Re-assessment of the genus Helmolepis Stensiö 1932 (Actinopterygii, Platysiagidae) and the evolution of the Platysiagids in the Early-Middle Triassic

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Re-assessment of the genus *Helmolepis* STENSIÖ 1932 (Actinopterygii: Platysiagidae) and the evolution of Platysiagids in the Early-Middle Triassic

RAOUL J. MUTTER

Key words: Basal Actinopterygii, Triassic, Systematics, *Helmolepis manis* sp. nov., Paleobiogeography

ABSTRACT

The type material of the rare, small actinopterygian *Helmolepis gracilis* Stensiö 1932 from the lower Griesbachian of East Greenland has been re-discovered in the Geologisk Museum of the University of Copenhagen. Two additional specimens, one presumably juvenile, have been identified in the same collection. More precise meristic features are reported and the reconstruction of the skull skeleton is considerably improved. Furthermore, another species, *Helmolepis manis* sp. nov. has been discovered in the Lower Triassic (Dienerian) of northwest Madagascar. The evidence of similar small-sized actinopterygian species in the Early Triassic suggests that platysiagids – recently also described from the Lower Smithian of western Canada – showed worldwide distribution at least by the Dienerian. Discovery of this new species further supports the assumption, that the Platysiagidae were not the offspring of derived Middle Triassic "perleidiform" actinopterygian fishes, but probably shared a common (unknown) ancestor older than the early Smithian, possibly of early Griesbachian age. The occurrence of closely related, small-sized actinopterygians in high latitudes by the early Dienerian and in the eastern Panthalassic Ocean by the early Smithian may be explained by an early or rapid dispersal event in combination with dwarfism in the recovery phase following the end-Permian mass extinction.

ZUSAMMENFASSUNG

Das Typusmaterial des seltenen, kleinen Strahlenflossers *Helmolepis gracilis* STENSIÖ 1932 aus dem unteren Griesbach von Ost-Grönland wurde wiederentdeckt im Geologischen Museum der Universität Kopenhagen. Zwei weitere Exemplare, eines vermutlich juvenil, sind in derselben Sammlung identifiziert worden. Genauere meristische Merkmale und eine verbesserte Rekonstruktion des Schädels werden vorgestellt. Ausserdem wurde eine weitere Art, *Helmolepis manis* sp. nov., entdeckt: sie stammt aus der Untertrias (Dienerian) von Nordwest-Madagascar. Die Evidenz ähnlicher kleinwüchsiger Aktinopterygier-Arten in der Untertrias lässt vermuten, dass die Platysiagiden – kürzlich auch aus dem unteren Smithian von West-Kanada beschrieben – eine weltweite Verbreitung spätestens zur Zeit des Dienerian aufwiesen. Die Entdeckung dieser neuen Art zeigt auch, dass die Platysiagidae keine Abkömmlinge der stärker abgeleiteten mitteltriassischen "perleidiformen" Aktinopterygier sind, sondern wahrscheinlich einen gemeinsamen (noch unbekannten) Vorfahren vor dem frühen Smithian, möglicherweise im frühen Griesbachian aufwiesen. Das Auftreten nahe verwandter, kleinwüchsiger Aktinopterygier in hohen Breiten im frühen Dienerian und im östlichen Panthalassa zur Zeit des frühen Smithian könnte durch ein frühes oder schnelles Dispersal-Ereignis von Zwergformen in der Erholungsphase nach dem Perm-Trias Massensterben erklärt werden.

1. Introduction

The Lower Triassic (?lower Griesbachian) Wordy Creek Formation of East Greenland is a classic fossil site, from where certain actinopterygians have been extensively described (i.e. Stensiö 1932; Nielsen 1935, 1936, 1942, 1949). Nybelin (1977) contributed a rather preliminary description of a small basal actinopterygian based on four specimens, one of which had briefly been noted both by Stensiö (1932; "group D") and Nielsen (1936), and the type series had seemingly been lost. Recent reevaluation of the collection of actinopterygians from the Wordy Creek Formation revealed that the Parasemionotidae and that the perleidid-like ?neopterygians ("*Perleidus*" *stoschiensis* STENSIÖ 1932) have been underestimated in counts of specimens (pers. obs.). "*Perleidus*" *stoschiensis* and other perleidid-like neopterygians differ from *Perleidus altolepis* in skull and caudal fin features. The study has also confirmed the taxon *Helmolepis gracilis* STENSIÖ 1932 is particularly rare in the lower Griesbachian at Cape Stosch (main sampling ground in the Wordy Creek Formation). Only two new specimens were identified while re-evaluating hundreds of specimens in this major but little studied collection of Triassic East Greenland fishes. In contrast to the scarcity of this group in Denmark, the (presumably mainly lower) Smithian layers of the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation

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in the Canadian Rocky Mountains yielded over 100 specimens of a new species, believed to be closely related to *Helmolepis gracilis* (Mutter 2004a; Neuman & Mutter 2005).

Reconstruction of the skeleton of the Canadian species *Helmolepis cyphognathus* NEUMAN & MUTTER 2005 highlights differences found between the two taxa. However, the type material of *Helmolepis gracilis* had been unrecoverable (Neuman & Mutter 2005). Only re-discovery and re-description of the type series stored at the Geologisk Museum of the University of Copenhagen (and 2 newly discovered specimens) allowed critical review of *Helmolepis gracilis* within Platysiagidae.

Re-investigation of Early Triassic "perleidids" found in nodules in northwest Madagascar (collection Natural History Museum, Stockholm) led to the discovery of a single specimen, which shows diagnostic features of the genus *Helmolepis*, and can readily be placed in a new species, *Helmolepis manis* sp. nov. The Madagasscan specimen does not only allow interpretation of species-specific features in the shoulder girdle due to its reasonably complete state of preservation, but also adds to our knowledge of the Triassic biogeographic distribution of platysiagids.

2. Material, Method and Institutional Abbreviations

2.1. *Helmolepis gracilis* STENSIÖ 1932

Material. – Holoype specimen MGUH VP 3219 (no. 47 in Stensiö [1932: 284]), specimen MGUH VP 563 mentioned by Nielsen (1936), and specimens MGUH VP 562-4 described by Nybelin (1977).

Newly described specimens. – MGUH VP 27740 and 27741.
Localities. – All specimens are from the Lower Triassic Wordy Creek Formation localities of East Greenland, largely known as the "Cape Stosch" site. Specimens MGUH VP 563 and 564 are from between Gaffeldal and Stribedal (probably zone 2, 245–280 m above sea level), and the holotype specimen MGUH VP 3219 is from section C (200–260 m above sea level); specimen MGUH VP 562 was found on Spath Plateau (350–390 m above sea level); one of the new specimens MGUH VP 27741 was collected in Kiledalens E. Vaeg, 396–427 m above sea level, and the second new specimen MGUH VP 27740 was also collected on Spath Plateau, River 13, 300–400 m above sea level.

Remarks. – Three of the 6 specimens are preserved in concretions; the holotype specimen MGUH VP 3219 and specimens MGUH VP 563 and 564. Specimen 27740 is an imprint with very little phosphatic remains. MGUH VP 562 and 27741 are fragmentarily preserved in silty sandstone ("shale"). The holotype specimen MGUH VP 3219 lacks most of the (characteristic) head but trunk and fins are almost completely preserved. As already mentioned by Nybelin (1977), specimen MGUH VP 563 is by far the best preserved specimen, and therefore the majority of observations and conclusions are based on the latter specimen.

2.2. *Helmolepis manis* sp. nov.

Only known specimen. – NRM-PZ P. 4375.
See description of species.

2.3. Method

The rubber used for positive casts in this study is a Smooth-On polyvinylsiloxan of low viscosity ("light body"). The terminology of fish bones follows Neuman & Mutter (2005).

2.4. Institutional Abbreviations

The material described is housed at the Geologisk Museum of the University of Copenhagen (MGUH) and at the Riksmuseet Stockholm (Natural History Museum, NRM). The acronyms "PZ" and "VP" indicate the sections "paleozoology" and "vertebrate paleontology" in the respective collection.

3. Systematic Paleontology

3.1. Description of the (re)discovered material

Class Osteichthyes HUXLEY 1880
Subclass Actinopterygii COPE 1887 (*sensu* Wooward 1891)
Order "Perleidiformes" BERG 1937 ([BERG 1940 in part] new usage *sensu* Mutter 2002)
Remark. – The "Perleidiformes" are a paraphyletic assemblage, whose interrelationships have not yet been successfully resolved (see also Mutter 2004b).

Family Platysiagidae BROUGH 1939
Helmolepis STENSIÖ 1932

Helmolepis gracilis STENSIÖ 1932 (Figs 1–6)
Formation. – Lower Triassic (?Griesbachian) Wordy Creek Formation of East Greenland (Denmark).
Locality. – For specific localities, see list of materials.
For diagnosis, see below.

Description of Specimen MGUH VP 27740. – This specimen is an anterior body half squashed in lateral view (Fig. 1). The phosphatic material is not preserved or at least badly weathered, leaving almost exclusively imprints of remaining parts of the head, dorsal and anal fin. The origin of the dorsal fin is at about scale row 23. The pelvic fin is partly preserved but dislocated, its probable origin is at scale row 15. At least 14 transversal scale rows are present in the anterior flank.

The proportions of the jaws and the outlines of the snout can be traced as imprints. The imprint of the lower jaw measures 9 mm in length and about 2 mm in depth. The maxilla is very slender and its posterior plate is deepened and curved postero-ventrally. Several imprints of tiny teeth are preserved in the posterior region of the borders of maxilla and dentary.

The snout is preserved in original outline (Fig. 1B) and shows the eye was large and placed far anterior. The wall of

Fig. 1 A

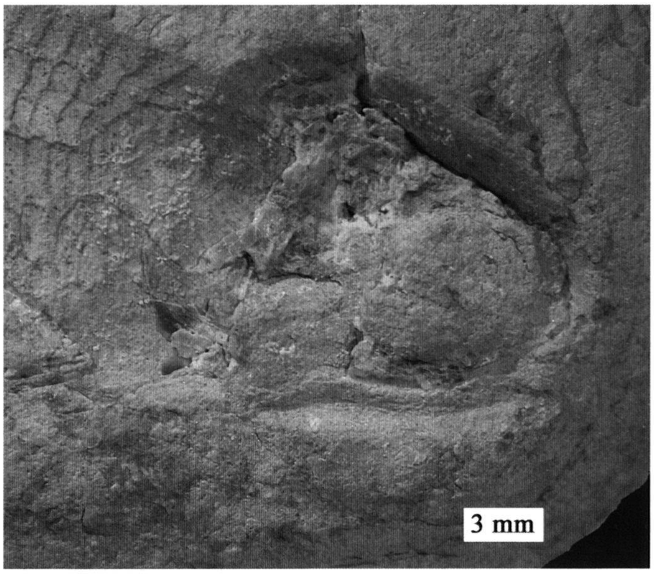

Fig. 1. *Helmolepis gracilis* Stensiö 1932, specimen MGUH VP 27740. – A) The concretion contains an imprint of head and trunk seen in mesial view. B) The close up shows the head's blunt shape, its large eye sockets, and the characteristic shape of the maxilla (compare with Fig. 3A).

the orbit in the ventro-anterior area was thin and very little room was available to accommodate the slender lachrymal. The lachrymal sutures another bone anteriorly, probably the antorbital. However, only a thin sheet of this bone is visible and its identification is interpretive. I was not able to find clear evidence of rostral bones but a vague imprint of a small fragment to the left of the nasal is interpreted as a small rostral.

Description of Specimen MGUH VP 27741. – This presumably juvenile specimen is a dorsal body half including the dorsal fin but missing the caudal fin, and it is preserved in lateral view (Fig. 2). The specimen measures about 49 mm in standard length. The origin of the dorsal fin is at longitudinal scale row 23. The dorsal fin counts 8 lepidotrichia that are almost entirely jointed. The segments are usually about twice as long as broad.

The squamation consists of relatively large and broad scales, compared to the specimen's body size, and the posterior border is serrated. The ganoin surface appears to be devoid of any conspicuous ornament pattern but faint grooves are visible on ideally preserved scales. Thirty-eight longitudinal scale rows are present from the cleithrum back to the end of the caudal peduncle.

The head is very poorly preserved and most bones are missing but a relatively very narrow dermopterotic and a short pair of broad frontals are visible.

Helmolepis gracilis – Specimens Described by Nybelin (1977)

Specimen MGUH VP 563 (Figs. 3–5A, in addendum to Nybelin [1977: 4–8]), the standard length measures 75 mm, the length of the head (posterior border of operculum to tip of snout) is 22 mm, and the dorsal fin adjoins the squamation at scale row 21.

New observations from Smooth-On peels taken from the nicely preserved head of specimen MGUH VP 563 (Fig. 3A) allow addition of new information to Nybelin's (1977) descriptions.

Head and Shoulder Girdle (Figs. 3, 6). – There are no premaxillae preserved, and the maxilla is slightly longer than the dentary (Fig. 3). In the snout area, imprints of the two nasals can be seen *in situ* in front of the frontals ("postrostral" by Nybelin [1977: p. 4] and a pit line can be traced in the left nasal). The two nasals meet at the midline of the snout dorsally and are sutured by the short rostral that is partly overlapped by the nasals. The rostral is edentulous, which is indicative of non-fusion with any premaxillary bones.

The branchiostegal rays are very short (almost half as wide as long) and rounded. The suboperculum is slightly larger than the operculum and there is no ventrally adjoining interoperculum (the "line" Nybelin [1977] refers to is a crack in the originally curved suboperculum). The dermohyal is small and wedge-shaped.

I was not able to trace the ossification "presupracleithrum" as suggested by Nybelin (1977: 6 and fig. 1). I interpret the vaguely delimited elevation in the position referred to as a thickened rim in the anterodorsal corner of the broad supracleithrum. Postcleithra appear to have been absent, and the cleithrum is almost entirely covered by the cheek bones.

Sensory Canals. – The visible tubuli of the infraorbital sensory canal number 4 in the jugal, and the preoperculum sensory canal has 8 short side branches – which seem limited to the dorsal portion of the preopercular sensory canal. Judged by the course of the oblong ganoin tubercles in the ornament of certain head bones, the course of the sensory canal can be discerned in the frontals and nasals.

*Fins (*caudal fin in Fig. 4*).* – The pelvic fin is not in articulation (rays are preserved around longitudinal scale row 11) and there is one enlarged scale or scute in front of the pelvic fin. The caudal fin is conspicuously forked and of classic abbreviat-

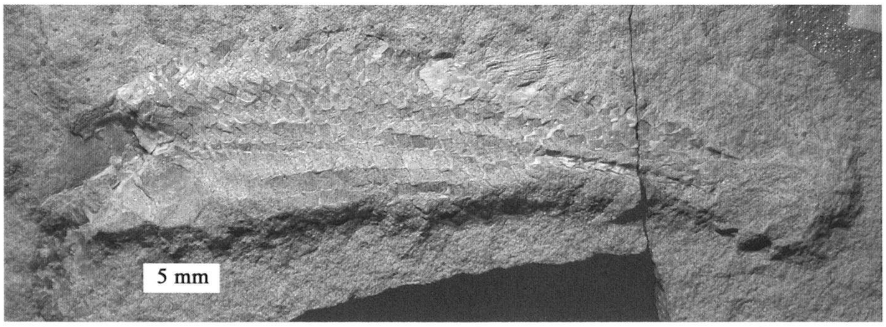

Fig. 2. A second new (probably juvenile) specimen (MGUH VP 27741) of *Helmolepis gracilis* STENSIÖ 1932 consists of a trunk and part of the head, A) seen in mesial view, B) close up of head.

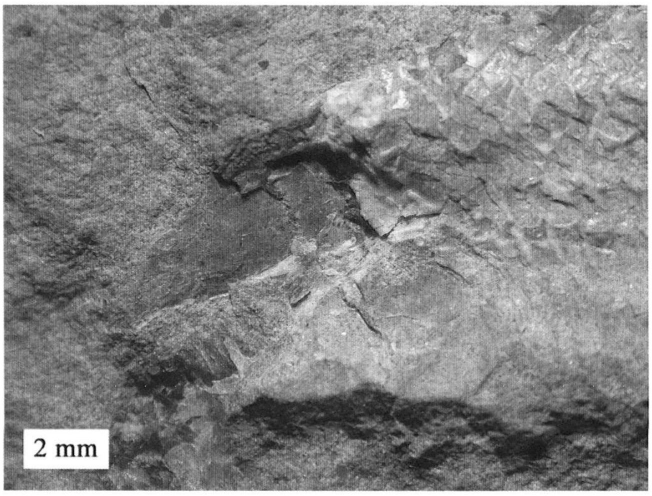

Fig. 2 B

ed heterocercal shape (Fig. 4). The scales diminish in size posteriad but the most distal segments of the lepidotrichia do not become members of the series of fulcra in the dorsal lobe (Fig. 4). Instead, the outermost scales adjoin the single row of caudal fin scales.

Squamation (Fig. 5). – The squamation consists of relatively large, flat scales, smooth or with a faint ornamentation. The ornamentation consists of up to six diagonally running, shallow ridges in the free scale surface. The posterior border is conspicuously serrated (Fig. 5). In the anterior flank, 4 transversal scale rows are slightly deepened if compared to the neighboring scales.

Thirty-eight longitudinal scale rows are present and about 15 transversal scale rows can be counted in front of the pelvic fin. There seems to be a faint ornament in the center of the free scale surface on scales of the anterior flank of holotype specimen MGUH VP 563 (Fig. 5A). However, in specimen MGUH VP 564, there is no ornament visible on the Smooth-On peel of imprints of anterior flank scales (Fig. 5B). The serration appears to be present on most scales, in particular in the anterior body half.

3.2. Revised Reconstruction of the Head of Helmolepis gracilis (Fig. 6)

The main improvements with respect to the former reconstruction concern the skull roof, the snout, the circumorbitals, and the definite absence of an interoperculum. Also, traces of the pectoral girdle (cleithrum and supracleithrum) are preserved in the holotype specimen. The supracleithrum overlaps the cleithrum just above the level of the dorsal border of the suboperculum. The cleithrum is ventrally broadened and reaches anteriad underneath the first branchiostegal ray.

As can be seen from the new Smooth-On peel of specimen MGUH VP 563 in comparison with the new specimens, the dorsal border of the suboperculum runs more obliquely than in Nybelin's (1977) reconstruction. The dentary and the maxilla are more slender in the holotype specimen and in specimen MGUH VP 27740 than suggested in Nybelin's (1977) composite drawing.

The snout is particularly typical of these Early Triassic platysiagids, because a very similar pattern of ossifications is also found in the Canadian species. For instance, the postrostral – normally present in stem actinopterygians – is absent, so that the large nasals meet at the midline over much of their length.

3.3. Diagnostic Features of Helmolepis gracilis

As a result, the revised diagnostic features of *Helmolepis gracilis*, in the light of *Helmolepis cyphognathus* from the Lower Triassic Sulphur Mountain Formation (Neuman & Mutter 2005), can be summarized as follows:

1. about four supraorbitals hem the skull roof laterally (pattern different or unknown in all other platysiagids)
2. oblong and dorsally fairly broad dermohyal (not seen in any other platysiagid)
3. few broad branchiostegal rays (more slender and more numerous in all other platysiagids)
4. broad nasals meeting at midline (probably shared with *Helmolepis cyphognathus* and *Platysiagum sclerocephalum* EGERTON 1872)

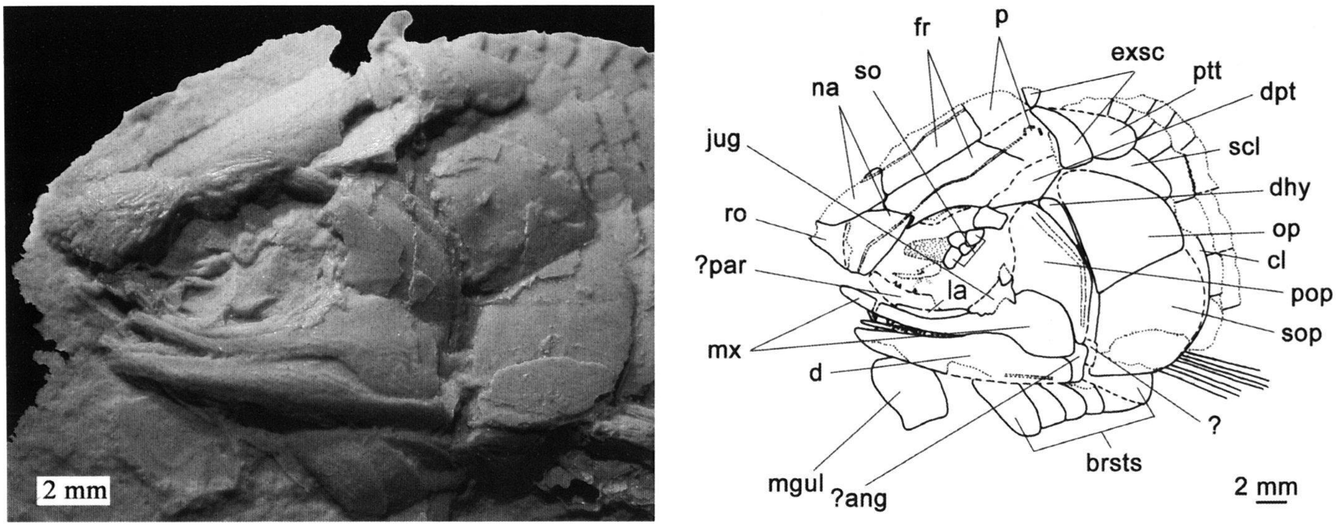

Fig. 3. Head of *Helmolepis gracilis* STENSIÖ 1932, specimen MGUH VP 563.- A) Smooth-On peel of the imprint of the head in left lateral view. B) Re-interpretation of the skull of *Helmolepis gracilis*. Note that there is no interoperculum but a series of fairly broad branchiostegal rays, and the rostral does not suture with the frontals but the nasals meet in the midline. Abbreviations: ang, an gular; brsts, branchiostegal rays; cl, cleithrum; d, dentary (dentalosplenial); dhy, dermohyal; dpt, dermopterotic; exsc, extrascapular; fr, frontal; jug, jugal; la, lachrymal; mgul, median gular; mx, maxilla; na, nasal; op, operculum; p, parietal; par, prearticular; pop, preoperculum; ptt, posttemporal; ro, rostral; sci, supracleithrum; so, supraorbital; sop, suboperculum.

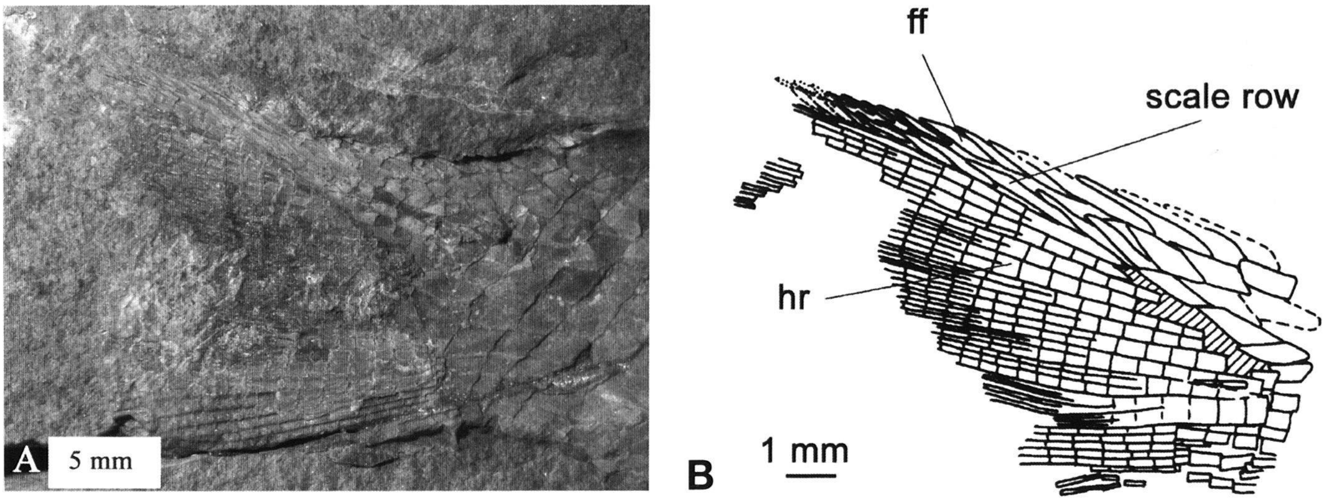

Fig. 4. A) The caudal fin of *Helmolepis gracilis* STENSIÖ 1932 in specimen MGUH VP 563, imprint of the caudal fin as preserved. B) Note the absence of epaxial rays; instead, there is the well-developed single series of oblong caudal fin scales ("scale row"). Abbreviations: ff, fringing fulcra; hr, hypaxial rays.

3.4. Helmolepis manis sp. nov. (Fig. 7): First Evidence of the genus Helmolepis in the Southern Hemisphere

Holotype and single specimen known. – NRM-PZ P. 4375.
Note. – The counterpart of the concretion belonging to this specimen may be recoverable; the part (P. 4375) was probably donated by J.-P. Lehman (Museum d'histoire naturelle in Paris).
Locality. – basin d'Ankitohazo, northwest Madagascar (horizon unknown; see also Lehman 1952).
Age. – Lower Triassic; lower Dienerian.
Etymology. – "man-" is derived from Ancient Greek, meaning "sparse" or "rare".
Preliminary diagnosis. – Thirty-five (possibly up to thirty-nine) longitudinal scale rows; posttemporal and supracleithrum conspicuously enlarged; postcleithrum absent.

Description of Specimen NRM-PZ P. 4375 (Fig. 7). – Specimen NRM-PZ P. 4375 is a small specimen of 53 mm standard

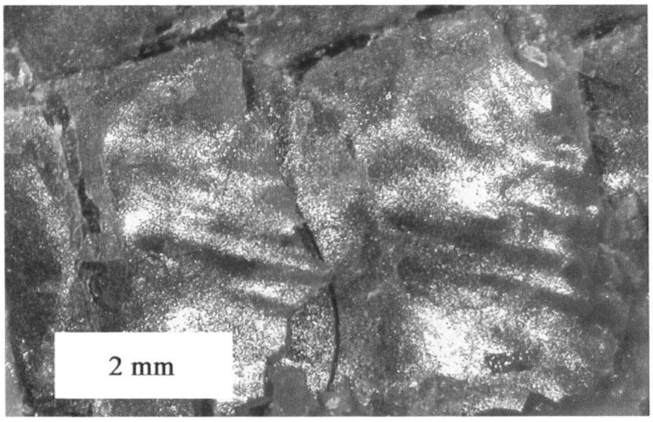

Fig. 5 A

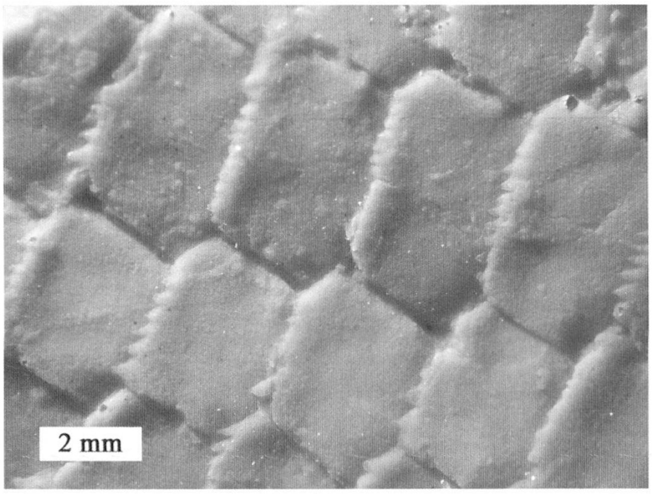

Fig. 5. Variation in anterior flank scales of *Helmolepis gracilis* STENSIÖ 1932. A) Moderate ornamentation and serrated posterior scale border in specimen MGUH VP 563 (anterior to left). B) Smooth scale surface and serrated posterior scale border as seen in Smooth-On peel of specimen MGUH VP 564 (anterior to right).

length. The specimen is preserved as an imprint and heavily weathered. The origin of the pelvic fin is at vertical scale row 13 or 14, and all other fins are missing or too fragmentarily preserved to yield counts of lepidotrichia.

Thirty-five longitudinal scale rows can be counted; there is room for 3–5 more vertical scale rows back to the end of the caudal peduncle. At the level of the pelvic fin, which adjoins the squamation between vertical scale row 13 and 15, are 14 or 15 horizontal scale rows.

Head (Fig. 7). – The head shows vague outlines and broken margins of all major dermal skull bones (Fig. 7A, B). The eye socket is very large and placed far anteriorly, and the skull roof is relatively very short and broad. The posttemporal is quite large and must have been almost the size of the posterior plate of the maxilla. The anteriorly suturing extrascapular cannot be delineated in its precise outlines but the course of its sensory canal suggests a relatively broader lateral side. The jaws are short: the dentary appears shorter than the maxilla but the anterior border of the dentary is broken. The suboperculum is slightly deeper than the operculum and seemingly broader; it projects dorso-posteriorly along the border of the operculum. The snout is too poorly preserved to allow description. However, the anteriormost large bone may be the left nasal, and it sutured a small adjoining bone ventrally, probably the antorbital.

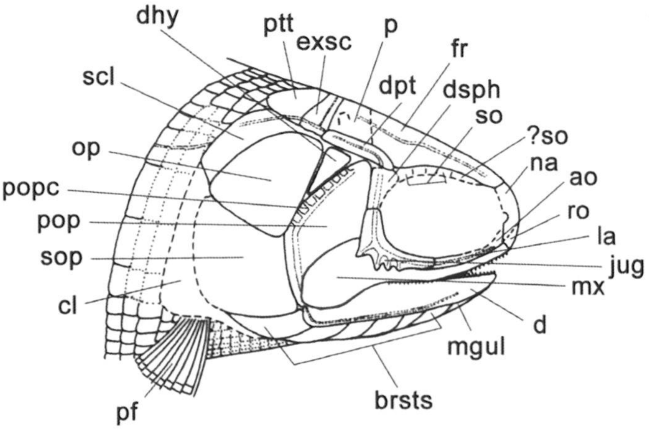

Fig. 6. Attempt at a schematic reconstruction of the head of *Helmolepis gracilis* STENSIÖ 1932, based on MGUH VP 563, 3219, 27740, and 27741. The dermopterotic and the supraorbital patterns are least well known. Abbreviations: ao, antorbital; brsts, branchiostegal rays; cl, cleithrum; d, dentary (dentalosplenial); dhy, dermohyal; dpt, dermopterotic; dsph, dermosphenotic; exsc, extrascapular; fr, frontal; jug, jugal; la, lachrymal; mgul, median gular; mx, maxilla; na, nasal; op, operculum; p, parietal; pf, pectoral fin; pop, preoperculum; popc, preopercular sensory canal; ptt, posttemporal; ro, rostral; scl, supracleithrum; so, supraorbital; sop, suboperculum.

The infraorbital canal of the lachrymal is partly mineralized although none of the circumorbital ossifications are preserved (Fig. 7C). Mineral-filled portions of the sensory canals in the supraorbital, extrascapular, preoperculum and dentary are preserved and their course is illustrated in Figure 7B.

Pectoral girdle. – The supracleithrum sutures the posttemporal with its broad dorso-anterior margin and it must have overlapped the cleithrum just above the suture of the suboperculum-operculum. The cleithrum is not visibly preserved but an imprint suggests that its posterior border runs parallel with the posterior margin of the opercular series and bulges out ventrally.

Squamation. – The free scale surface is smooth but the posterior free scale surface shows up to 7 or 8 parallel antero-posteriad running grooves in the anterior flank, and the posterior scale border is serrated (not illustrated in Fig. 7). The scales in the posterior body half also show this ornament but the grooves become fewer in concert with the diminishing depth of scales.

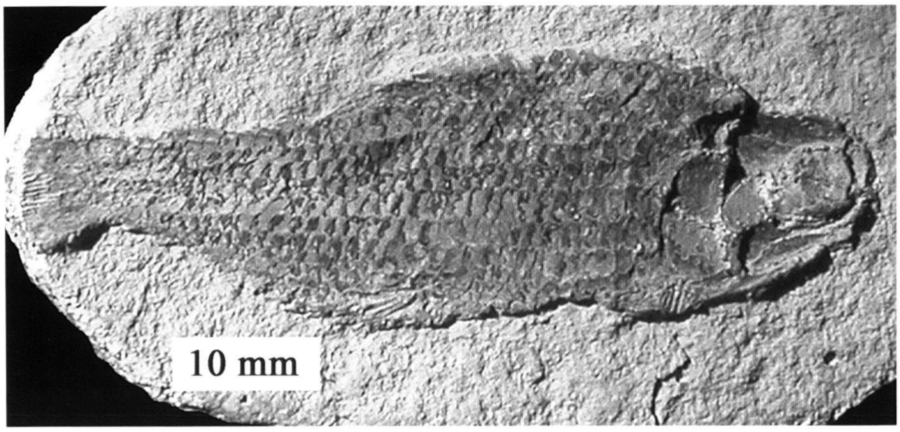

Fig. 7 A

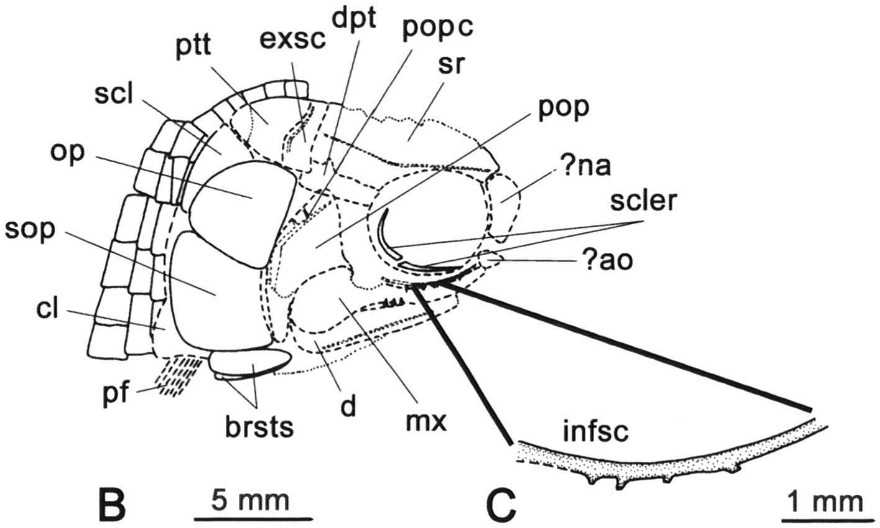

Fig. 7. A) Calcareous concretion with specimen NRM-PZ P. 4375 in right lateral view identified as *Helmolepis manis sp. nov.*, representing the only known evidence of the genus *Helmolepis* from the Southern Hemisphere (Lower Triassic of Madagascar). B) Tentative line drawing of specimen NRM-PZ P. 4375 as preserved with C) a close-up of the prominent ossified tube for the infraorbital sensory canal. Note the presence of several slightly deepened scale rows in the anterior flank. Abbreviations: ao, antorbital; brsts, branchiostegal rays; cl, cleithrum; d, dentary (dentalosplenial); dpt, dermopterotic; exsc, extrascapular; infsc, infraorbital sensory canal; mx, maxilla; na, nasal; op, operculum; pf, pectoral fin; pop, preoperculum; popc, preopercular sensory canal; scl, supracleithrum; scler, slerotic ring; sop, suboperculum; sr, skull roof.

4. Discussion: Platysiagid Origin and Biogeography

The misinterpretation of a crack in the antero-ventral corner of the suboperculum led Nybelin (1977) to believe that *Helmolepis gracilis* possessed an interoperculum; this mistake impeded understanding of the origin of the whole group of platysiagids (see Gardiner & Schaeffer 1989; Cloutier & Arratia 2004). Most other features show clear affinities with primitive "perleidiforms", but were denied bearing a systematic significance because of the purported presence of an interoperculum. However, Bürgin (1992: p. 54) hinted at a scenario favoring a more isolated phylogenetic lineage of platysiagids, having re-described the hitherto little-known *Platysiagum minus* BROUGH 1939 in the Anisian/Ladinian of the northern Tethys. And, in the light of recent discoveries, including numerous specimens of *Helmolepis cyphognathus* in the Lower Smithian of north-eastern Panthalassia, the platysiagids show a changing and surprisingly widespread distribution throughout the Early Mesozoic, with major evolutionary changes observed in the skull skeleton (Fig. 8).

The re-discovered, evidently scarce species *Helmolepis gracilis* from the lower Griesbachian of East Greenland and the Dienerian *Helmolepis manis* sp. nov. from Madagascar are remarkable records, and the phylogenetic position of these species has become highly important. The Middle Triassic to Early Jurassic genus *Platysiagum* EGERTON 1872 and the Early Triassic genus *Helmolepis* can be placed within Platysiagidae with confidence – despite the considerable stratigraphic gap in the Late Triassic (see below). Lombardo (2002) recently described a basal actinopterygian from the upper Ladinian of the northern margin of the Tethys, *Caelatichthys nitens* LOMBARDO 2002, that shows affinities to *Platysiagum* and *Helmolepis* in the shape and composition of cheek bones, maxilla and its dentition, lachrymal and jugal. The main differences – but plesiomorphic features if compared to amblypterids – include the break-up of the preoperculum, the more derived snout (if compared to *Helmolepis)*; presence of premaxilla and rostro-postrostral ("rostral" in Lombardo 2002), and the presence of a large, undivided dermopterotic (if compared to *Platysi-*

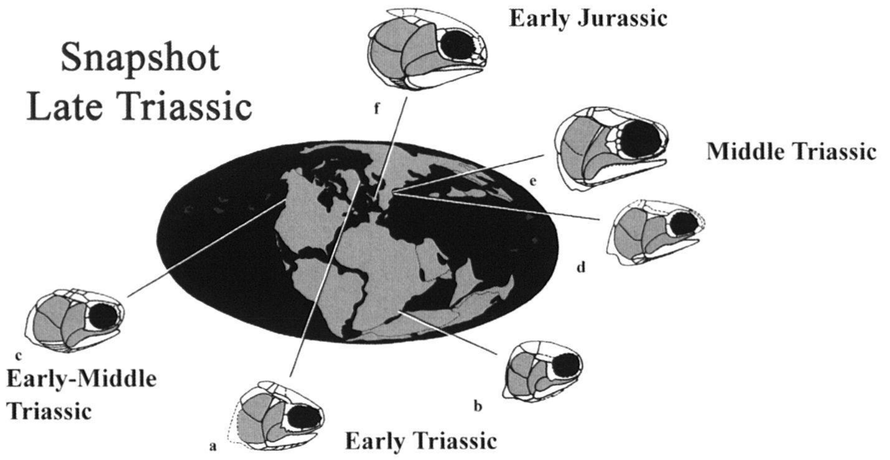

Fig. 8. Revised occurrence of platysiagid actinopterygians from the lowest Triassic to the Liassic: the main changing patterns in skull ossifications through time are counts of branchiostegal rays, the cheek area and the preoperculum, jaw proportions, and the maxilla including dentition. a: *Helmolepis gracilis* STENSIÖ 1932 (Griesbachian, East Greenland); b: *Helmolepis manis*. sp. nov. (Dienerian, NW Madagascar); c: *Helmolepis cyphognathus* NEUMAN & MUTTER 2005 (Smithian, western Canada); d: *Platysiagum minus* BROUGH 1939 (Anisian-Ladinian, Italy/ Switzerland); e, *Caelathichthys nitens* LOMBARDO 2002 (Ladinian, Italy/ Switzerland); f, *Platysiagum sclerocephalum* EGERTON, 1872 (Liassic, Great Britain).

agum). Despite these differences, the taxon is at present most parsimoniously placed in Platysiagidae.

As mentioned above, the systematic position of Platysiagidae has commonly been assessed as advanced "perleidiform" (Mutter 2002; Cloutier & Arratia 2004), but because the "Perleidiformes" are paraphyletic among neopterygians (Gardiner & Schaeffer 1989; Mutter 2002), and because their earliest "members" after the end-Permian mass extinction show affinities to the Platysiagidae (Neuman & Mutter 2005), the genus *Helmolepis* may have occupied a phylogenetic "key position" relative to other Platysiagidae, to some "perleidiforms" (e.g. *Meridensia* BROUGH 1939 (see Bürgin 1992)) and possibly to other stem neopterygians.

H. gracilis retains plesiomorphic characters, such as the absence of epaxial rays, the posterior plate of the maxilla overlapping with the dentary, and the broad preoperculum. Features of perleidid affinities are the lack of an interoperculum, the upright suspensorium of the lower jaw and the shape of the preoperculum, the slender-short dermopterotic, the pattern of circumorbital ossifications (the oblong-slender lachrymal in particular), and the presence of several rows of slightly deepened flank scales. The combination of presumably derived features, which characterize the genus *Helmolepis*, are: absence of a postrostral, conspicuously broadened sensory canals, the structure of the caudal fin, and the shape of the maxilla, including a single series of tiny and delicate conical teeth on the jaw margins, extending far back on the maxilla. Some of these features are also present in *Platysiagum* and *Caelatichthys* as primitive characters.

The fact that platysiagids were widespread in the Early Triassic and occurred with at least one species even in the lower Dienerian of the Southern Hemisphere, raises interesting questions. The nearly worldwide presence of large-sized pelagic fishes in the Early Triassic, such as the palaeonisciform actinopterygians *Saurichthys* AGASSIZ 1834 and *Birgeria* STENSIÖ 1921, could be explained, because the ability of marine nektonic predators to survive the end-Permian mass extinction had been put in context with hypercapnia (Knoll et al. 1996), and the absence of Lazarus-taxa in the Scythian had commonly been used to support the scenario of the worldwide end-Permian mass extinction (e.g., Wood 1999). The presence of modern-looking, small-sized actinopterygians (±60 mm) such as *Helmolepis* in the earliest Scythian, however, does not easily fit this scenario. Although Platysiagidae were known from the middle-upper Liassic (Early Jurassic in age: Egerton 1872) and in the upper Ladinian and Anisian-Ladinian (Middle Triassic: Bürgin 1992; Lombardo 2002; Herzog 2003) in Europe, their probable origin and relatively common occurrence in the Early Triassic had been overlooked or misinterpreted (Schaeffer & Mangus 1976; Nybelin 1977; Neuman 1992; Neuman & Mutter 2005). It is now possible to trace the evolutionary pathway of this phylogenetically isolated lineage throughout the Triassic.

Platysiagids show a considerable distribution over space and time (Fig. 8). The skull skeleton undergoes major changes, whereas the postcranium remains relatively conservative (ganoin cover on scales, abbreviated heterocercal caudal fin, ±constant size and position of all fins). In the earliest representatives, *Helmolepis gracilis* and *Helmolepis manis* sp. nov., the maxilla is comparatively deep and the preoperculum-cheek region is comparatively short. In the late Early Triassic *Helmolepis cyphognathus*, the maxilla has become extended backwards and the cheek has expanded as in the Middle Triassic *Platysiagum minus* BROUGH 1939. In the late Middle Triassic *Caelatichthys nitens*, the dermopterotic can be found to be expanded, but the preoperculum has become subdivided in 2 anamestic postorbitals and a dermohyal. These patterns are distantly reminiscent of amblypterids, less so of paramblypterids (see Gardiner 1963; Dietze 1999), and probably represent plesiomorphic features. The Early Jurassic *Platysiagum sclerocephalum* EGERTON 1872 is almost ten times larger than any Triassic platysiagid (600 mm); this species exhibits no subdivisions of the preoperculum, but instead it possesses a subdivided dermopterotic, another putative plesiomorphic amblypterid character. Platysiagid interrelationships are not yet understood, because single species are spread in space and time and differ considerably in ossification patterns in snout and skull roof. However, in addition to their large orbit and the posteriorly expanded maxilla with its minute teeth, they all share a slender-oblong lachrymal and an increasing number of branchiostegal rays through time. All species are marine, but the composition of their respective faunal context alters substantially during the late Early Triassic (Mutter 2003). No Late Triassic remains of platysiagids have yet been reported, but two facts may account for this deficiency: First, the teeth are minute and not easily recoverable (see Bürgin 1992). Second, the scales are fairly inconspicuous and, when isolated, probably indistinguishable from typical Early-Middle Triassic actinopterygian scales, such as those of parasemionotids or "perleidids". Scales, teeth or (less distinctive) remains such as isolated skull bones and segments of fin rays therefore may have been overlooked in samples retrieved from screen washing – the standard method in preparing many Late Triassic sediments for study.

Interestingly, the platysiagids show a distributional pattern comparable to the biogeography of the Ptycholepidae, another isolated, conservative actinopterygian lineage (Mutter & Bürgin in prep.). In both lineages, the latitudinal distribution peaks in the earliest Mesozoic, which would be indicative of an early dispersal event following the end-Permian mass extinction. However, the longitudinal distribution peaks in the middle Mesozoic (Fig. 8), and great differences in body size can be observed between early and middle Mesozoic platysiagids. The comparatively small size of Early Triassic *Helmolepis gracilis* and *Helmolepis cyphognathus* and in particular, *Helmolepis manis* sp. nov., may be related to dwarfism of the macrofauna following the great end-Permian extinction event with reduced primary production (e.g., Brookfield et al. 2003).

The global distribution of *Helmolepis* in the Early Triassic may not only be explained in the light of dwarfism occurring in taxa recovering from the end-Permian extinction event, but may also serve as an example of successful adaptation to the high-stress environment in the post-extinction marine realm and subsequent, successful radiation.

According to gross morphology and stratigraphic occurrence, the known platysiagids may provisionally be subdivided in 4 distinctive groups: group I, *Helmolepis gracilis* and *Helmolepis manis* sp. nov.; group II, *Helmolepis cyphognathus* and *Platysiagum minus*; group III, *Caelatichthys nitens*; group IV, *Platysiagum sclerocephalum*, whereas groups III and IV show differing primitive retentions.

Helmolepis cyphognathus and *Platysiagum minus* may be closely related and should be placed in a the same (new) genus, but the supraorbital and snout region are still poorly known in the latter species, and such action must await discovery of new material of platysiagids and a phylogenetic analysis using possible (currently unknown) outgroups.

Although the origin of platysiagids remains unknown, it has become clear that they represent an isolated phylogenetic lineage that can be traced back to the beginning of the Mesozoic.

5. Conclusions

The platysiagids represent a fairly isolated phylogenetic lineage from the Middle Triassic to the Lower Jurassic, but the morphology of their earliest known representatives clearly discloses "perleidiform" affinities by the Griesbachian. No possible ancestors can yet be identified among the Permian marine fish assemblages, e.g., from central or northern Europe, and a palaeoniscoid or amblypterid origin is entirely hypothetical (see above and Gardiner 1967; Hutchinson 1973). There is currently no better explanation available for the cosmopolitan presence of very small-sized actinopterygians such as *Helmolepis* in the earliest Triassic except for the theory of dwarfism due to reduced primary production. Origin of platysiagids in the Late Permian seems unlikely but remember the end-Permian extinction event was selective and group-specific. Other, not closely related fish groups, such as coelacanths and dipnoans, exhibit a peak in diversity in the Early Triassic, although overall diversity in fish assemblages can be shown to be much lower in the Early than in the Middle Triassic (Mutter 2003, 2004c; Schultze 2004).

No patterns of diversity or radiation can yet be mapped for platysiagids throughout the Triassic. However, it may be assumed, that either an early or rapid dispersal event involved "platysiagid" and "perleidiform" ancestors alike, and that this event had taken place clearly before the Early Smithian, probably in the Griesbachian. The ancestors or basal-most of "perleidiform" fishes may rather be discovered among the small and rare actinopterygians close to the Paleozoic-Mesozoic boundary.

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