The skull of *Grossius aragonensis*, an onychodont from the Middle Devonian of Spain

by

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Description: Only the head of this large fish (1 m or longer, with an estimated head length of 25 cm) is present; the rostral end and the rear section are missing. The whole head was recovered from a lime nodule with some plastic deformation, the right side being flattened. Because the whole right side was exposed by preparation, the bones are better seen here than on the [other less distorted] side. The strongly distorted fracture surfaces at the anterior and posterior ends were ground, so that the bones became more visible in cross-section. A further vertical break goes through the Orbita, it developed through a hammer blow on the nodule while prospecting. In addition, the roof of the skull can be removed along a break line.

The head has a pointed, three-cornered shape, which gives a strongly sharpened profile to the rostral region. The ventral length of the head as recovered is 13.5 cm, the length of the skull roof (from the recovered rostral end, to and including the median extrascapular) about 21 cm, the height at the recovered posterior margin about 14 cm. The large orbits (length 3.9 cm, height of 2.8 cm) lie well posterior to the rostrum. Individual sclerotic plates (*scl*) and/or parts or castings of them were recovered. A reconstruction of the sclerotic rings based on the size of the recovered plates, gives a number—typically high for onychodonts—of about 20 plates for the entire sclerotic ring. Anterior to the orbit lies a single external naris (*na*, about 1 cm in diameter), which appears larger than it probably was, since the edges of the surrounding bones forming the margin of the naris were not recovered. Clear sutures cannot be followed anterior to the

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orbit. The lacrimal (*La*) forms the anterior border of the orbit and probably the posterior border of the naris. Between the lacrimal and the jugal (*J*) is inserted the single infraorbital bone (*Io*). The jugal reaches the orbit only straight one [along?] at the posteroventral corner. The preserved jugal contains the anterior part of the infraorbital canal, which proceeds posteriorly and appears to involve the first squamosal [????], and so can be interpreted as parts of the preopercular line. Part of the postorbital section of the infraorbital canal can be observed in the postorbital (*Po*), as well as channels branching from it which have been exposed by weathering. The dorsal section of the postorbital is about twice as long as the ventral. Dorsal to the postorbital lies an elongate intertemporal (*It*), with a posteroventrally oriented posterior portion reaching the second squamosal. The intertemporal articulates posteriorly with two bones: the supratemporal (*St*) (which joins the postparietal with a zigzag suture), and the extratemporal (*Et*). Posterior to these two bones is located the tabular (*T*), the rounded posterior margin of which was completely preserved. The postorbital canal, with numerous branching channels, is well-exposed by weathering. It extends [posteriorly along] the length of the intertemporal and, by way of the supratemporal, reaches the tabular. In the supratemporal, a channel branches [ventrally] to the extratemporal, where the canal divides into numerous small branches.

Behind the jugal lies the first squamosal (Sq1). It extends dorsally to the ventral edge of the postorbital, but does not reach the dorsal margin of the cheek region. The extremely large second squamosal (Sq2) fills most of the postorbital space. The path of the preopercular canal could not be established in either of the two squamosals, nor in the cross section (fig. 6e). Only the anterior section of the opercular region, which lies between the second squamosal and the tabular, was recovered.

The jaws are formed from two slim bones, the maxilla and the dentary, both of which gradually become taller posteriorly. Anterior to the maxilla lies the premaxilla, which is typical of the onychodonts. Its outline cannot be specified at this time. Beyond the

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anterior end of the dentary the anteriormost section of the parasymphysial tooth spirals extend upward. The two parasymphysial tooth spirals both curve up and back to approximately the height of the center of the orbits, bearing a large number (7 counted, but probably more than 10) posterolingually curved main teeth (with points not directed upwards) beside which, laterally to a small tooth and the symphysis, are a medium sized tooth and a small tooth (fig. 6c). All these teeth show the striations typical of onychodonts (40-50 per mm on the lingual side). The maxillary teeth are positioned lingual to the ventral margin of the maxilla, so they are not visible in lateral view. The dentary teeth are implanted in a gutter (figs. 6d, 6e). As is usual for onychodonts, none of the teeth have folded dentine. Schultze (1969). The oral canal (*orc*) runs along the dentary, as also described by Jessen (1967, fig. 12B) for *Onychodus sigmoides*. The canal can be observed on the transverse breaks near the orbit (fig. 6d), but not, however, on the cross section at the posterior margin of this specimen. Ventral to the dentary are found the infradentary (*Id*) and submandibular (*Smb*). These are relatively narrow, uniform bones. The right and left gulars overlap (fig. 6e). Reconstructing the original overlapping relationship among the gulars and the submandibulars, one recovers a rather angular cross section for the back of the head. The gulars end approximately at the same height as the center of the orbits, directly behind the parasymphysial tooth whorls.

The skull table (fig. 6a1) is formed mainly by long postparietals (*Pp*, about 10 cm long). The parietals were destroyed. The rostral region is covered by bones (the overall rostronasal bone cover is discussed below), but only the median seam can be determined. Under these bones lies a dorsal lamella of the premaxilla (Pmx), visible in the cross section at the rostral end (fig. 6c). If one lifts off the postparietal shield (fig. 6a2), then one can follow the bones which were observed at the rear plane of section anteriorly (fig. 6e). The horizontal break [*i.e.* the fracture line which permits removal of the parietal shield] runs somewhat diagonally through the skull at the level of the upper section of the second squamosal, somewhat more deeply on the right (through the postorbital) than on the left (through the intertemporal). On the right side, therefore, the most dorsal section shows the entopterygoids (*Pt*) medial to the second squamosal. Medial to the maxilla—thus directly ventral to the entopterygoid—is located one small bone with a

strong ventral recess [plural?], possibly a fragment of the ectopterygoid displaced posteriorly (*?Ept*). The lower jaw and gular bones have been discussed above. Between these lie cross-sections of further bones, such as the spindle-shaped cross-section of a basibranchial element (*Bb*). The bones lateral to the basibranchial element probably also belong to the branchial skeleton. These (*Chy*) are conveniently observed in cross-section and are interpreted here as the bony covering of the certatohyal. The prearticulars are missing. Between the two entopterygoids lie three endoskeletal elements. The two ventral elements are observed in diagonal cross-section surrounding the notochordal canal (*Ch*). Over the canal rises a vertical element (*ne*) with only a short anterior extension (fig. 6a2). Without serial sections, it cannot be determined whether this represents an occipital element (the fact that this bone is found isolated, without a further anterior element, suggests a neurocranial segment) or whether it is the dorsal section of the neural arch of one of the anterior vertebrae. Ventrally, as well, the bone surrounding the notochordal canal (*db, vb*) cannot be clearly identified with respect to the neurocranium. The interpretation preferred here would mean that these are vertebral elements (*ne* = neural arch, *db* = pleurocentrum, *vb* = intercentrum) continuing the spinal column far into the head, anterior to the articulation between the quadrate and the lower jaws. Ventral to the ventral vertebral elements are transversely cut pieces of bone, which are probably related to [act as? are?] the small, denticle-bearing bone plates on the roof of the branchial region.

Dorsal to the entopterygoids—and deeply recessing them dorsally—is the hyomandibular (*Hy*), which bears a channel for the mandibular ramus of the VIIth nerve. In dorsal view (fig. 6a2) one can follow the right hyomandibular as far anteriorly as the left, since the right side of the head is shifted posteriorly compared to the left posterior to the rostrum. In the cross section at the posterior end of the head, the palatoquadrate is not observed, while it is strongly ossified more anteriorly. Thus one sees the ascending process of the palatoquadrate (*pr.a*) projecting into the orbit. Posteriorly, behind the ascending process, the dorsal edge of the palatoquadrate also rises to the dorsal edge of the entopterygoids (in contrast to *Eusthenopteron*, Jarvik 1954, text-Fig. 23B). In the orbital region, the palatoquadrate (autopalatine portion) articulates with the ethmosphenoid (fig. 6d1,2);

medial to the palatoquadrate, still another bone is found, which is attached to the anterior part of the entopterygoids here [vomer!?]. The ethmosphenoid is strongly ossified. It surrounds the cranial cavity, forming the olfactory canals (*c.olf.*, fig. 6a1). The ethmosphenoid cavity in the orbital region is delimited ventrally by the *pars medialis ethmosphenoidis* (*p.m.*), which supports a tall parasphenoid (*Ps*). The *pars medialis* and parasphenoid separate two deep hollows (*cv.in*) in the roof of the mouth, which accommodate the teeth of the parasymphysial tooth spirals. More anteriorly, the ethmosphenoid cavities become deeper, and are separated only by the external bone wall of the ethmosphenoid. At the anterior margin of the orbits, where the ethmosphenoid ossification expands laterally to form the anterior wall of the orbits, the wall is pierced by foramina [opening into the orbit] (*ö.d.*, *ö.m.*, *ö.v.*) which communicate with the ethmosphenoid cavities [this is a very free translation]. Since these were the only openings observed in the ethmosphenoid wall, they must represent the foramina for the *profundus* nerve (through ö.m), *nervus ophthalmicus lateralis* (through ö.d) and blood vessels. It is also possible that the anterior oblique eye muscles (*musculus obliquus superior* and *inferior*) communicate through these foramina with the anterior Ethmosphenoid. On the inner wall of the orbits, one can follow, at least, a seam, which separates the lateral ethmosphenoid wall into a ventral (p.l.v) and dorsal (l.d) sections. At the transverse break (fig. 6d2) the ethmosphenoid ossification seems to be still further partitioned. However it is difficult to decide whether or not this subdivision is an artifact of additional fractures in the material [or marks left by internal sutures of the rostral shield]. The ethmosphenoid ends under the anterior section of the postparietal (fig. 6a1, d2). Few ossifications were recovered from the otoccipital region (fig. 6a2), and these could not be interpreted.

The ornamentation of the cranial bones is observed only in a very few places. The bones appear smooth. Under strong magnification can one see that flat, shining tubercles, very closely spaced, form the surface. (Table 34, Fig. 1b). In addition, the scales, which are shifted relative to those on the right side of the head, show no detectable ornament on the free surface. The overlapped area of the scales carries single flat, tubercles (Table 33, Fig 2) over the radial strip [??], as found in *Onychodus* and the Rhipidistia (Ørvig 1957). The

inner surface of the scales is smooth with clearly visible concentric lines.

Grossius n. gen.

Definition: onychodontid with angular, three-cornered head, low rostral region, and tall occipital region. Postorbital long and large; extratemporal present. First squamosal much smaller than second squamosal. Maxilla gradually increasing in height posteriorly. Dentary, infradentary, and submandibular low. Parasymphysial tooth spiral with small teeth beside the main teeth: two medially and one laterally. Ethmosphenoid with large cavity ventral and anterior to the cranial cavity. Autopalatine section of the palatoquadrate robust, with ascending process reaching the height of the posterior border of the orbit. Monotypic.

Derivation: in honor of Professor Dr. W. Gross
Type Species: *Grossius aragonensis* n. sp.

Grossius aragonensis n. sp.

Definition: Large onychodontid (estimated overall length 1 m or more). Single postparietal occupies half of the skull table. Inter -, supra -, and extratemporals long and low. Dorsal section of postorbital twice as long as ventral section. First squamosal very low, contacting only the posteroventral corner of the postorbital. Ten or more posterolingually curved main teeth on both parasymphysial tooth spirals, lingual sides of teeth with enamel striations (40-50 per 1 mm). Blunt, conical marginal teeth in a gutter of the dentary and/or lingual to the ventral lamella of the maxilla. Deep internasal cavity, in which the main teeth of the parasymphysial tooth spirals insert. Dermal skull bones covered with small, tightly-packed tubercles (general impression: smooth surface with fine raster). Round scales; scale surface probably unornamented, portions of the overlapped sections with isolated small, dorsal tubercles.

Location & Stratigraphy: Moyuela Formation, lower Middle Devonian 50 m southeast of

the Loscos Monforte Road, North Rio Moyuela (Carl *et al*. 1972, Fig. 5:Grid point 11 "Carraloscos N"; Area designation "Azarollo Pass"), Province of Aragon, Spain.

Holotype and only specimen: Gö 709-1 (head in 3 parts).

Derivation: for the Province of Aragon.

Comparisons: Like *Quebecius*, this specimen may be immediately recognized as an onychodontid by the parasymphysial tooth spiral and posteriorly curved teeth with the typical lingual side enamel striations. As is the case for *Quebecius*, and, further, in agreement with *Strunius* and *Onychodus*: all are palaeoniscids with similar maxillae and large numbers of sclerotic plates. *Grossius*, like *Onychodus*, is among the large forms within the Onychodontida. *Grossius* differs from *Onychodus* in the shape of its low maxilla, which posteriorly becomes only gradually taller, and is still lower than the maxilla of *Onychodus*, although the suborbital maxillary region is taller than in *Strunius*. Although the form of the premaxilla is not known in *Grossius*, the recovered portion under the rostronasal bone cover (fig. 6c) shows that the premaxilla of this onychodont had an overlaid lamella at the dorsal margin as with *Strunius rolandi* and *Onychodus obliquidentatis* (Jessen 1967 fig. 11F, G) contrary to other species, which are assigned to the same genera (Jessen 1967, fig. 11E, H; Ørvig 1969, text-fig. 11). Also very much like *O. sigmoides* (Jessen 1967, fig. 11C), the upper marginal dentition is hidden by an outer lamella of the maxilla. Unlike *Strunius* and *Onychodus*, the dentary teeth lie in a gutter. The anterior end of the dentary is flat under the parasymphysial tooth spiral -- without a bulging, thickened end as in *Strunius*, or weakly bent upward as with *Onychodus* (Jessen 1967, Fig. 13). The parasymphysial tooth spiral bears a large number of main teeth and, in contrast to *Strunius*, *Quebecius*, and *Onychodus*, three side teeth. All of these characteristics clearly separate *Grossius* from *Onychodus*. It should be mentioned that both species lived at about at the same time. Thus the holotype of *G. aragonensis* was found at a stratigraphic level (Carl's et al. 1972), within the range of *Onychodus* fossils in the USA (Early to Late Devonian with highest frequency in the Early Middle Devonian, based on existing material in museums).

The principle characters differentiating Grossius from the two small onychodonts, *Strunius* and *Quebecius* are the head shape, the make-up of the cheek region (*Grossius* with small first squamosal adjacent to a large second squamosal, with broad postorbital), the presence of an extratemporal, etc. The opercular region of *Grossius* may resemble that of *Strunius*. In any case, it appears unlikely that the opercular region was developed as in *Quebecius*. It thus appears here justified to establish a new genus and species for this unique type specimen.

The ethmosphenoid of *Grossius* possesses a cavity, quite unlike the Rhipidistia, where a massive *septum nasi* develops in this region (Jarvik *et al*. 1964, text-fig. 19). In the Actinopterygii (anterior myodome) and the Actinistia (Bjerring 1971, text-fig. 2: comparing Actinistia with Rhipidistia) a cavity is present in the anterior region of the ethmosphenoids. However its slight degree of expansion and its location (not sufficiently far back under the cranial cavity) do not compare well with the structure in *Grossius*. In the case of the Holoptychiida, recesses (*cv.in*) develop on both sides the internasal septum which are functionally adapted for the admission of the long main teeth of the parasymphysial tooth spirals. Hence Jessen (1967, S. 367) assumed that the same occurred in the Onychodontida. The palatoquadrate, to this extent, may be similar to that found in actinopterygians, as it seems to rise sharply behind the *processus ascendens* (to judge by the entopterygoids), before it drops to the glenoid. The hyomandibular is similar to the actinopterygian and rhipidistian condition, since it lies close to the palatoquadrate and/or the entopterygoid (unlike the case of the Actinistia).

This description of two new genera shows that the Onychodontida is a polymorphic group, variable in the construction of the fins, in the structure and form of the head, and even in the course of the sensory lines. Despite this large variability, characteristics nevertheless remain which permit unambiguous assignment of specimens to the Onychodontida. Some important characteristic are the simple, unfolded teeth, which are curved posterolingually on the tooth spiral, but are otherwise simple conical forms with a unique character (Jessen, 1967, Schultze 1969) in that the lingual face bears more or less

closely spaced enamel striations. In particular, the last-mentioned characteristic makes it possible to assign even isolated teeth unambiguously to the Onychodontida. The parasymphysial tooth spirals, which Jessen (1967) described in detail, are certainly most remarkable -- although, to be sure, the tooth spirals of *Grossius* are more on than after the toothrows, which Jessen (1967, S. 376) would not permit for the onychodontids. Additional, better finds will give us knowledge in more detail of the anatomy of this group—above all, the endocrania—so that perhaps soon, from the mosaic of characteristics, we will see a more exact picture of the showing a closer relationship to one or the other of the crossopterygian groups.