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ON THE PARASPHENOID OF THE BRACHYTHORACI

Abstract. — A description is given of the Brachythoraci parasphenoid as compared with the corresponding structure in Acanthaspidiidians and some Crossopterygiidians (Polepidae), and with the Acanthodian anterior-basal.

INTRODUCTION

The first description of the parasphenoid of the Arthrodires was made by E. S. Hills (1936) upon discovering in the endocranial floor of the *Coccosteus* (= *Buchanosteus*) *osseus* the presence of a „thickened part composed of solid bone“ with a somewhat complicated structure.

A dermal element, coating the very same region of endocranium of *Kujdanoviaspis buczacziensis* but showing a much simpler structure, was described by E. A. Stensiö (1942).

In an addendum to his next paper on the cranium and cervical joint of the Dolichothoraci (Acanthaspida) (1945), Stensiö is led to the conclusion that the dermal element, described by him and by Hills, constitutes the parasphenoid. In the same paper Stensiö writes that in certain Brachythoracid Arthrodires from Wildungen (*Erromenosteus*, *Trematosteus*, *Brachyosteus*) he had ascertained the presence of the parasphenoid, shaped as a powerful bone, extending, as it does in the Crossopterygiidians and most of the Palaeonisciformes, backwards to underneath the transitional part between the orbito-temporal and the otic regions of the endocranium. E. A. Stensiö believes that this element is provided with a paired processus ascendens.

In their paper on the anterior superognathal of *Gorgonichthys*, D. H. Dunkle and P. A. Bungart (1946) published a drawing representing the parasphenoid of *Dinichthys terrelli* and *Heintzichthys gouldii* mentioning in the text that the superognathal elements are intimately associated with a parasphenoid-like plate which is apparently to be homologised with the anterior-basal element of the Acanthodians.

The most recent reference to this element, here under consideration, is to be found in a paper by E. Jarvik (1954). When speaking of his hypothesis concerning the development of parasphenoid in fishes, that

author expresses an opinion that in the Arthrodires the bone, as mentioned above, represents a primitive type of structure, apparently without ascending processes. Basing his statement on an unpublished paper by Stensiö he also alleges that the development of the parasphenoid in Arthrodires is characterised by disintegration and reduction.

Kujdanoviaspis buczacziensis and *Buchanosteus osseus* are the only representatives of the Arthrodires whose parasphenoids have been reported upon at any length. Since, as shown by Stensiö, both, the latter of these forms, as well as *Kujdanoviaspis*, belong to the Arctolepida, no detailed description of the parasphenoid of Brachythoraci is thus far available.

There are three specimens of these bones in the fossil material deposited at the Muzeum Ziemi (Museum of the Earth) in Warszawa and collected by late Mrs. Z. Gorizdro-Kulczycka in the Upper Devonian of Kielce. Two of them were discovered in association with other skull fragments belonging to *Dinichthys* cf. *pustulosus*, and to the representative of a new genus of Brachythoraci, probably closely related to *Pholidosteus*. A description of these fragments will be given in a forthcoming paper. No fossil remains were found associated with the third specimen, and its generic and family appurtenance, cannot, therefore, be established. Nevertheless its close resemblance to the parasphenoid of *Dinichthys terrelli* and *Heintzichthys gouldii* as figured in the drawing by Dunkle and Bungart, testifies to its referability to the Brachythoraci. This specimen is in the most complete state of preservation of the three at the writer's disposal. Through treatment in acetic acid some of its very delicate structural details have been disclosed and it is on this specimen that the writer has based his present description of the parasphenoid of Brachythoraci.

The writer's thanks are due to Professor D. W. Obrutschew of Moscow and to Dr. D. H. Denison of Chicago for the valuable hints received from them by way of correspondance while he was working on his description of Devonian fishes from the Holy Cross Mts. He is also particularly indebted to Professor W. Gross of the Berlin Humboldt University for making accessible to him the collection of fossil fishes at the university's palaeontological institute, and for the friendly advice extended to the writer during his brief visit at the laboratory operated under the management of Prof. Gross.

DESCRIPTION

The parasphenoid of the Brachythoraci displays a rather complicated structure. Two parts may be differentiated in this bone, namely the anterior (*pa*) in the form of a strong plate with a sub-cordate outline,

terminating in a sharp apex projected anteriorly, and the posterior (*pp.*) transversally elongated, thick around the midpoint and thin around the edges.

Transversally the anterior cordate part (*pa.*) is somewhat concave on the ventral side, and convex dorsally. At the same time its lateral edges rather turn up in the dorsal direction, particularly so in its broad posterior region. Longitudinally the anterior cordate part bends gradually dorsad as it approaches its anterior limit. On the ventral side, along the mid-line, a longitudinal crest (*cr. m.*) occurs in some forms (though absent in the specimen *incertae familiae*, showing the best state of preservation), more or less sharply edged, with height increasing anteriorly. Its basal width increases in the same direction. The crest is particularly distinct in the parasphenoid of *Dinichthys* cf. *pustulosus* where it reaches to the anterior end of the element and terminates in a sharpened process. In this form the longitudinal crest passes posteriorly into a rather small flat area (*a. tub.*) spotted by minute tubercles identical to those found on the external surface of the dermal bones of the skull. A longitudinal groove runs dorsally along the mid-line of the anterior cordate part of the parasphenoid (*sm.*). The free bone edge is grooved and serrated.

The posterior part (*pp.*) is unfortunately in a state of incomplete preservation. The lacking details are the more delicate marginal parts, in the form of thin lateral lamellar processes (*prl. v.*), situated ventrally, whose outline has been figured by Dunkle and Bungart (1946) in their drawing of the parasphenoid of *Dinichthys terrelli* and *Heintzichthys gouldii*. On the base of the cited drawing it may be inferred, that these processes are very well developed in *Dinichthys terrelli*, while in *Heintzichthys gouldii* they are rather rudimentary.

The posterior part of the parasphenoid of Brachythoraci transversally somewhat concave, presents a perfectly smooth and even ventral surface, lacking any details. It is separated from the anterior cordate part by a distinct transverse groove (*s. tr.*) whose course across the element is traced at an angle with anteriorly pointed apex. Medially the groove is partitioned by a bone lamella pierced by a large foramen communicating with the left and right portions of the groove. This gives the semblance of a delicate bone-bridge spanning the central region of the groove (*p.*). The ventral side of the bridge passes with no signs of demarcation to the ventral surface of the anterior cordate part, while from the posterior part it is separated by a narrow groove communicating at both ends with the transverse groove which transects the whole element. Close to the bone margin a minor groove branches off on both sides into the transverse groove (pl. II, fig. 7) and traverses the lateral surface running an-

teriorly to the dorsal side of the anterior cordate part of the element, where it soon disappears. In the mid-part of the groove, on both sides of the median bridge, there are two symmetrically arranged, fairly large foramina (*c. aci.*) separated by a bone lamella (pl. I, fig. F; pl. II, fig. 6), vertically piercing the parasphenoid and communicating with a basin-like depression situated centrally on the dorsal side of the element. A rather small ridge (*cr. fh.*) is found between the two foramina of the depression, with its one end coalescing imperceptibly with the front wall of the depression, while the other end terminates as a free process on the back wall. From the foramina at the floor of the hypophysial depression (*fh.*), two somewhat divergent furrows run across the front wall. The walls of the depression which, frontally, rather gently partition off the posterior part of the parasphenoid from the anterior cordate part, at the back drop down steeply toward the thin list of the posterior rim. On the sides they form sub-even, triangular processes (*prl. d.*), transected by a deep notch. From underneath these, branch off lamellar lateral processes of the dorsal side, as mentioned here above.

The present description has been based on the shape of the parasphenoid in *Brachythoraci incertae familiae* and of the specimen referable to *Dinichthys cf. pustulosus*. As figured in the drawing by Dumle and Bungart, it also agrees with the structure of the parasphenoid in *Dinichthys terrelli* and *Heintzichthys gouldii*.

Though the bad state of preservation is a hindrance in the way of observations, yet it would seem that the parasphenoid belonging to a new representative of *Brachythoraci* is of a somewhat different structure. It shows a similar curve in the anterior part; ventrally it also is provided with a longitudinal crest though not so strongly developed as in *Dinichthys cf. pustulosus*. Further, it probably lacked the transverse groove as well as the bridge and foramina piercing the element at mid-line. In its dorsal region there probably existed a single, blind, funnel-like pit poorly walled in.

DISCUSSION

In its shape the parasphenoid of the *Brachythoraci* differs considerably from the corresponding element in *Kujdanoviaspis buczacziensis* where it is a flat rhombiform plate, strewn with minute tubercles and pierced at mid-point by the hypophysial foramen. In this representative of the *Arctolepida* the element here considered is in no way related to the internal carotids which penetrate the skull laterally from the parasphenoid.

The shape of the parasphenoid in *Buchanosteus osseus* is an intermediate form between that in *Kujdanoviaspis* and in such representatives

of Brachythoraci as *Dinichthys* and *Heintzichthys*. It is also a rhombiform plate strewn with tubercles arranged along a somewhat radial pattern. On the other hand, instead of the single hypophysial foramen, two foramina will be here encountered ad mid-point, partitioned by a bone lamella. Behind these foramina there is a transverse groove which, in the opinion of E. S. Hills, unites with the blind sac-like pits and communicates on each side with the canal which opens on the lateral bone margin. E. S. Hills favours the supposition that these two foramina are the hypophysial canals, in spite of his own assertion that he knows of no case in which hypophysis, either in embryonic or adult stages, was paired. That author also supposes that the lack of lamina in the hypophysial foramen in *Kujdanoviaspis* may have resulted from the bad state of preservation of the specimen (1946, p. 218: „...although in a poorly preserved specimen it is quite possible that the duplicate nature of this canal would not be observable“).

This interpretation may be doubted not only owing to the unpaired nature of the hypophysis but also the structure of the parasphenoid in *Dinichthys* and *Heintzichthys*. As may be inferred from the preceding description, the paired foramen is in these forms situated within the transverse groove, which testifies to the mutual association of these two structures. Further, in between the groove foramina a bone-bridge is encountered, which must have served as protection of some connecting structure. It seems rather improbable for the glandular ducts to have developed a network of this kind. It might rather be inferred that internal carotids, connected by anastomosis running underneath the bridge, passed through the paired foramen. As mentioned by Hills and as is to be seen from his drawings, the parasphenoid in *Buchanosteus osseus* has been damaged in the region of the „blind sac-like pits“ and canals leading to the transverse groove. It would appear that this might have led to want of exactitude in reconstruction and that the „blind sac-like pits“ may be parts of canals opening on the lateral margin of the parasphenoid. Yet on the other hand, the absence of any grooves or canals whatever, leading to the hypophysial foramen in the *Kujdanoviaspis buczaciensis* bars all other interpretations and suggests incorrectness in Hills' supposition that the bad state of preservation may be responsible for the absence of the bone lamella.

It is the probable absence of paired foramina, as well as that of the transverse groove on the parasphenoid of the representative of the new genus of Brachythoraci that prohibits full certainty in confirming the correctness of interpretation in the case of these foramina. More constancy is to be expected in vessels of such significance, though in the case of rays, for instance, they vary their behaviour, entering into the

skull cavity either independently by means of paired foramina, or again by means of a single one.

As above cited, the form here considered probably approaches genus *Pholidosteus*, which, with respect to some of its characters, is more primitive than the *Cocosteus* and represents an independent line of evolution of the Brachythoraci. There is a chance, therefore, that a somewhat different course was taken by its internal carotids which penetrated the skull laterally in relation to the parasphenoid, as in the case of *Kujdanoviaspis buczacziensis*, while the transverse anastomosis, if it did exist, might have run very superficially, either on the ventral or on the dorsal side, without leaving signs of its course on the parasphenoid.

In conformity with the above, the parasphenoid in *Buchanosteus osseus* and in Brachythoraci would not be provided with the hypophysial foramen present in *Kujdanoviaspis buczacziensis*. Since the presence of the hypophysial foramen is a primary character, while its absence a secondary one, we must recognise when accepting the above interpretation, that the parasphenoid in *Kujdanoviaspis buczacziensis* represents a more primitive stage than that encountered in *Buchanosteus osseus* and the Brachythoraci.

Similarity in structure of the parasphenoid, referable to *Buchanosteus* and that of Brachythoraci, is one more proof testifying to the close relationship between the latter forms and Arctolepida.

As mentioned above, the presence of the hypophysial foramen on the parasphenoid of *Kujdanoviaspis buczacziensis* implies small probability to the suggestion that simplicity of structure in this element is referable to secondary simplification. In this connection it is to be inferred that the evolution of the parasphenoid within both, Arctolepida and Brachythoraci, had taken place independently from that within other stocks of fishes. The resulting characteristic shape of the bone persisted in Brachythoraci to the end of their existence. Inasmuch as the relationship between other representatives of the Arthrodires with those under consideration, has not been adequately clarified and taking into account that no decisive evidence has been supplied showing some stage of reduction of the parasphenoid in Arthrodires (it must be added that not long ago the Arctolepida and Brachythoraci were regarded as lacking this skeletal element) — suggestions concerning the disintegration and reduction of the parasphenoid in the Arthrodires does not seem justifiable in the light of data now available.

The external appearance of the parasphenoid of Brachythoraci resembles that element in Porolepidae as described and figured by Gross (1936) and Jarvik (1954). In these fishes the parasphenoid is also relatively short and broad, with a distinct anterior part separated from the

posterior one by what Jarvik (1954) has called prespiracular groove. In *Glyptolepis* there is a hypophysial foramen in the mid-line of this groove. At first sight these morphological details may appear identical with the transverse groove and the paired foramen associated with it, as described above. Yet, in *Porolepidae*, the prespiracular groove lies superficially only covered with a mucous lining of the oral cavity. This is testified by the presence of ornamentation. Contrarywise, the ornamentation of the parasphenoid of *Brachythoraci*, persisting in *Dinichthys* cf. *pustulosus*, occurs in the anterior cordate part only, while it is lacking in the groove. This condition and the presence of the „bone-bridge“, whose only purpose could have been the protection of underlying structures, both testify that the groove must have been associated with certain anatomic structures by the present writer believed to have been the internal carotids. It would thus seem that the prespiracular groove and foramen on the parasphenoid of *Porolepidae* cannot be homologised with the groove and foramina on the parasphenoid of *Brachythoraci*.

By its external appearance the parasphenoid of *Brachythoraci* also resembles the anterior-basal element of the *Acanthodians*, described by Watson (1937), this being stressed by Dunkle and Bungart (1946). Still — in opposition to the parasphenoid of *Brachythoraci*, which is a typical dermal bone as testified by its histological structure and also by the presence of ornamentation persisting on the parasphenoid of *Dinichthys* cf. *pustulosus* — the anterior-basal element in the *Acanthodians* shows perichondrial ossification only. Neither foramina nor grooves for the internal carotids are to be found on the ventral side of the anterior-basale of the *Acanthodians*. The foramen of the hypophysial canal is situated in the centre of this element. Furthermore, the anterior-basal element differs from the parasphenoid of *Brachythoraci* by a number of other, less significant characters.

The lack in the available specimen of *Brachythoraci* of that part of endocranium adjacent to the parasphenoid, makes impossible a close analysis of this dermal element in its relation to the endocranium, or of the relation of its lateral processes to similar structures on the anterior basal of the *Acanthodians* and the ascending processes of the *Crossopterygians* and *Actinopterygians*.

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O PARASFENOIDZIE RYB BRACHYTHORACI

Streszczenie

Notatka zawiera opis parasfenoideum *Brachythoraci* z górnego dewonu Kielc oraz porównanie z odpowiednim elementem u *Acanthaspida* i niektórych *Crossopterygii* (*Porolepidae*), jak również z antero-basale *Acanthodii*.

OBJAŚNIENIA DO ILUSTRACJI

Pl. I

A antero-bazalny element *Acanthodii* (wg Watsona), B parasfenoid *Buchanosteus osseus* (wg Hillsa), C parasfenoid *Dinichthys terrelli* (wg Dunkle'a i Bungarta), D parasfenoid *Heintzichthys gouldii* (wg Dunkle'a i Bungarta), E parasfenoid *Glyptolepis*, F podłużny przekrój przez parasfenoid *Brachythoraci*, G parasfenoid *Dinichthys cf. pustulosus*, H parasfenoid *Brachythoraci incertae familiae*, A, B, E, G powierzchnia brzuszna, C, D, H powierzchnia grzbietowa.

a. tub. pole pokryte guzkami, bs. ślepe workowate zagłębienie, ca. kanał dla anastomozji tętniczej, c. aci. kanał dla arteria carotis interna, c. hyp. kanał przysadkowy, cr. fh. grzebień zagłębienia przysadkowego, cr. m. grzebień środkowy, fh. zagłębienie przysadkowe, gr. psp. rowek prespirakularny, p. mostek kostny, p. a. przednia sercowata część, pp tylna część parasfenoideu, prl. d. grzbietowy wyrostek boczny, prl. v. brzuszny wyrostek boczny, sc. mały rowek z tyłu kostnego mostka, sm. rowek środkowy, s. tr. rowek poprzeczny, t. guzek.

Pl. II

Fig. 1-2. Parasfenoid *Brachythoraci* n. gen.; 1-strona grzbietowa, 2-strona brzuszna; $\times 1,5$.

Fig. 3. Parasfenoid *Dinichthys* cf. *pustulosus*, strona brzuszna; wielk. nat.

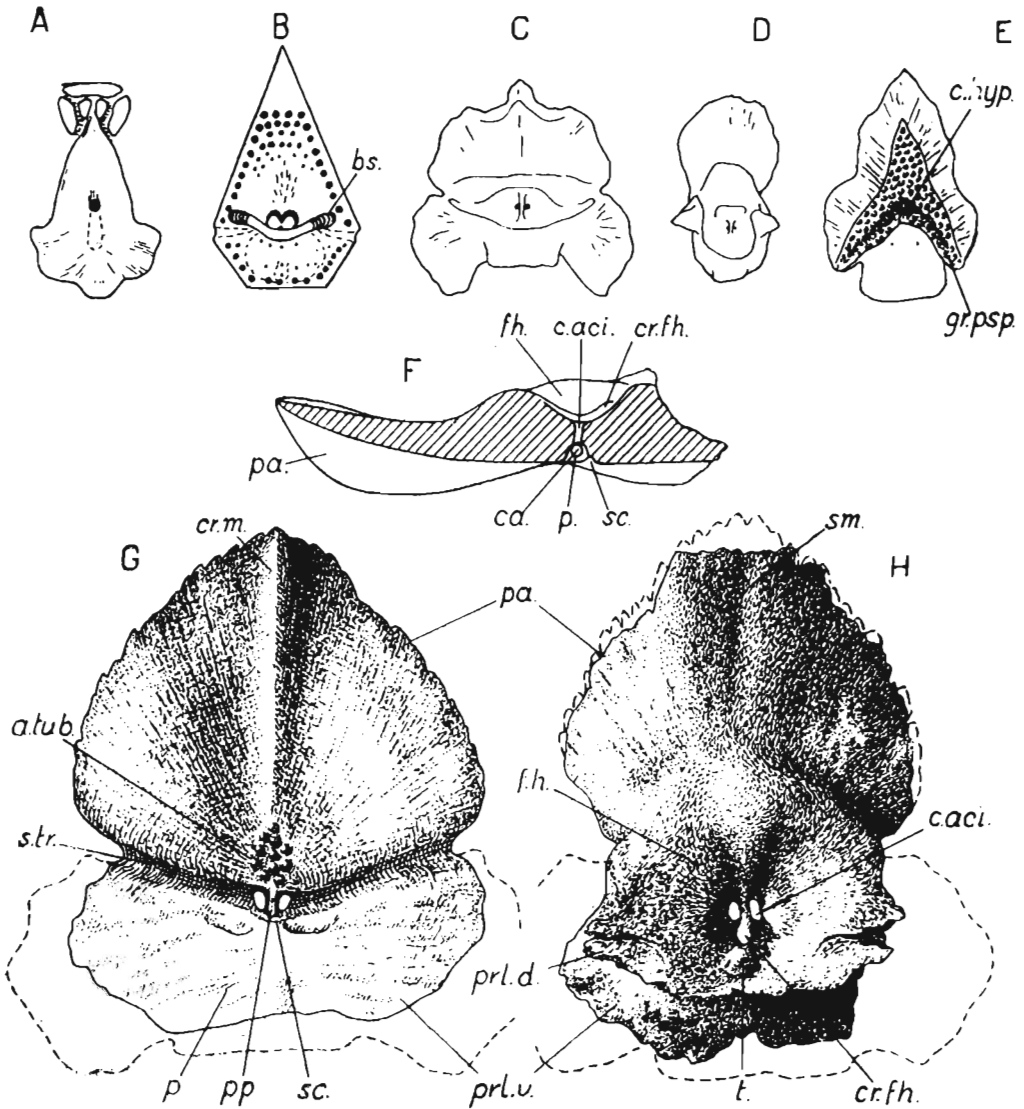
Fig. 4-7. Parasfenoid *Brachythoraci incertae familiae*; 4-strona brzuszna, 5-strona grzbietowa, 7-strona boczna, $\times 1,5$; 6-środkowa część poprzecznego rowka w rzucie ukośnym, ukazującym otwór pod kostnym mostkiem dla anastomozy tętniczej; $\times 3$.

ЮЛИАН КУЛЬЧИЦКИ

О ПАРАСФЕНОИДЕ РЫБ BRACHYTHORACI

Резюме

Предлагаемая статья содержит описание парасфеноида рыб *Brachythoraci* из верхнего девона Кельц и его сравнение с соответствующим элементом представителей *Acanthaspida* и некоторых *Crossopterygii* (*Porolepidae*), а также с антеробазальным элементом *Acanthodii*.



A anterior-basal element of the Acanthodians (after Watson). B parasphenoid of *Buchanosteus osseus* (after Hillis), C parasphenoid of *Dinichthys terrelli* (after Dunkle & Bungart), D parasphenoid of *Heintzichthys gouldii* (after Dunkle & Bungart), E parasphenoid of *Glyptolepis*, F longitudinal section of the parasphenoid of *Brachythoraci*, G parasphenoid of *Dinichthys cf. pustulosus*, H parasphenoid of the *Brachythoraci incertae familiae*, A, B, E, G ventral aspect, C, D, H dorsal aspect.

a. tub. tuberculated area, bs. blind sac-like pit, ca. canal for the arterial anastomosis, c. aci canal for the arteria carotis interna, c. hyp. hypophysial canal, cr. fh. crest of the hypophysial depression, cr. m. median crest, fh. hypophysial depression, gr. psp. preopercular groove, p. bone-bridge, pa. anterior cordate part, pp. posterior part of the parasphenoid, prl. d. dorsal lateral process, prl. v. ventral lateral process, sc. smell groove behind the bone-bridge, sm. median groove, s. tr. transverse groove, t. tubercle.

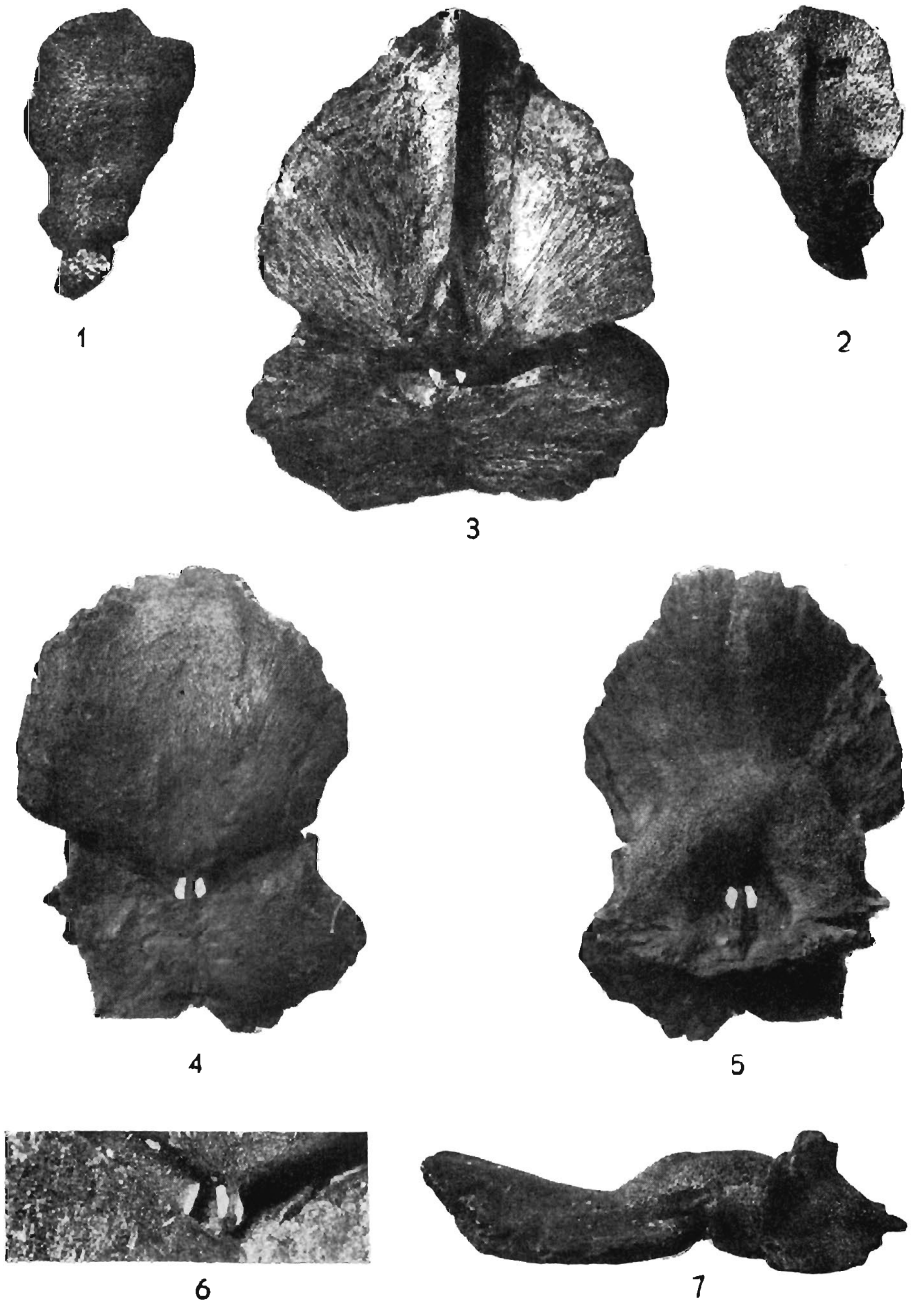


Fig. 1-2. Parasphenoid of *Brachythoraci* n. gen.; 1-dorsal, 2-ventral aspects; $\times 1,5$.
 Fig. 3. Parasphenoid of *Dinichthys* cf. *pustulosus*; ventral aspect; nat. size.
 Fig. 4-7. Parasphenoid of *Brachythoraci incertae familiae*; 4-ventral aspect, 5-dorsal aspect, 7-lateral aspect, $\times 1,5$; 6-mid-part of the transverse groove in oblique projection showing the anastomotic foramen under the bone-bridge, $\times 3$.