: for instance *Palaeoniscus* (Fig 2D; Aldinger 1937), *Cycloptychius*, *Elonichthys* (Moy-Thomas & Dyne 1938), *Boreosomus* (Nielsen 1942; Lehman 1952), *Dicellopyge* (Brough 1931).

Schaeffer's description suggests that the Redfieldiidae (Fig. 2E) probably also had this anterior notch (1967: 307, 308): "As the mandibles are about the same length as the infraorbital ramus of the maxilla, the toothlike denticles along the ventral margin of the rostral and the antorbital could not have functioned in seizing prey. Furthermore, it has not been possible to reconstruct [...] the snout [...] in a way that would permit the rostral teeth to meet the mandibular ones, even if the lower jaws were actually longer. Part of the space between antorbitals must have been occupied by the mandible when the mouth was completely closed, but we have been unable to eliminate the resulting space between the ventral margin of the rostral and the mandibular symphysis." The presence of an anterior notch is confirmed, according to us, by the characteristic protruding snout in side view, as explained above.

In this peculiar redfieldiid snout, covered with a quantity of small dermal tubercles, what could be the function of an anterior notch? First it could cause a smaller aperture of the mouth and, thus, increase the inhaling strength during expansion of the mouth: this would facilitate

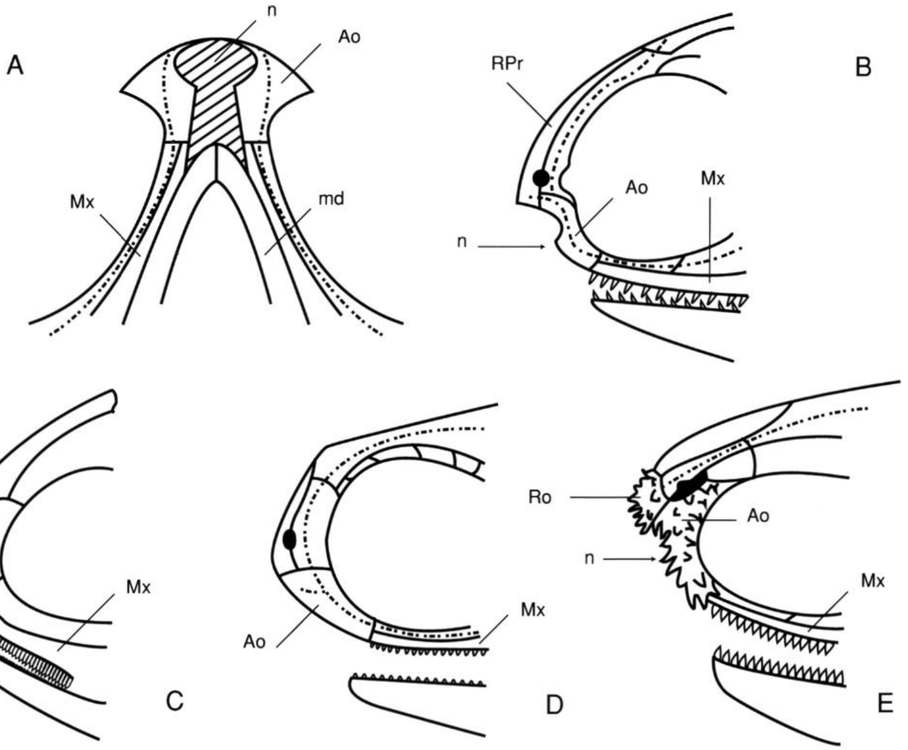

FIG. 2. — Dermal snouts: **A**, ventral view; **B**-**E**, left lateral view. **A**, **B**, Rhadinichthyid from Bear Gulch (after Lund & Poplin in prep.); **C**, *Aeduella* (after Heyler 1969, fig. 92); **D**, *Palaeoniscus freieslebeni* (after Aldinger 1937, fig. 25B); **E**, *Cionichthys greeni* (after Schaeffer 1967, fig. 7). **Ao**, antorbital; **Mx**, maxillary; **md**, mandible; **n**, notch; **Ro**, rostral; **RPr**, rostro-postrostral.

suction in a benthic feeding mode (Lund *et al.* 1985). Indeed, this combination of an armored projecting snout and the notch would permit these fishes to root around (like hogs), using the denticles to stir up the sediment and the notch to facilitate suction upon those prey items that were scared out of their hiding places. Moreover, Schaeffer and Hutchinson emphasize that these fishes could have had a thick fleshy lip supported by these denticles and overhanging the mouth: this lip helped them to feed at the sediment-water interface, somewhat like the protrusive mouth of recent teleosts. In this hypothesis could an anterior notch have been linked to a very short appendage like a tiny trunk? Like the protrusive premaxillae in recent teleosteans, this would increase the buccal volume during abduction of the lower jaw, as well as just after the food was engulfed and the mouth was closed again (Alexander 1967).

The existence of this anterior notch raises the question of the anatomy of the underlying endocranial and visceral regions: ethmoidal endoskeleton and vomers, as well as oral valves, if there were any in these fishes. In the total absence of data it is difficult to answer.

DISCUSSION ABOUT THE PRIMITIVE STATE AND FURTHER EVOLUTIONARY TRENDS OF THE ACTINOPTERYGIAN PREMAXILLARY

The anatomical variety of the premaxillary in primitive fossil actinopterygians, briefly described above, leads to two fundamental questions:
– What was the condition of the premaxillary, in the ancestral morphotype of actinopterygians?
– What does this variety indicate about the relationships of the main actinopterygian lineages?

In the past the three following hypotheses (absent, fused to other bones, present) have been proposed concerning the ancestral condition of the premaxillary in actinopterygians.

HYPOTHESIS 1

Absence of the premaxillary: Westoll (1937) was among the first to speculate about the fate of the premaxillary. He noticed that the holostean and teleostean premaxillary was quite complex and different from what was known of paleoniscoids at his time. Therefore he thought that the very first actinopterygians had no premaxillary and he proposed four schemes to explain the existence of a premaxillary in the upper actinopterygians: (1) it is a neoformation; (2) it results from a fragmentation of the paleoniscoid rostral; (3) the primitive maxillary has been split into maxillary and premaxillary; (4) or the lineages which gave rise to the upper actinopterygians have been separated very early from the paleoniscoid ones, which implies that premaxillaries developed independantly in both groups. Westoll considered this last hypothesis as improbable. The first of Westoll's suggestions can now be discarded since all other osteichthyan groups share the plesiomorphous occurrence of a premaxillary. Westoll's other schemes are early previews of the subsequent hypotheses stated below (premaxillary produced by fragmentation of compound bones, very early separation of the lineages leading to paleoniscoids and neopterygians, parallelism of eventual structures).

HYPOTHESIS 2

Presence of the premaxillary as a compound bone, macromeric snout: many authors, such as Pehrson (1947, 1958), Gardiner (1963, 1984) and Jessen (1968) suggested that a premaxillary was present in the first actinopterygians but as a rostro-premaxillo-antorbital. This view, based on the observation that this compound bone is present in the most primitive Devonian forms and in the Recent *Polypterus*, is part of the more generalized hypothesis of a macromeric primitive pattern of the dermal snout (Gardiner 1963; Patterson 1975). Later in actinopterygian history, different and successive splittings of the rostro-premaxillo-antorbital would have led to the various dispositions observed in paleoniscoids and to the mesomeric snout anatomy of neopterygians (Fig. 3).

HYPOTHESIS 3

Presence of an individualized premaxillary: mesomeric snout evolving by fragmentations. The ancestral actinopterygian morphotype *has* indeed independant premaxillaries in a mesomeric snout (Pearson 1982; Schaeffer 1984; Long 1988; Gardiner & Schaeffer 1989). This is more consistent with the mesomeric snout disposition of sarcopterygians and of the larval *Polypterus* than with Westoll's first three schemes or with that of a macromeric primitive pattern. We note that this hypothesis fits better with the more recent data about the pattern of occurrence of separate premaxillaries among the paleoniscoids.

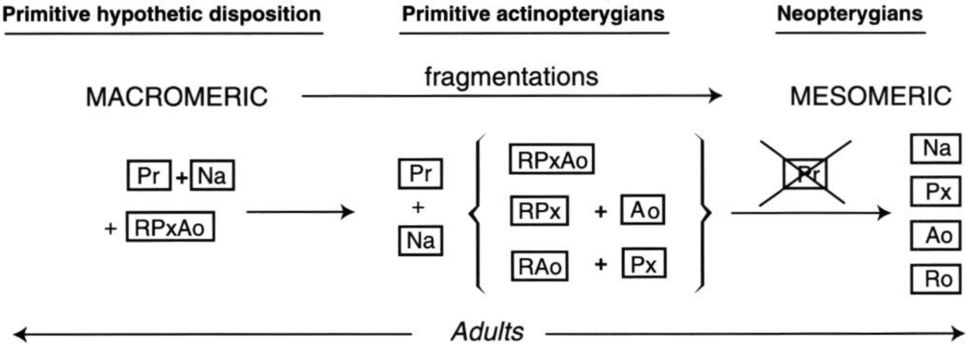

FIG. 3. — Hypothesis about the evolution of the dermal snout after Pehrson (1947, 1958), Gardiner (1963, 1984), Jessen (1968), and others (see text). **Ao**, antorbital; **APx**, antorbito-premaxillary; **Na**, nasal; **Px**, premaxillary; **Pr**, postrostral; **RAo**, rostro-antorbital; **Ro**, rostral; **RPx**, rostro-premaxillary; **RPxAo**, rostro-premaxillo-antorbital; **RPr**, rostro-postrostral.

The lack of premaxillary is better explained as a mere lack of its territory in the embryo rather than as an involution during later development (Poplin & Lund 1995). In order to specify this third hypothesis, Schaeffer (1984: 5) adds that "[...] the pattern in the 24 mm *Polypterus* represents the primitive actinopterygian larval condition, whereas that in the mature *Polypterus* [...] may be regarded as the primitive adult condition."

Therefore, based on this view, the third hypothesis is completed as follows when we add the recent data (Fig. 4). The primitive larval pattern of the snout in actinopterygians was mesomeric with separate postrostrals, rostrals, nasals, premaxillaries and antorbitals. Different processes during development and maturation led to the various dispositions observed in the primitive fossil adult actinopterygians: (1) fusions leading to the variety of macromeric snouts observed in primitive fossil actinopterygians; (2) precocious disappearances during development of its territory resulting in the absence of premaxillary; and (3) neoteny maintaining the larval pattern in adults (Jollie 1969). The neopterygian adult pattern (also characterized by the absence or fusion of a postrostral) sprung after paedomorphosis either from already known lineages of mesomeric primitive actinopterygians, or directly from the primitive hypothetic larval pattern.

CONCLUSION

We propose the following hypothesis about the mechanisms which gave rise to the main patterns of the dermal snout in actinopterygians: the primitive mesomeric snout evolved and diversified either through heterochronous processes, such as neoteny and paedomorphosis, either through fusions or disappearances. This hypothesis leads to the following considerations.
– The ancestral larval morphotype of the acti-

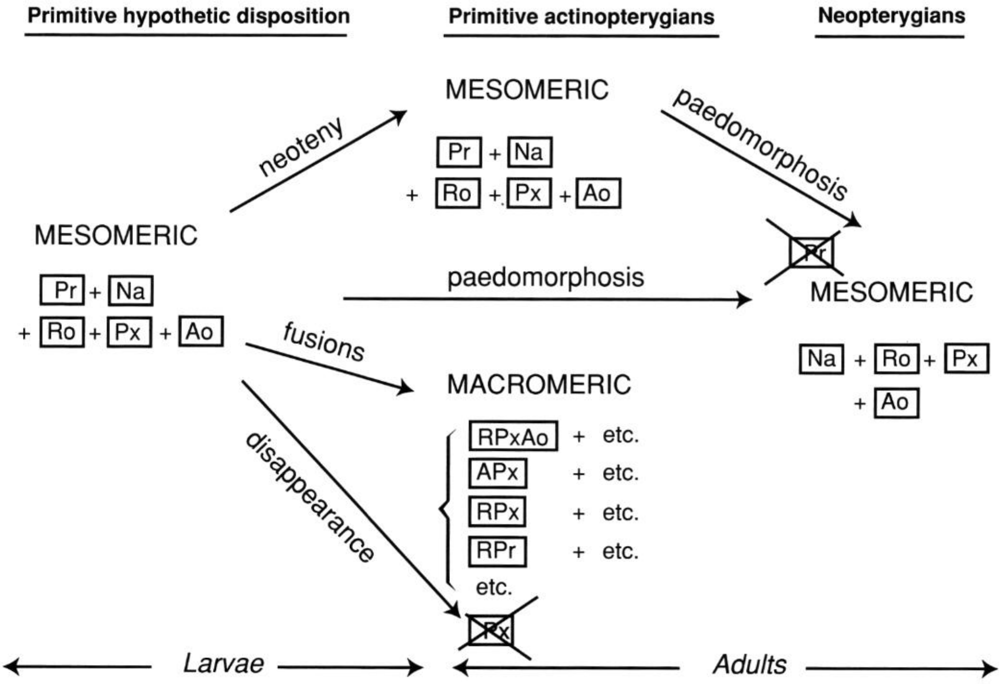

FIG. 4. — Hypothesis proposed in this paper about the evolution of the dermal snout, based on those of Pearson, Schaeffer, Long, Gardiner & Schaeffer (see text). **Ao**, antorbital; **APx**, antorbito-premaxillary; **Na**, nasal; **Px**, premaxillary; **Pr**, postrostral; **Ro**, rostral; **RPx**, rostro-premaxillary; **RPxAo**, rostro-premaxillo-antorbital; **RPr**, rostro-postrostral.

nopterygians is likely to have been provided with a separate premaxillary.

– It is more parsimonious, from a phylogenetic point of view, to think that the lineages with a mesomeric disposition and possessing a premaxillary are more closely related to neopterygians than the other lineages (macromeric and/or lacking premaxillaries).

– The multiple states of the premaxillary (particularly its loss) and their systematic distribution indicate that, at least some of them could have appeared more than once. These data and new informations on the actinopterygian relationships of *Polypterus* can be interpreted as supporting the hypothesis that the lower actinopterygians conveniently called "paleoniscoids" may not be a natural group.

Finally, this review of the problems concerning the primitive pattern of the premaxillary, and of its subsequent evolutionary trends, is a demonstration of the parallel evolution of knowledge and ideas. It is rather amusing to notice that Westoll's first three schemes are invalidated by recent data, and that his last scheme, that he considered as the less likely, turned to be the one favoured herein. In sixty years from now, what will remain of the analysis exposed in this paper?

Acknowledgments

We are thankful to Richard Cloutier and John Long who revised the manuscript and to Henri Lavina who computerized the drawings and tables.

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Submitted for publication on 8 January 1996;
accepted on 28 May 1996.