# 9. Notes on the Endocranium of a Devonian Cladodus.

By

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## Preface.

The present paper is based on an imperfect *Cladodus*-endocranium from the Upper Devonian of Wildungen that had been prepared by the late professor O. JAEKEL of Greifswald. Though it cannot be determined with full certainty as to species, however, I have here adopted for it the species-name *Cladodus wildungensis*, proposed by JAEKEL. The endocranium belongs to the Geological-Palaeontological institute of the University of Berlin. For the opportunity of describing it I am indebted to the late professor O. JAEKEL and to professor H. STILLE of Berlin.

## Description.

The *Cladodus* endocranium here under consideration lacks the ethmoidal region, the most dorsal part of the orbitotemporal region, the dorsal and the most posterior parts of the otic region, and the whole occipital region; and it is thus represented only by the main ventral parts of the orbitotemporal and otic regions (figs. 1, 3). As in its present state of preservation it is approximately 5 cm. long its total length may be estimated to about 7—9 cm., and accordingly it is from a fairly large individual.

In general shape the endocranium must have been broad and fairly low. Specially characteristic for it is that its basal face is broad and that its postorbital process is strikingly long. At least the otic and orbitotemporal regions are in several respects suggestive of the corresponding regions in *Chlamydoselachus* (cf. figs. 2, 4).

As normally in Selachians the endocranium is calcified, and also as normally in Selachians its calcifications occur as thin layers of lime prisms. In the otic and orbitotemporal regions such a layer of lime prisms lines

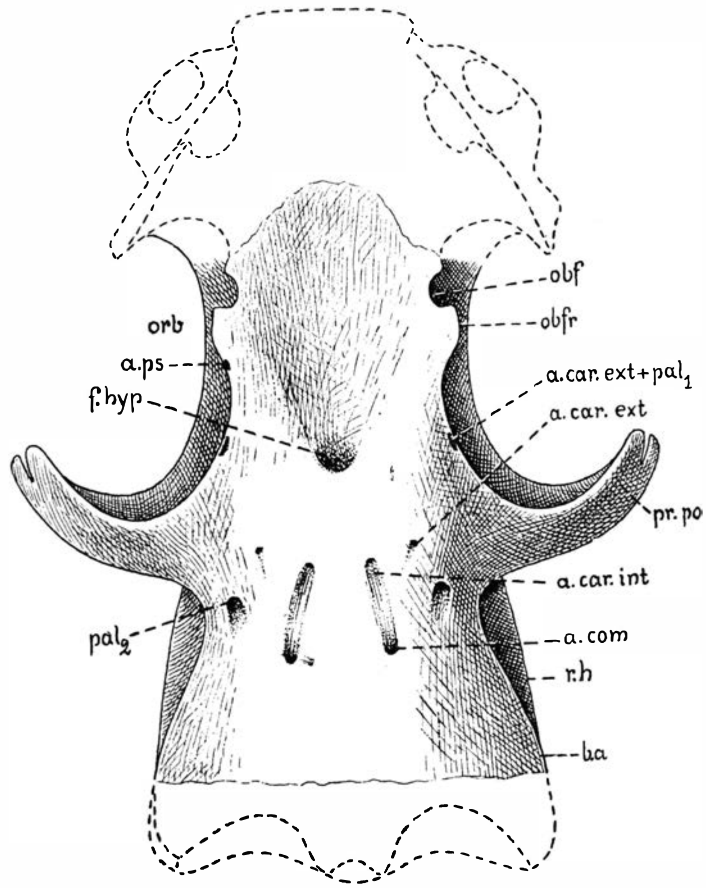


Fig. 1. *Cladodus wildungensis* n. sp. Otic and orbitotemporal regions of the endocranium in ventral view. × 1 ½ diam. approximately.

*a.car.ext*, groove and canal for the a. carotis externa; *a.car.ext* + *pal*$_1$, common canal for the a. carotis externa and for the anterior branch of the r. palatinus VII; *a.car.int*, groove and canal for the a. carotis interna; *a.com*, canal for the a. carotis communis; *a.ps*, canal probably for the a pseudobranchialis efferens (cf. fig. 6); *b.a*, bulla acustica; *f.hyp*, fenestra hypophyseos; *obf*, articular facet for the orbital process (of the palatoquadrate); *obfr*, ridge behind the articular facet for the orbital process; *orb*, orbit; *pal*$_2$, canal for the presumed posterior branch of the r. palatinus VII; *pr.po*, postorbital process; *r.h*, horizontal ridge on the lateral face of the otic region.

the lateral and ventral faces except for an area laterally to the saccular division of the labyrinth cavity, below the articular facet for the hyomandibula, and an area between the opticus and trigeminus exits developed in relation to the eye stalk (figs. 3, 7). A layer of lime prisms lines also certain parts of the labyrinth cavity, e. g. the saccular division and the divisions for the semicircular canals. Moreover layers of lime-prisms are also found lining several canals for nerves and vessels. And finally a layer of lime prisms was probably also present on a large part of the dorsal face of the endocranium, though only isolated fragments are found of it in the present state of preservation of the endocranium. At least with regard to the extent of the one of these layers that lines the ventral and lateral faces of the otic and orbitotemporal regions the endocranium shows a striking agreement with *Chlamydoselachus* (cf. ALLIS 1923, pl. 8, figs. 8, 9; pl. 9, fig. 11).

Otic region. — The otic region (figs. 1, 3, 6, 7) is approximately as long as the orbitotemporal region and somewhat rectangular in a transverse section; and in both these characters it thus agrees with that in *Chlamydoselachus*. It is broadest in its posterior part, thence tapering forwards as far as to close behind the postorbital processes; and as the tapering in this case takes place more in the basal than in the dorsal parts the region is in ventral view suggestive of that in *Chlamydoselachus*. However, whereas in *Chlamydoselachus* its maximum height is situated at the transition to the orbitotemporal region it seems here to have layn further back.

The postorbital process (*pr.po*, figs. 1, 3, 6)[1] is, as has already been mentioned, long, so long even that its length almost equals the breadth of the region just posteriorly to it. In its dorsal part, which is lacking in the present state of preservation, the process was probably fairly broad; in its ventral preserved part it is thin with a narrow, almost edge-like ventral margin. It is curved somewhat forwards and downwards and at the distal extremity it has a broad notch by means of which it is divided there into a dorsal and a ventral branch in a fundamentally similar way to that in *Chlamydoselachus*. Whether as in *Chlamydoselachus* (figs. 2, 4), it was pierced by any foramina for dorsal branches from the n. buccalis lateralis is impossible to make sure, since, as has already been mentioned, its dorsal part is absent in the fossil. The preserved part of its posterior face is in a dorsi-ventral direction concave in the dorsal and convex in the ventral portion, whereas the preserved part of its anterior face in a corresponding direction is concave throughout its height. From its detailed appearance, particularly, however, from the absence of an articulation facet on it, it is evident that the process, quite as that in *Chlamydoselachus*, gave no articulation to the palatoquadrate (cf. ALLIS 1923, p. 151). Accordingly there was no postorbital articulation here between the palatoquadrate and the endocranium.

The proximal part of the postorbital process is extended ventrally on the lateral side of the region down to the cranial base so as to form a lateral boundary of two rostro-caudal canals and certain branches from one of those canals. This ventral part of the process is anteriorly continuous

[1] According to information given to me by professor N. HOLMGREN the ontogenetic development of the endocranium seems to show that the postorbital process in reality belongs to the orbitotemporal region. For practical reasons, however, I have described it here together with the otic region.

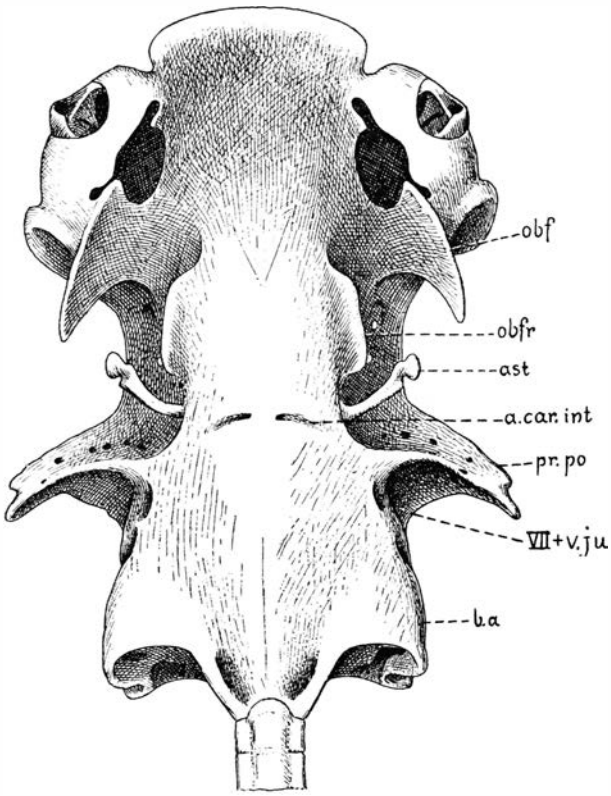


Fig. 2. *Chlamydoselachus anguineus*. Endocranium in ventral view. After ALLIS 1923. *a.car.int*, canal for the a. carotis interna; *ast*, eye stalk; *b.a*, bulla acustica; *obf*, articular facet for the orbital process of the palatoquadrate (not correctly indicated in the figure. The broken line from *obf* should be continued to the anterior margin of the part *obfr*); *obfr*, ridge bounding the articular facet for the orbital process on the posterior side; *pr.po*, postorbital process; VII + *v.ju*, canal for the v. facialis and the v. jugularis.

with the subocular shelf as in recent Selachians (cf. DE BEER 1926, pp. 276—277).

The dorsal wall of the region is lacking in the fossil. How this wall was with regard to details is therefore impossible to make sure; but it is conceivable that a spheno-pterotic ridge (ALLIS 1923, p. 155) was present though it may have been fairly low and indistinct (cf. fig. 4).

Owing to the circumstance that the labyrinth was strongly developed the lateral wall of the region is thick, constituting about a third or more of the entire breadth of the region. Its lateral (external) face is bounded from the ventral face by a broad obtuse ridge, which, at least as far back as it is preserved, resembles the similarly situated ridge in *Chlamydoselachus*. More precisely that ridge begins anteriorly, immediately behind and ventrally to the posterior opening of the rostro-caudal canal which, as we shall see, transmitted the tr. hyoideomandibularis VII (VII h, figs. 3, 7) and goes backwards laterally to the saccular division of the labyrinth cavity on which it probably continued as far back as to the posterior face of the endocranium. The dorsal boundary of the face was, as we shall see, formed by the sphenopterotic ridge already referred to. On the postero-ventral part of the face, immediately dorsally to the ridge forming the ventral boundary of the face, there was in all probability a lateral bulge (*b.a*, figs. 1, 3, 7), caused by the saccular division of the labyrinth cavity, and there was thus here conceivably a somewhat distinct bulla acustica. The part of the face situated on and just dorsally to the bulla acustica must be the articular facet for the hyomandibula (*f.hm*, figs. 3, 7), though it is lined by a layer of lime prisms and in no way differs from the adjacent parts of the face. The part of the face following in front of the ones just described, thus the one immediately behind the preserved part of the postorbital process is like the articular facet for the hyomandibula concave in a dorsi-ventral direction. Both it and the articular facet for the hyomandibula are bounded dorsally by a pronounced horizontal ridge, a ridge (*r.h*, figs. 1, 3) which begins close above the posterior opening of the canal which, as will be shown, transmitted the v. jugularis (*v.ju*) and goes backwards externally to the division of the labyrinth cavity for the external semicircular canal and the ventral part of the division of the labyrinth cavity for the posterior semicircular canal. This ridge, which will be termed the horizontal ridge, thus corresponds to the horizontal ridge described by ALLIS on the lateral face of the otic region in *Chlamydoselachus* below the spheno-pterotic ridge (*r.h*, fig. 4; ALLIS 1923, p. 157) and to a similarly situated ridge in *Acanthias* (WELLS 1917). As pointed out by ALLIS (1923, p. 157) this ridge of the recent Selachians agrees in certain-respects with the opisthotic ridge of the *Teleostomi*, but as in regard to other characters it differs much from the last-mentioned ridge there is no reason to assume that it should be homologous with that.

The presence of the horizontal ridge as defined just above on the lateral face of the region is of special interest for us in this connection. In the recent Selachians in which it is found this ridge is always situated more or less far below the upper margin of the lateral face and it is therefore fully evident that it must have had a similar position here too and that the lateral wall therefore must have continued somewhat upwards above it. Accordingly we find that a dorsal part of the lateral wall is missing in the fossil. This dorsal missing part which probably also includes the most dorsal portion of the postorbital process had behind that process a lateral face which thus was situated dorsally to the horizontal ridge and which conceivably was bounded from the dorsal face of the region by the spheno-pterotic ridge (cf. preceding page). As we thus see the lateral wall of the region seems with regard to the detailed shape of its lateral face to have been as in the recent *Acanthias* (WELLS 1917) but particularly as in *Chlamydoselachus* (figs. 2, 4).

The ventral wall of the region was probably rather thin. It has in the fossil condition no canal or cavity for the notochord, but despite this we may be justified in assuming that the notochord was present and that it probably had a somewhat similar forward extent as in recent Selachians. In this connection it should also be pointed out that, as will be dealt with more in detail below (p. 136), the common carotid went in a canal in the ventral wall and that the a. carotis interna during its passage below the endocranium for a fairly long stretch seems to have layn in the very layer of lime prisms lining the ventral face of the region. For comparison it

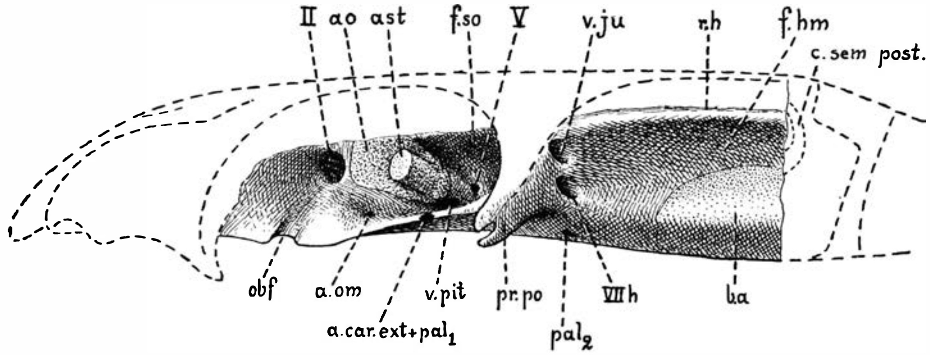


Fig. 3. *Cladodus wildungensis* n. sp. Otic and orbitotemporal region in lateral view. Areas without lining of lime prisms dotted. $\times$ 1 $^1/_2$ diam. approximately.

*a.car.ext* + *pal*$_1$, common canal for the a. carotis externa and the anterior branch of the r. palatinus VII; *ao*, eye stalk area (without lining of lime prisms); *a.om*, canal probably for the a. pseudobranchialis efferens (cf. fig. 6), *ast*, eye stalk process; *b.a*, bulla acustica; *c.sem.post*, division of the labyrinth cavity for the c. semicircularis posterior; *f.hm*, articular facet for the hyomandibula; *f.so*, foramen probably for a supraorbital branch of the r. ophthalmicus superficialis; *obf*, articular facet for the articulation with the orbital process of the palatoquadrate; *pal*$_2$, canal for the posterior branch of the r. palatinus VII; *pr.po*, postorbital process; *r.h*, horizontal ridge on the lateral face of the otic region; *v.ju*, canal for the v. jugularis; *v.pit*, canal for the v. pituitaria; II, opticus canal; V, trigeminus canal; VII h, rostro-caudal canal for the n. facialis.

should be mentioned here that in recent Selachians both the vessels just referred to run wholly beneath the ventral wall of the region, though in certain forms (*Chlamydoselachus*, ALLIS 1923, p. 156) they may be situated in a special tough connective tissue, closely adhering to the ventral wall of the region. As this connective tissue seems to be able to chondrify easily, and as in addition it agrees in its position with the most ventral part of the ventral wall of the fossil form under consideration it is probable that it really represents that and that it thus probably has arisen by a sort of reduction of cartilage originally belonging to the ventral wall. (A similar process of reduction in certain recent Selachians seems also to have taken place below the proximal part of the postorbital process and around the sub-cranial part of the a. carotis externa).

Returning to *Cladodus* we find in this that the ventral face of the ventral wall of the region (figs. 1, 3, 7) is somewhat convex in a transverse direction and broad. It is broadest in its posterior part, thence decreasing somewhat in breadth forwards as far as to a transverse plane just behind the postorbital processes. In regard to its general configuration it is suggestive of the corresponding face in *Chlamydoselachus,* (fig. 2), but whereas in that form it has a distinct bulge caused by the labyrinth cavity, it seems in *Cladodus* to have been entirely destitute of such a formation. However, the labyrinth cavity has in *Cladodus* a quite similar position in relation to the ventral wall and the ventral face as in *Chlamydoselachus*.

Between the ventrally produced part of the postorbital process that has already been described above and the lateral wall proper of the region under description there are, as has been mentioned, two rostro-caudally running canals, a ventral and a dorsal one, which both lead from the orbit to the posterior side of the postorbital process.

The ventral one of these two canals (VIII *h*, figs. 3, 7) is situated fairly close to the cranial base. If we follow it from in front backwards we find that we may distinguish four parts in it: an anterior short and somewhat narrow part, which goes downwards and somewhat backwards; a ventral horizontal part which is wide and sinus-like; a narrow ascending part, which is almost vertical; and finally a posterior somewhat wider part which goes almost horizontally and which opens outwards behind the postorbital process. In the most anterior descending part opens a fairly fine transverse canal, *V l* (fig. 7), which comes from the cranial cavity, and in the posterior horizontal part we find the external opening of a fairly wide canal, VII (fig. 7), which also is transverse and which also comes from the cranial cavity. From the wide sinus-like part of the canal two branches, $pal_1$, $pal_2$, go downwards to the ventral side of the region, and from the posterior horizontal part one branch, *rd*, (fig. 7) leads upwards to the dorsal rostro-caudal canal (*v.ju*). Of the two downward passing branches the anterior one, $pal_1$ (figs. 1, 3, 7) which is the narrowest of the two, goes forwards and downwards to and joins the canal for the a. carotis externa, whereas the posterior one, $pal_2$ (figs. 1, 3, 6, 7), goes backwards and slightly posteriorly to the ventral face of the region somewhat postero-medially to the postorbital process.

The dorsal one of the two rostro-caudal canals just under description (*v.ju,* figs. 3, 7) begins in the orbit somewhat postero-dorsally to the ventral one (VII h) and goes posteriorly and somewhat upwards in such a way that its posterior opening lies just ventrally to the most anterior part of the horizontal ridge of the lateral face of the region. A broad groove leads from below to its anterior opening, from the anterior opening of the ventral rostro-caudal canal.

From its position and relations it is easily understood that the dorsal rostro-caudal canal *v.ju*, just described was traversed by the v. jugularis which ascended to it from the postero-ventral corner of the orbit. This canal may therefore be termed here the jugular canal. After leaving the posterior opening of the canal the jugular vein must obviously have gone close below the horizontal ridge (*r.h*) dorsally to the hyomandibula in a corresponding way as in the recent Selachians.

As the dorsal rostro-caudal canal thus is the canal for the jugular vein the ventral rostro-caudal canal must obviously be at least in the main a nerve-canal developed for the n. facialis and certain of its main proximal branches. On account of its function it will be termed the rostro-caudal facialis canal.

The branches $pal_1$ and $pal_2$ of the rostro-caudal facialis canal were in all probability traversed by the anterior and posterior branch respectively

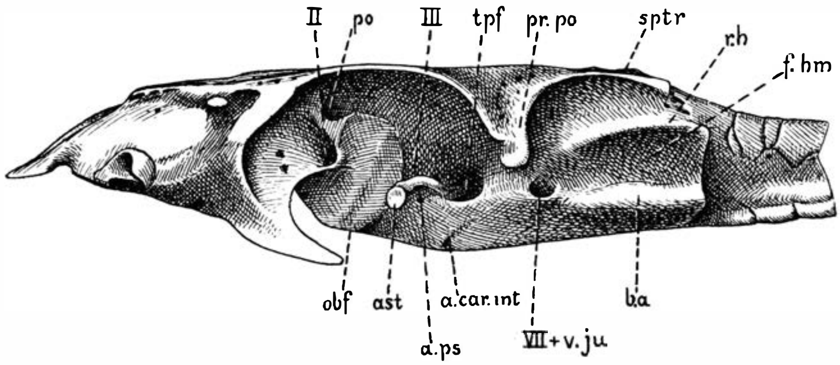


Fig. 4. *Chlamydoselachus anguineus*. Endocranium in lateral view. After ALLIS 1923. *a.car.int*, canal for the a. carotis interna; *a.ps*, canal for the a. pseudobranchialis efferens; *ast*, eye stalk; *b.a*, bulla acustica; *f.hm*, articular facet for the hyomandibula; *obf*, articular facet for the orbital process of the palatoquadrate; *po*, preorbital canal; *pr.po*, postorbital process, *r.h*, horizontal ridge on the lateral face of the otic region; *sptr*, spheno-pterotic ridge; *tpf*, trigemino-pituitary fossa; II, opticus canal; III, oculomotorius canal; VII + *v.ju*, canal for the n. facialis and the v. jugularis.

of the r. palatinus VII, whereas the tr. hyoideomandibularis VII went backwards in the normal way and left the rostro-caudal facialis canal through the posterior opening. In such circumstances it is clear that the facialis ganglionic complex must have occupied a considerable portion of the rostro-caudal facialis canal, in fact probably not less than the three posterior parts of that. The transverse canal V *l* could not be followed inwards and it is therefore uncertain at which place it issues from the cranial cavity, but judging from its position somewhat behind the trigeminus foramen it is not impossible that it was traversed by the roots of the laterales fibres for the trigeminus branches, and if this was so, these roots must have reached the orbit through the anterior opening of the rostro-caudal facialis canal. As we shall see it is not quite impossible that also an arterial branch may have entered and traversed the anterior half of the rostro-caudal-facialis canal.

The branch *rd*, which is situated above the exit of the facialis roots, in the rostro-caudal facialis canal and by which that canal is in communication with the canal for the v. jugularis, may perhaps have transmitted a lateralis branch to some dorsal part of the preopercular sensory canal groove or to the spiracular neuromast or else a dorsal branch of the facialis proper; but it is of course also not impossible that it was traversed by a vessel. Any definite interpretation of it can thus not be given as yet.

The n. glossopharybgeus probably traversed the cranial wall in a similar way as in the recent Selachians, and thus the external opening of its canal may have layn either on the lateral face of the region behind the articular facet for the hyomandibula, as in most Selachians, or else on the posterior face of the endocranium close to the external opening of the vagus canal as in *Chlamydoselachus* (cf. GEGENBAUR 1872, p. 44; ALLIS 1923, pp. 159—160).

In the posterior half of the ventral wall of the region there is a paired, fairly wide, rostro-caudal canal, *a.com* (figs. 1, 6), which lies somewhat internally to the layer of lime prisms lining the ventral face and which is provided with a layer of lime-prisms of its own. This canal reaches forwards to a point somewhat postero-medially to the ventral opening of the canal for the presumed posterior branch of the r. palatinus VII ($pal_2$), from where it is continued forwards by a fairly wide antero-medially running groove, *a.car.int,* (figs. 1, 6), which anteriorly in the region is converted into a canal situated in the layer of lime prisms lining the ventral face.

Somewhat anteriorly and laterally to the groove *a.com,* there is a fairly narrow groove which leads into the canal, denoted with the letters *a.car.ext* (figs. 1, 3, 6, 7). The canal *a.car.ext* goes forwards and laterally in the layer of lime-prisms lining the ventral face of the region finally meeting and joining the canal for the anterior branch of the r. palatinus VII ($pal_1$). The common canal thus formed ($a.car.ext + pal_1$, figs. 1, 3, 6, 7), which is fairly wide, opens anteriorly in the lateral margin of the subocular shelf somewhat in front of the postorbital process and thus in the posterior part of the orbitotemporal region.

With the knowledge which at present we possess concerning the blood vascular system in the recent Elasmobranchs it is not difficult to conclude that the paired canal *a.com* lodged the a. carotis cummunis, that the groove and canal *a.car.int,* were developed for the a. carotis interna, and that the groove *a.car.ext,* though it seems to have been narrower than the former, conceivably was caused by the a. carotis externa (cf. ALLIS 1911, 1912; 1923; O'DONOGHUE & ABOTT 1928; PARKER 1886; DANIEL 1922). In this connection it should be emphasized that, as the groove and canal for the a. carotis externa seem to be narrow, it is not impossible that a branch from the a. carotis communis corresponding to a part of the a. carotis externa might have been given off to the rostro-caudal facialis canal (VII *h*) through the canal for the presumed posterior branch of the r. palatinus VII (*pal*$_2$). If the lastmentioned arterial branch really was present it must have traversed the three anterior parts of the rostro-caudal facialis canal in order to reach the orbit.

Labyrinth cavity. — The labyrinth cavity is large. As has already been mentioned parts of it are lined by a thin layer of lime-prisms. More precisely the three divisions for the semicircular canals with their ampullae,

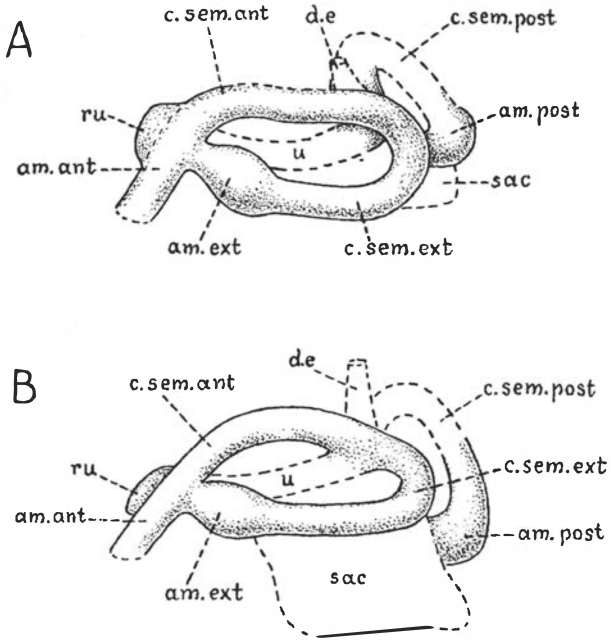


Fig. 5. *Cladodus wildungensis* n. sp. Attempted restoration of the labyrinth cavity, A, in dorsal, B, in lateral view. Parts not preserved or very imperfectly preserved indicated with broken lines. × 2 diam.

*am.ant*, part of the labyrinth cavity probably for the ampulla anterior; *am.ext*, swelling for the ampulla externa; *am.post*, swelling for the ampulla posterior; *c.sem.ant*, *c.sem.ext*, *c.sem.post*, divisions of the labyrinth cavity for the canalis semicircularis anterior, the c. semicircularis externus and the c. semicircularis posterior respectively; *d.e*, probably place of the canal for the ductus endolymphaticus; *ru*, division probably for the recessus utriculi; *sac*, saccular division; *u*, utricular division (crus commune).

a part of the division for the utriculus and a part of the division for the sacculus were lined by such layers. With regard to its extent it should be mentioned that the labyrinth cavity reaches from a point close postero-medially to the postorbital process backwards probably almost or practically throughout the length of the otic region.

The saccular division (*sac*, fig. 5) is fairly large and seems, as in recent Selachians, to have been rather independent of the other division. As it is imperfectly preserved nothing certain can be said of its shape.

The utricular division (*u*, fig. 5) was probably not in direct cummunication with the division for the posterior semicircular canal and it must obviously have had its largest extent in an oblique direction from above downwards and forwards. A somewhat rounded swelling (*ru*, fig. 5) ventrally to the anterior part of the anterior semicircular division probably lodged the recessus utriculi. As is clear from the position and shape of its cavity the utriculus must have been of the same type to that in recent Selachians.

The division for the canalis semicircularis anterior (*c.sem.ant*, fig. 5) is fairly short and lies somewhat close to the utricular division. Its ampullary swelling seems to be partly preserved (*am.amt*).

The division for the canalis semicircularis externus (*c.sem.ext*, fig. 5) is long with an anterior horizontal part situated medially to and causing the horizontal ridge of the lateral face of the otic region, and a posterior part which curves medially and upwards and opens into the upper end of the utricular division together with the division for the c. semicircularis anterior. The swelling which lodged the ampulla (*am.ext*) is well shown.

Finally the division for the c. semicircularis posterior (*c.sem.post*, figs. 3, 5) is imperfectly preserved, but despite this it is clear that as in recent Selachians it must have formed a complete or almost complete ring, which probably was in communication only with the saccular division.

Anything of a canal for the ductus endolymphaticus is not known, but it is very likely that such a canal was present as normally in Selachians although it is not preserved.

From the structure and configuration of its cavity it is evident that the membranous labyrinth in all main respects must have been of the same type to that of the recent Selachians. And as we thus see that type of a membranous labyrinth must be very old.

Orbitotemporal region. — As has already been mentioned the orbitotemporal region practically equals the otic region in length (figs. 1, 3). Ventrally it is somewhat narrower than the otic region, whereas dorsally it probably was approximately as broad as that. However, no quite certain statements can be given of the breadth of the dorsal parts. The ventral wall projects laterally far beyond each lateral wall, forming in this way a broad subocular shelf which posteriorly is continuous with the ventral part of the postorbital process of its side. On account of the presence of the subocular shelf the region is about twice as broad in its ventral wall as immediately dorsally to that, thus than in the part formed by the lateral walls. Any basal angle (»Basalecke») is not present. The height of the region which posteriorly equals that of the anterior parts of the otic region probably decreases somewhat most anteriorly towards the ethmoidal region.

The dorsal wall of the region is not preserved and nothing can therefore be said of it.

The lateral wall of each side is fairly thin, much thinner than the lateral wall of the otic region. Its lateral face (figs. 3, 7) taken as a whole

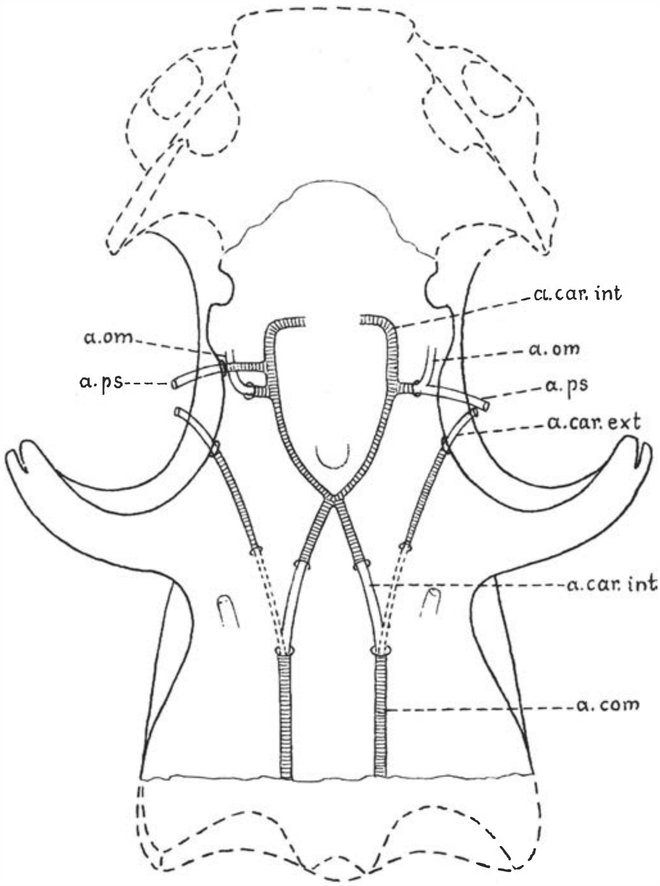


Fig. 6. *Cladodus wildungensis*. Outlines of endocranium in ventral view with an attempted restoration of the main arterial trunks of the head. Parts of the arteries situated in the cranial walls indicated with transversal lines. × 1 ½ diam. approximately.
*a.car.ext*, a. carotis externa; *a.car.int*, a. carotis interna; *a.com*, a. carotis communis; *a.om*, a. ophthalmica magna; *a.ps*, a. pseudobranchialis efferens.

is fairly strongly concave in a dorsi-ventral direction and somewhat concave in a rostro-caudal direction. A little posterior to the middle of its length this face has a fairly large oval area, the eye stalk area (*ao*, figs. 3, 7), which is destitute of lime-prisms. The layer of lime-prisms immediately posterior to this area is raised, projects antero-laterally and is anteriorly concave in a dorsi-ventral direction in such a way that there is reason to assume that it formed the posterior lining of an antero-dorso-lateral process (*ast*, figs. 3, 7). From its position in relation to the nerves and vessels of the region it is, as we shall see, very likely that this presumed process formed the insertion place for the eye stalk or even represented the proximal part of that structure. In this connection it deserves also to be pointed out concerning the process that dorsally to it goes a deep groove for the r. ophthalmicus superficialis V and the n. ophthalmicus lateralis, and that immediately ventrally to it there is a pit in which, as we shall see, the pituitary vein emerged (*v.pit,* figs. 3, 7). On the anterior ventral part of the face fairly close behind the ethmoidal region we find the articular facet for the orbital process of the palatoquadrate, thus the facet for the »palato-basal» articulation. This facet (*obf,* figs. 1, 3, 7) which is lined by lime-prisms, forms a fairly narrow groove which extends from above downwards and somewhat forwards. Ventrally it is very well pronounced, being bounded both anteriorly and posteriorly by a ridge, whilst more dorsally its boundaries are obscure. The ridge bounding it posteriorly (*obfr*), which is rounded, is particularly thick and strong.

The ventral wall of the region, which as has already been pointed out, forms a broad subocular shelf and which therefore is broad seems to have been at least somewhat thick. Its posterior part is pierced by a fairly small, rounded fenestra hypophyseos (*f.hyp,* figs. 1, 6) whilst its lateral margin anteriorly bears a deep notch which is the ventral end of the articular facet (*obf*) for the orbital process. The ventral face of the wall rises somewhat forwards towards the ethmoidal region so as to be directed a little forwards. Otherwise it should be pointed out concerning it that this face in the median part has a broad shallow rostro-caudal groove bounded by a low broad longitudinal ridge on each lateral side and that accordingly a transverse section through it is somewhat convex laterally and concave in the middle part.

The n. opticus had its exit through a short wide canal (II, figs. 3, 7) which opens into the orbit somewhat postero-dorsally to the articular facet for the orbital process, close in front of the eye stalk area. The external opening of this canal faces antero-laterally.

The n. oculomotorius must have pierced the cranial wall somewhat behind the n. opticus in the anterior part of the eye stalk area, but nothing is known so far of its canal. The n. trochlearis probably reached the orbit somewhere dorsally to the opticus, but nothing is known of its canal either.

The n. trigeminus proper or, perhaps more precisely, its roots, i. e. the somatic sensory and visceral motor roots (cf. NORRIS & HUGHE 1920), emerged through a fairly fine canal, V (figs. 3, 7), which opens into the orbit somewhat posterior to the eye stalk area, in a deep wide pit bounded by the subocular shelf below and the postorbital process behind. In this pit are also the anterior opening of the canal for the v. jugularis (*v.jug*) and the anterior opening of the rostro-caudal facial (VII h) canal of which the former lies fairly far postero-dorsally and the latter posteriorly to the external opening of the trigeminus canal. As has already been mentioned above in the description of the rostro-caudal facialis caudal (p. 135) it is possible that the roots of the lateralis fibres for the n. trigeminus had their exit from the cranial cavity through the canal denoted V *l* (fig. 7) into the most anterior ascending part of the rostro-caudal facialis canal from which they finally reached the orbit.

As the conditions are with regard to the exits of the trigeminus roots through the cranial wall we must assume that the trigeminus ganglionic complex was situated mainly outside the cranial wall in the pit bounded by the subocular shelf and the postorbital process and that the lateralis fibres reached it in that pit through the anterior opening of the rostro-

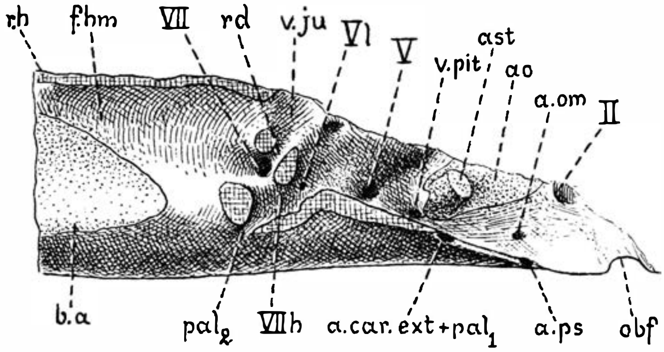


Fig. 7. *Cladodus wildungensis* n. sp. The parts preserved of the otic and orbito-temporal regions seen from the right side with the postorbital process and certain other parts removed. Section areas indicated with crossing lines; areas without linie prisms dotted. × 2 diam.

*a.car.ext* + *pal*$_1$, common canal for the a. carotis externa and the anterior branch of the r. palatinus VII; *a.o*, eye stalk area; *a.om*, canal probably for the a ophthalmica magna (cf. fig. 6); *a.ps*, canal probably for the a. pseudobranchialis efferens (cf. fig. 6); *ast*, eye stalk process; *b.a*, bulla acustica; *f.hm*, articular facet for the hyomandibula; *obf*, articular facet for the orbital process of the palatoquadrate; *pal*$_2$, canal for the posterior branch of the r. palatinus VII; *rd*, canal connecting the canals *v.ju* and VII *h*; *r.h*, horizontal ridge of the lateral face of the otic region; *v.ju*, canal for the v.jugularis; *v.pit*, canal for the v.pituitaria; II, opticus canal; V, trigeminus canal; V *l*, canal probably for the roots of the lateralis fibres to the trigeminus branches; VII, canal for the facialis roots; VII *h*, rostro-caudal facialis canal.

caudal facialis canal. From the ganglionic complex the r. ophthalmicus superficialis V and the n. ophthalmicus lateralis must have taken an antero-dorsal direction and have gone in the pronounced groove which, as has already been mentioned, is present dorsally to the eye stalk area and eye stalk process. The r. ophthalmicus profundus in all probability had its course ventrally to the eye stalk process. Immediately after its origin from the ganglionic complex the n. buccalis lateralis probably gave off the r. oticus dorsally to the canal for the v. jugularis through the roof of which it reached the dorsal face of the endocranium. The r. mandibularis must have passed straight laterally across the dorsal side of the subocular shelf in a shallow groove which passes off in a lateral direction from the trigeminus foramen.

The canal for the a. carotis interna (*a.car.int*, figs. 1, 6) which, as we have seen, from the ventral wall of the otic region continues forwards into the ventral wall of the region here under description approaches in this the median line and joins its fellow of the other side close behind the fenestra hypophysea, then soon separating again from that, continuing antero-latero-dorsally within the lateral cranial wall. For a fairly long distance in this direction it is narrow. Somewhat postero-ventrally to the opticus canal it joins a fairly wide transverse canal, *a.om* (figs. 3, 6, 7) from the ventral part of the orbit, and immediately after this it becomes much wider and takes a somewhat more decided upward direction to the opticus canal in which it opens on the ventral side.

On the right side of the specimen we find close in front and ventrally to the canal *a.om* a second transverse canal, *a.ps* (figs. 1, 6, 7). This canal, which is approximately as wide as the canal *a.om,* begins at the very lateral margin of the subocular shelf and goes medially and somewhat upwards in a direction towards the internal carotid canal. It could not be traced quite to the internal carotid canal but despite this it is very probable that it lead to and opened in that.

As it actually begins below the orbit, it is very unlikely that the canal *a.ps*, transmitted the a. ophthalmica magna which as is well known goes to the eye. We are therefore lead to the conclusion that it was traversed by the a. pseudobranchialis efferens. And if this conclusion is true the a. ophthalmica magna must of course on the right side have reached the orbit through the canal *a.om*.

On the left side of the specimen no traces are found of the canal *a.ps,* but whether this really means that it was absent or that it is not preserved, because it was destitute of a lining of lime prisms or because its lining with such prisms had become destroyed, is impossible to make sure. But if it really would be so that it was absent on the left side of the specimen the conclusion seems inevitable that the canal *a.om* on that side was developed for the a. pseudobranchialis efferens and that the a. ophthalmica magna there as in recent Selachians (ALLIS 1923, figs. 52, 60; DANIEL 1922; etc.) was given off from the a. pseudobranchialis efferens already before that artery entered the canal *a.om* (cf. fig. 6).

The canal for the a. carotis externa (*a.car.ext,* figs. 1, 6) passes in the region forwards and laterally in the layer of lime-prisms lining the ventral face. Fairly soon it fuses, as we have seen, with the canal for the supposed anterior branch of the r. palatinus ($pal_1$, figs. 1, 3, 6, 7) and the common canal thus formed continues forwards and laterally to the lateral margin of the subocular shelf where it opens. More precisely the anterior opening of this common canal is situated opposite the posterior part of the eye stalk area.

As we find from the description just given of their canals the a. carotis interna and the a. carotis externa had within the region a fundamentally similar course as in the recent Selachians. However, it is of importance to note that they passed here to a much larger extent within the cranial walls than in any recent Selachian. Particularly interesting is to find that the a. carotis interna here in *Cladodus* entered the cranial cavity first as far forwards as at the opticus canal, whilst in all the recent Selachians where its cource is known in detail it definitely enters the cranial cavity already in the ventral part of the fossa hypophyseos from where it goes upwards and forwards along the medial face of the lateral cranial wall (and thus within the cranial cavity) to the opticus exit.

The circumstance that thus the carotids here to a large extent were situated within the cranial walls seems to show that these walls in the geologically older Selachians were thicker and better developed than in the recent representatives of these. In any case we may be justified in suspecting that the cranial walls in the geologically younger Selachians may be somewhat reduced in thickness as compared to those in the earlier appearing Selachians. And, as we have seen (p. 133 above), not only the orbitotemporal region but also the otic region shows conditions which lead us to such suspicions.

As has been mentionnd already above in the desciption of the region there is on the lateral face of this, immediately below the eye stalk process, a deep pit at the bottom of which a canal opens. This canal (*v.pit,* figs. 3, 7) which comes from the fossa hypophyseos and leads to the orbit must have been traversed by the v. pituitaria, which thus had its normal course and position.

Finally before finishing the description of the region it should be specially pointed out that the eye stalk process was situated exactly at the place at which the eye stalk of recent Selachians abuts against the cranial wall, and that it therefore may be assumed either that it was a basal part of an eye stalk, in which case the eye stalk would belong to the lateral wall of the region, or else that it formed a thick process against which the eye stalk rested with its basal face.

## Concluding remarks.

Though being imperfect the *Cladodus* endocranium described here is of much interest. It shows that the endocranium of the Cladodontids was of the Selachian-type and that at least in regard to the otic and orbitotemporal regions it was in several respects much as that in *Chlamydoselachus* among the recent Notidanids. In addition it shows that the labyrinth was very Selachian-like; that an eye stalk probably was present; that the cranial nerves in most respects were as in *Chlamydoselachus* and the Notidanids in general; and finally that also the vascular system of the head must have been fundamentally as in the recent Selachians.

The fact that with regard to their cranial anatomy they agree so well with each other indicates that the Cladodontids and the recent Selachians belong more closely together than what has been suspected. In fact one is even lead to the suspicion that the Notidanids and among them particularly *Chlamydoselachus* may in some way be descendents from a stock fairly closely related to the Cladodontids. Be this as it may, it is fully clear that the Selachian plan of organisation has arisen already in the Lower Palaeozoic and has remained almost unchanged up to the present time. The Selachians are thus with regard to their cranial anatomy a very conservative group of lower gnathostome vertebrates, in fact a much more conservative group than could be anticipated. It is even possible that in the respect just mentioned they are the most conservative group of lower gnathostome vertebrates known at present.

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