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The Genus Gephyrostegus

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STUDIES ON EARLY TETRAPODS

III. THE GENUS *GEPHYROSTEGUS*

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CONTENTS

Gephyrostegus bohemicus Jaekel from the Upper Carboniferous of Nyran is the oldest and most primitive member of the Seymouriamorpha. A new description is given based partly on the described material, but mainly on two hitherto undescribed specimens. These specimens are remarkably complete and make possible a description of the palate, previously unknown, and also a comparative study of the development of the vertebrae.

The single specimen, also from Nyran, described by Watson (1926) as *Diplovertebron punctatum* is made the type of a new species *G. watsoni*.

The position of *Gephyrostegus* in the Seymouriamorpha is discussed. Its primitive nature is emphasized and a comparison is made with later more specialized forms. The relationship of early tetrapods is considered and a new classification suggested.

Introduction

Gephyrostegus has been known for a long time, but no full description of the structure of this genus exists. The best specimen known hitherto was the skull described by Jaekel of which only the outer surface was figured. The two new specimens now available allow us to give a more complete description of the skull and much of the post-cranial skeleton.

This new material has been generously lent to us by the Méstké Museum Historiké, Pilsen (M.P.) and the Narodni Museum, Prague (C.G.H.). Professor D. M. S. Watson (D.M.S.W.) has also lent us two specimens from his private collection. We are glad to record our thanks to Professor Watson and these institutions. The place of origin of material is indicated in the text by the use of the letters given above in parentheses.

Gephyrostegus bohemicus **Jaekel**

Jaekel (1902, text-fig. 1); Watson (1926, p. 238) (*Diplovertebron punctatum* Fritsch); Broili (1905, Pl. 1, fig. 1), (1924, pp. 3–11, Pl. 1, text-figs. 1–2); Pearson (1924, pp. 338–343, text-figs. 1–2).

Type, a single specimen in counterpart from Nyran showing a skull associated with a number of scattered vertebrae, part of a shoulder girdle and the scattered remains of a forefoot. The skull of this specimen was figured by Jaekel (1902).

Gephyrostegus bohemicus was regarded by Watson as synonymous with *Diplovertebron punctatum* (Fritsch 1889, vol. 2, Pls. 50, 52, 53), the type of which consists of scattered bones including a pelvic girdle in which the ilium has an anterior and very long posterior process associated with two isolated vertebrae in which the neural arch is associated with two centra of equal size. New material described in this paper shows that in the vertebrae of *Gephyrostegus* the intercentra are always small, so that this association cannot be maintained. The generic name of *Gephyrostegus* is therefore reinstated and the specimen described in Watson's paper made the type of a new species, *Gephyrostegus watsoni*.

Solenodonsaurus was founded by Broili 1924 on a single specimen, in counterpart, one-half of which had been previously incorrectly described as a rachitimous labyrinthodont (Broili 1905). Broili's type of *Solenodonsaurus janenschi* is identical with the type of *Gephyrostegus bohemicus*.

The following material figured and described in this paper also belongs to *G. bohemicus*.

Specimen I (C.G.H. IIIB. 21. *c.* 587) and its counterpart (M.P. 451). Impressions of an almost complete skeleton showing the outer surface of the skull and palate, lacking most of the tail (Figure 10*A*, *B*).

Specimen II (C.G.H. 3027). Impression of a skeleton showing the dorsal surface of the skull and lacking the end of the tail (Figure 10*C*).

Specimen III (D.M.S.W. B. 65). A specimen showing the anterior part of the skull with an impression of part of the cheek and skull table with a few neural arches, ribs, scales and limb bones. This specimen was described by Miss Pearson in 1924.

The relative sizes of all these skulls is given in figure 1, specimen I being the smallest and Broili's type the largest. This is all the known material of *Gephyrostegus*, it comes from the cannel coal beds of Nyran in the Plzen basin, Czechoslavakia, which are said to be Upper Westphalian in age.

Technique

The nature of the material makes it necessary to include an account of the method of drawing used. In specimens I and II the bones have been lost naturally and the remaining fragments dissolved away by weak hydrochloric acid, so that a clear and sharp impression of the skeleton is left on the cannel coal matrix. In both these specimens the skeleton is almost complete and undisturbed and this condition, combined with the fine texture of the matrix, ensures that even minute details of structure are perfectly shown. In specimen I, for example, the bones of the skull are so delicate that superimposed on the sharp impression of the outer skull surface is an impression of the palate, while in the counterpart an impression of the palatal bones also carries a delicate imprint of the inner surface of the skull roof and cheeks. The light ossification of ths skull means that there is little surface relief, so that in observing either the impression on the actual specimen or Plasticene squeezes taken from it, the general pattern was not clear. Indeed, skulls preserved in this way often appear to show no details of structure, but the sutures, though delicate, are present and the confusion of detail which cannot be followed by direct observation can be resolved in the following way. The outlines of bones on the actual specimen were painted in gradually under a low-power binocular microscope by means of a fine camel-hair brush and chinese white. The specimen so outlined was then drawn by camera lucida on transparent tracing paper. The chinese white was removed and the drawing carefully checked against the actual specimen. Plasticene squeezes were then made and the drawing rechecked against these. Such a transparent drawing allows any doubtful structure to be referred directly either to the Plasticene squeeze (which represents the actual bones) or to their impression on the cannel coal slab. This is a great advantage in dealing with material of this type. The final drawing on the transparent paper was transferred to scraperboard.

Description of material

The detailed account of the structure of *Gephyrostegus* in the present paper is based mainly on the new material, specimens I and II, particularly specimen I.

Skull

The smallest known skull, that of specimen I, is preserved in counterpart so that both the outer surface and the palate are known (figures 2*A*, *B*, 4). Over a range in size (figure 1)

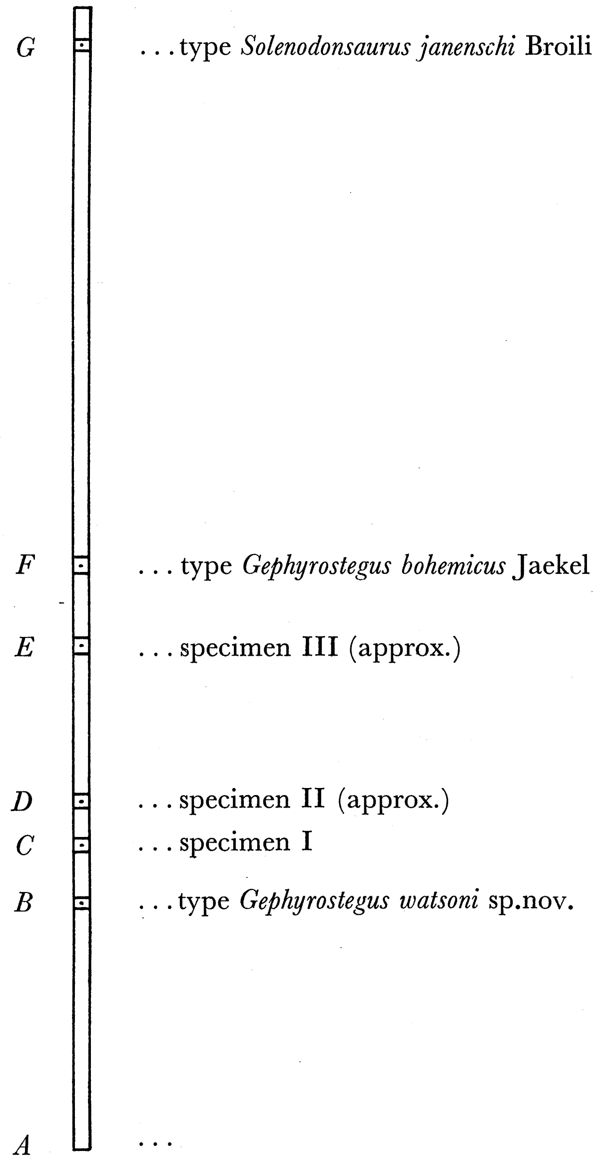

FIGURE 1. *Gephyrostegus* skulls. Length measured in the mid-dorsal line. *AB*, *AC*, etc. (× 1.)

from this to that of Broili's skull little difference in proportion or shape is shown (cf. figures 3, 4).

The skull bones of specimen I are very lightly ossified and the surface ornament, as one would expect in a young skull, consists of a very delicate reticulate ornament in the centre shading to striae at the margins of the individual bones. In the larger skulls this condition still persists and a true reticulate ornament is never developed. Broili and Jaekel both comment on the lack of dermal ornament and the light ossification in their larger skulls.

Lateral line canals even when they are undoubtedly present leave no imprint on the dermal bones of young skulls and are apparent only as ornament develops and the bones become more heavily ossified. At least this is so in *Microbrachis*. There is no trace of lateral line canals in any skull of *Gephyrostegus*, except for a line of shallow elongate pits on the dentary in specimen I which would appear to represent a lateral line canal. The assumption therefore is that lateral line canals are present at least in early growth stages of *Gephyrostegus*, but in view of the light ossification of the dermal bones not recorded in fossil specimens.

The skull table is of reptiliomorph type in which the tabulars meet the parietals so that the post-parietals only suture with these two bones. As shown in Jaekel's skull (figure 3) both an intertemporal and supratemporal are present. This is also shown in specimen I, though here in the collapse of the skull during preservation the pterygoid-parasphenoid articulation on the palate leaves an imprint on the skull table bones in this region.

In the posterior row of bones of the skull table the post-parietals have an ornamented exposure on the skull table from which smooth flanges extend on to the occipital surface. The tabulars are ornamented bones, no occipital flanges are apparent.

The bones of the cheek and preorbital region bear the normal relationship to one another. The dorsal border of the jugal carries a deep notch, a feature which occurs sporadically and in such an unrelated genus as *Urocordylus*.

The dorsal border of the squamosal is in contact throughout its length with the inter- and supratemporals both in this and Jaekel's skull, leaving part of the lateral margin of the tabular free. The attachment of the squamosal to the deck of the skull could therefore be presumed to be sutural but there is no certainty on this point. In *G. watsoni* the cheek is displaced from the skull table, i.e. a free articulation. In *Microbrachis* where a free articulation of squamosal and skull table exists the cheek is often preserved in full contact with the skull table in fossil specimens. In *G. bohemicus* therefore a free articulation is probably present.

There is a complete ring of thirty-three sclerotic plates (figure 3). Sclerotic plates are also present in specimen II (figure 2*C*) but in specimen I, in a very complete and well preserved skull, they are absent and may not be ossified at this early stage.

The marginal teeth on the maxilla and dentary in specimen I are small, their apices slightly recurved and their outer margins smooth except for a longitudinal furrow in some teeth representing the collapsed tooth cavity. Carroll (1965, p. 306) records a single enlarged tooth on the maxilla as a canine but Jaekel's larger skull shows no canine teeth.

The only known palate of *Gephyrostegus* is that of specimen I (figure 2*B*), where its structure is partially obscured by the two lower jaws which lie across it. All the palatal bones are covered by a shagreen of minute teeth. A few larger teeth are carried by the

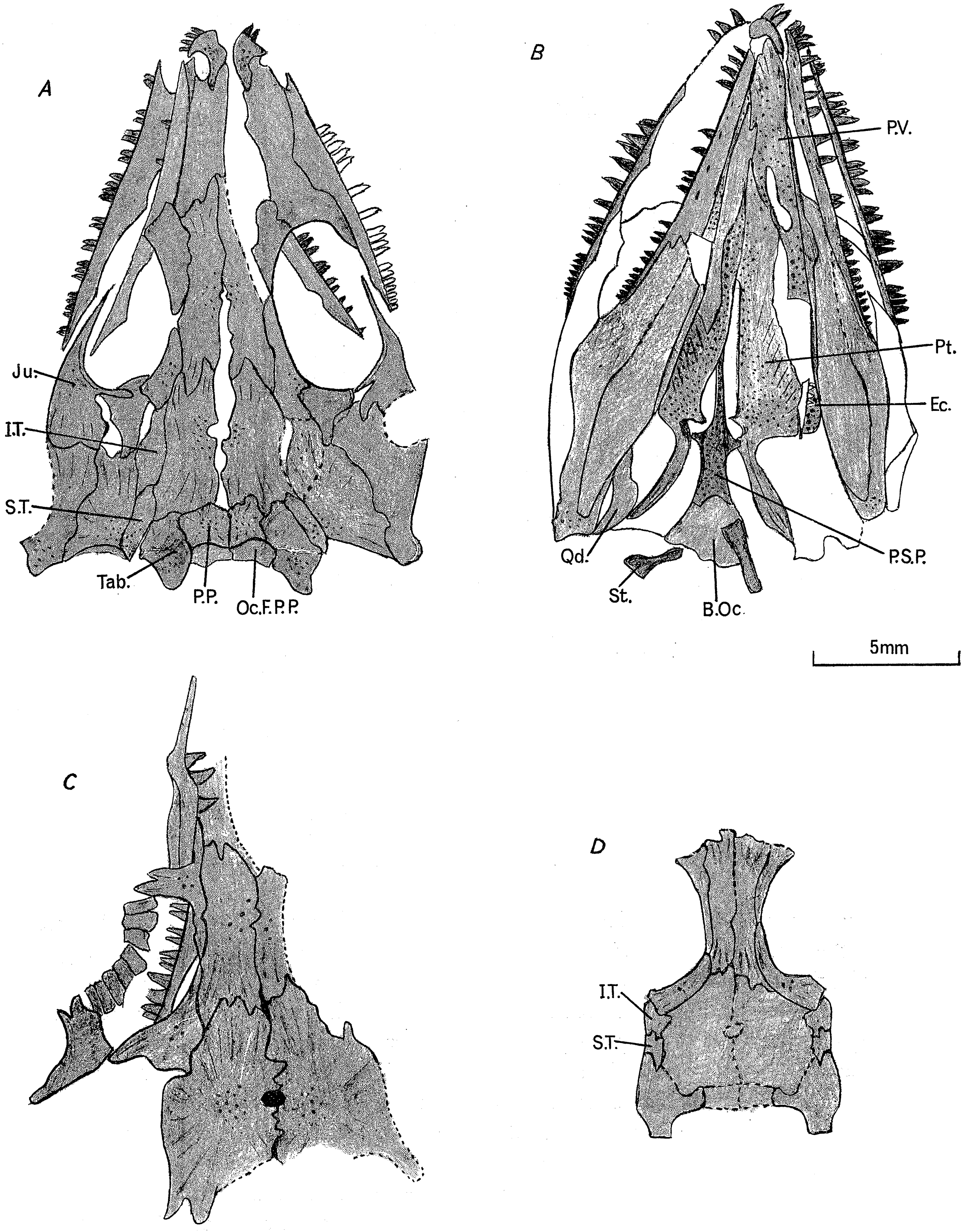

FIGURE 2. *Gephyrostegus bohemicus* Jaekel. *A*, *B*, specimen I; *C*, specimen II; *D*, *Gephyrostegus watsoni* sp.nov.

ectopterygoid but there are no tusks. Jaekel (1902, p. 129) refers to two stronger teeth in the anterior palatine region in his larger skull and it is therefore assumed that larger palatal teeth develop with increase in size.

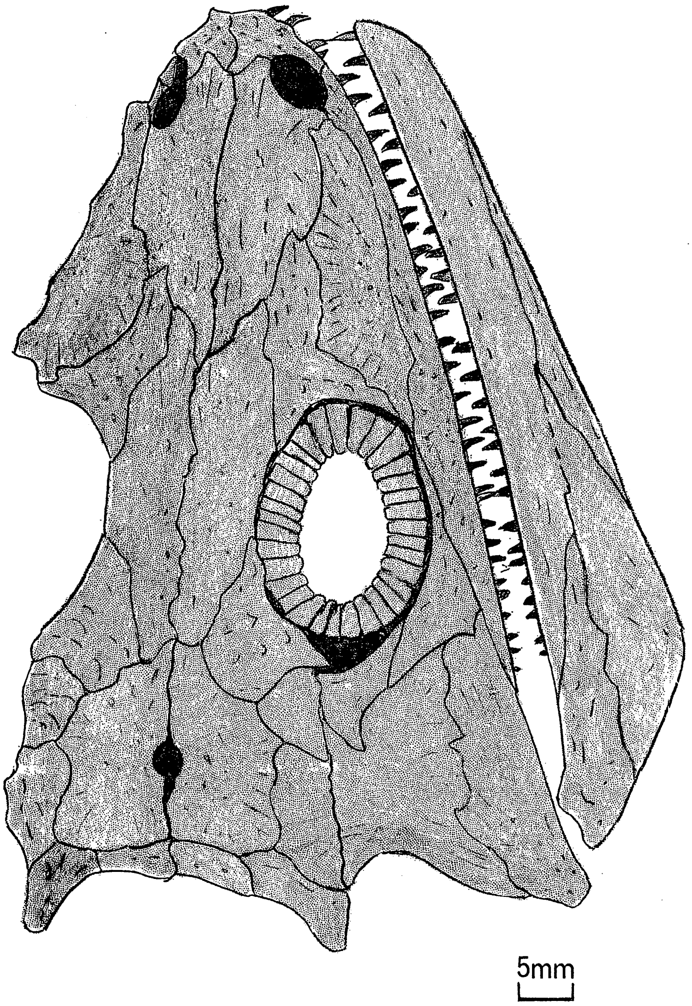

FIGURE 3. *Gephyrostegus bohemicus* Jaekel. Type skull after Jaekel.

The prevomers and palatal flanges of the pterygoid are large so that the anterior two-thirds of the palate is solid, the interpterygoid vacuities being small and not extending far anteriorly, the quadrate ramus of the pterygoid is relatively short. The body of the parasphenoid is narrow and united suturally with the basioccipital which is a wider bone. The basipterygoid processes of the parasphenoid though small are well shaped and fit into a deep groove on the pterygoid, the anterior face of which is strongly buttressed. It is these ossifications which in the fossil show through the lightly ossified skull table bones in the dorsal view of the skull. Between the parotic plate of the pterygoid and the quadratojugal an ossified quadrate is present (figure 2*B*).

The ectopterygoid is a small bone carrying, as already mentioned, a line of larger teeth. Its position in regard to the palatal ramus of the pterygoid is a little uncertain but it does appear to be in natural articulation with it (figure 2*B*) and has been so placed in the restoration of the palate (figure 4). If this position is correct there is no extension anteriorly of the subtemporal fossa and no free pterygoid flange as there is in later seymouriamorphs such as *Seymouria* (White 1939) and *Kotlassia* (Bystrow 1944).

Carroll (1965, p. 306) regards the pterygoid of *Gephyrostegus* as having a true reptilian transverse flange. The prominence of the transverse flange in captorhinomorphs and other

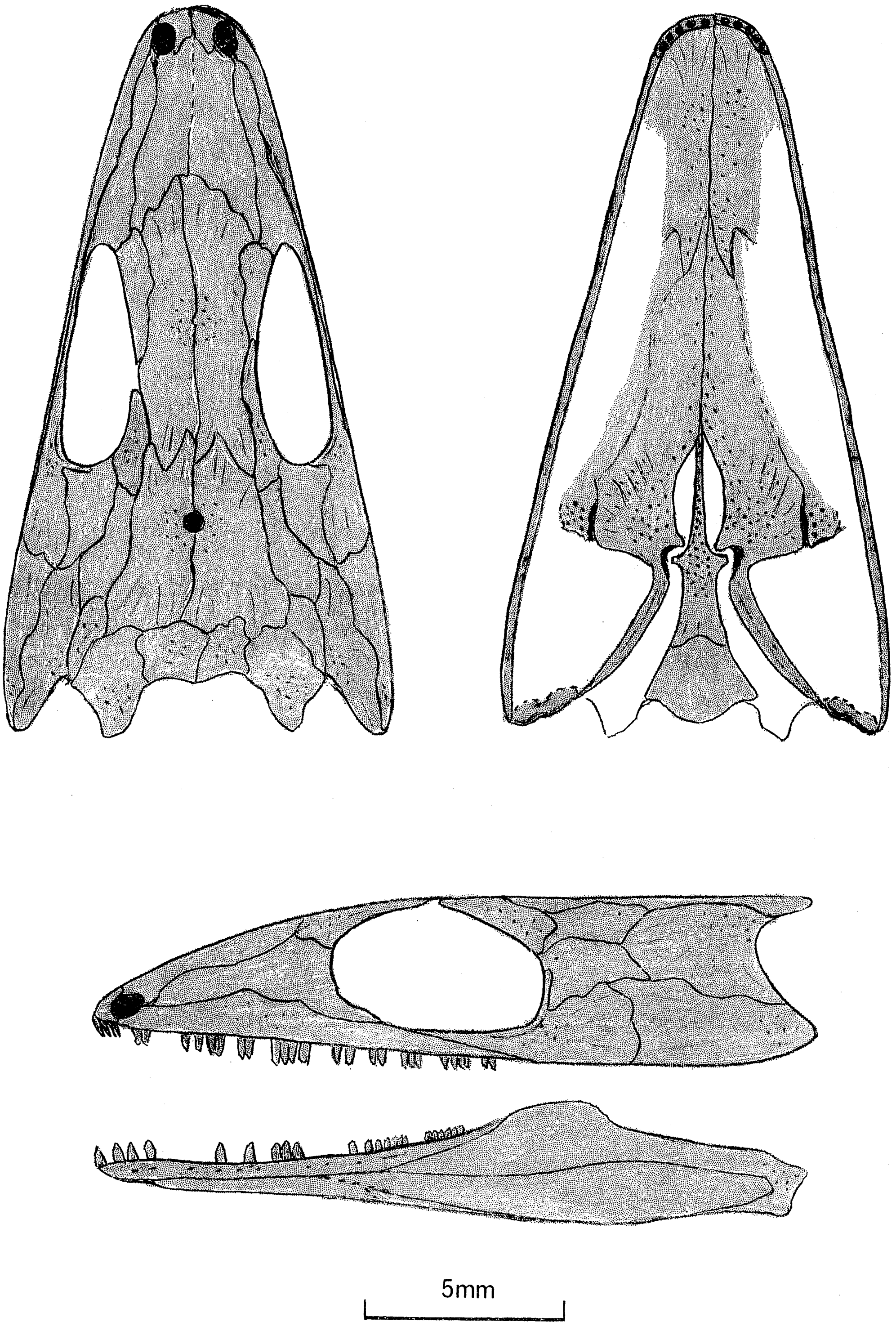

FIGURE 4. *Gephyrostegus bohemicus* Jaekel. Reconstruction of the skull based on specimen I.

primitive reptiles is correlated with the extension anteriorly of the subtemporal fossa which leaves the outer lateral margin of the palatal ramus of the pterygoid free. *Gephyrostegus* is more primitive than later seymouriamorphs in apparently lacking the extension anteriorly of the subtemporal fossa.

In specimen I the otic bones appear to be unossified. Two stapes with a short columella, an expanded foot plate and no stapedial foramen are present (figure 2*B*). The lower jaw is shown in figures 2*B* and 4.

Vertebral column (figures 5, 10*A* to *C*).

The vertebral column in *Gephyrostegus* is known complete, except for the tail in specimens I and II and some twelve vertebrae lying behind the shoulder girdle are present in Broili's specimen. The vertebrae in specimen I are preserved in counterpart so that each vertebra can be looked at from either side and its undisturbed condition is indicated by the fact that only the centrum of the 17th vertebra is missing.

The neural arch does not articulate with the full length of the centrum and the transverse process lies close to the prezygapophyses both lying above the parachordal process from which the post-zygapophyses sweep back free over the posterior part of the centrum. Both pre- and post-zygapophyses are well rounded with horizontal zygapophysial facets. The neural spines are low, rising little above the level of the zygapophyses even in Broili's much larger specimen.

The centra are spaced from one another suggesting that an intercentral cartilaginous pad was present between them and there is a post-pedestal rise. This seems to indicate a fairly large intercentral structure which was substantially cartilaginous, ossifying only in the ventral region to give the typical bony intercentrum. If this interpretation is correct it shows how the seymouriamorph vertebra corresponds with the embolomerous type. The dorsal length of the centrum is always longer than the mid-ventral length and the posterior ventral edge of the centrum is bevelled to accommodate the intercentra.

The range in size of the vertebrae is shown in figure 5, and the following growth changes can be observed in this series (centrum length of 3 mm to 13 mm).

In specimen I the neural arch ossifications are separate from the centrum ossification and the neural arch is in two halves. The zygapophyses in relation to the body of the neural arch are so well ossified that they form a distinct ridge running along the length of the vertebral column. There is no trace of an ossified facet for the capitulum of the rib adjacent to the transverse process. The centra are waisted and ridged. The intercentra are not preserved and were probably unossified as this vertebral column is little disturbed. In specimen II the neural arches are still in two halves (figure 10*C*) and small ossified intercentra are present in the dorsal and caudal regions. In the 13 mm vertebrae of Broili's specimen the neural arches are now single elements and fused with the centra. The transverse process has extended to the anterior margin of the centrum so that the rib capitulum, according to Broili, articulates with an ossified facet adjacent and contiguous with that of the transverse process. The width of the rib head and its slight emargination confirm this. The centra have filled out so that the waisted appearance and the ridges present in the smallest centra have disappeared. The intercentra like those of specimen II are small and independent.

The shoulder girdle is always situated some distance behind the skull and as is clearly shown in specimen II a true neck region distinguished by cervical ribs is present (figure 10 *C*). The sacral vertebrae are little differentiated. The transverse processes of two vertebrae at the level of the pelvic girdle are larger than those of the adjacent vertebrae. These two vertebrae are taken as sacral vertebrae. The vertebral count in specimen I is therefore 32 presacral vertebrae, the sacral vertebrae being 33 and 34.

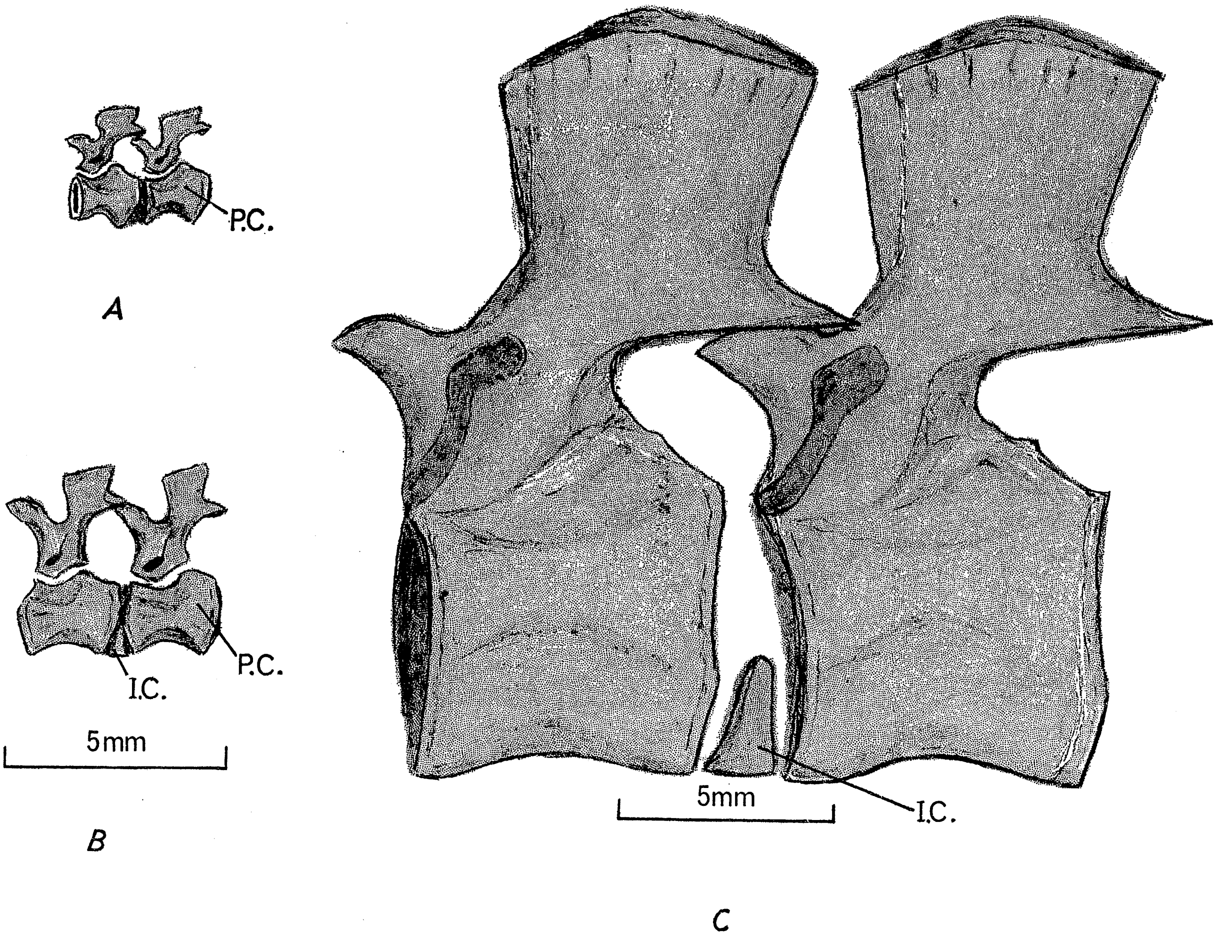

Figure 5. *Gephyrostegus bohemicus* Jaekel. Reconstruction of growth stages of vertebrae from the mid-dorsal region. *A*, specimen I; *B*, specimen II; *C*, after Broili.

In specimen II, at the level of the pelvic girdle two vertebrae again show enlarged transverse processes and are therefore taken as the sacral vertebrae, 33 and 34. In both specimens I and II the shoulder girdle lies at the level of the 8th to 10th vertebrae.

Cervical ribs are present in specimen II as far as the 9th dorsal vertebrae. These ribs (figures 10 *C*, 8 *A*) are short, their distal ends widened, the proximal ends, at least in the anterior cervical ribs, deeply bifid. The change from cervical to dorsal rib is abrupt.

In specimen I, short cervical ribs are present on vertebrae 2 and 3, the posterior cervical ribs are shorter than the dorsal ribs but show none of the specializations present in the cervical ribs of specimen II.

Sacral ribs are unknown in specimen I but a single sacral rib is preserved in specimen II (figure 10*C*). It is short and small but comparable with the 1st sacral rib in *Seymouria* (White 1939) or the single sacral rib of *Kotlassia* (Bystrow 1944).

The dorsal ribs in all specimens are long, curved, double-headed with the capitulum and tuberculum close together. Stages in development of the rib head are shown in figure 8. The articulation of the rib capitulum adjacent to the transverse process, even in the anterior body region, is very unusual and quite unlike the condition in *Seymouria* or *Kotlassia*, where the primitive connexion with the intercentrum is retained. Caudal ribs are present in specimens I and II.

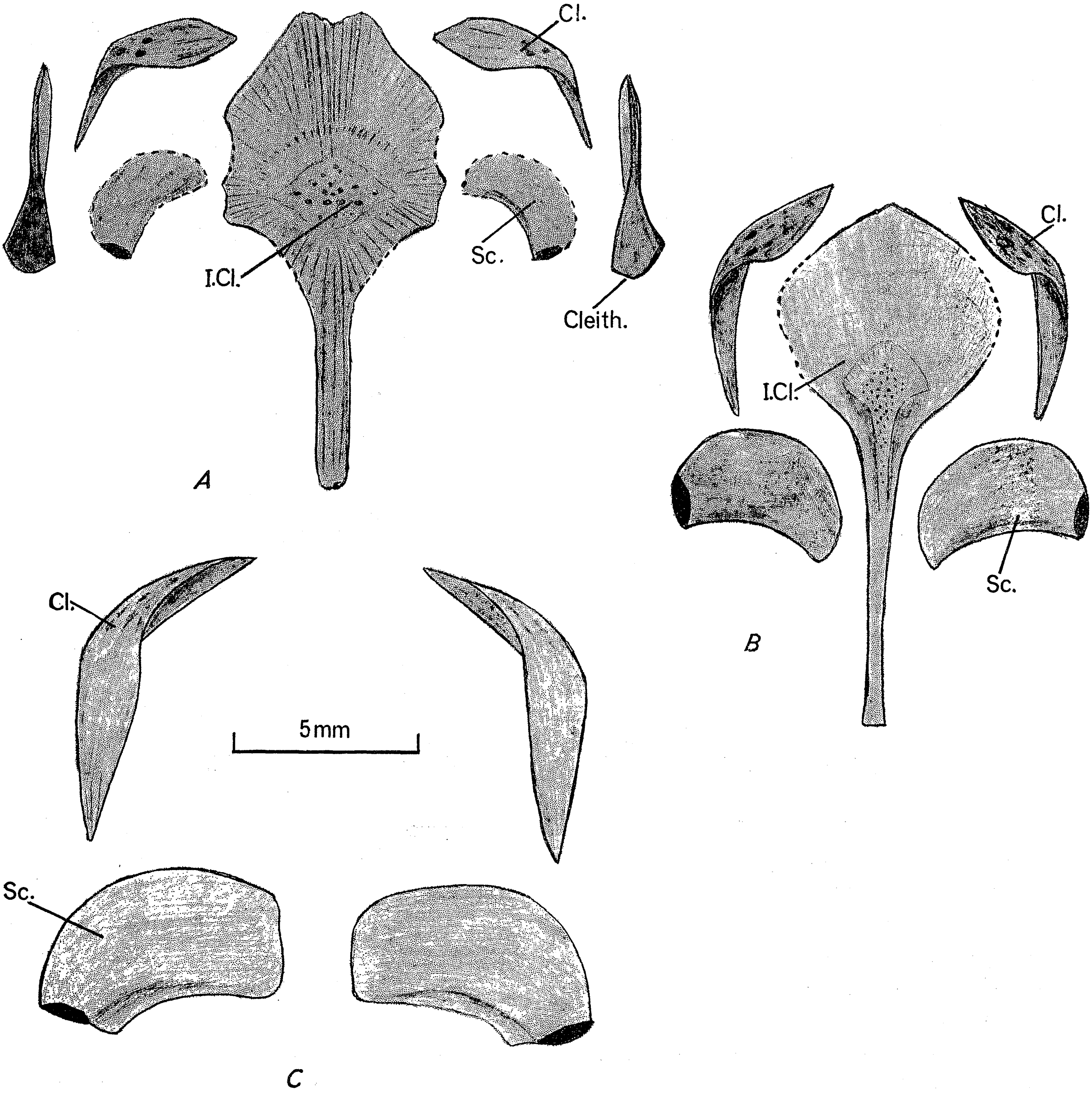

FIGURE 6. Shoulder girdle. *A*, *Gephyrostegus watsoni* sp.nov. *B* to *C*, *Gephyrostegus bohemicus* Jaekel. *B*, specimen I; *C*, specimen II.

Limbs and girdles

Remains of limbs and girdles occur in all specimens but those preserved in specimen I are the most complete (figure 10, *A*, *B*, *D*.).

The shoulder girdle (figure 6 *B*) has an interclavicle with a long parasternal process. The scapula in specimens I and II is not fully ossified. The humerus in specimen I (14 mm in length) is preserved as a flat bone, the proximal and distal ends lying in the same plane and no trace of an entepicondylar foramen is present. The humerus described by Broili (70 mm in length) is still without ossified condyles but an entepicondylar foramen is present and the head and distal ends of the bone are in two markedly different planes. Radius and ulna are more than half the humerus length and five digits are present, the first being reduced in size.

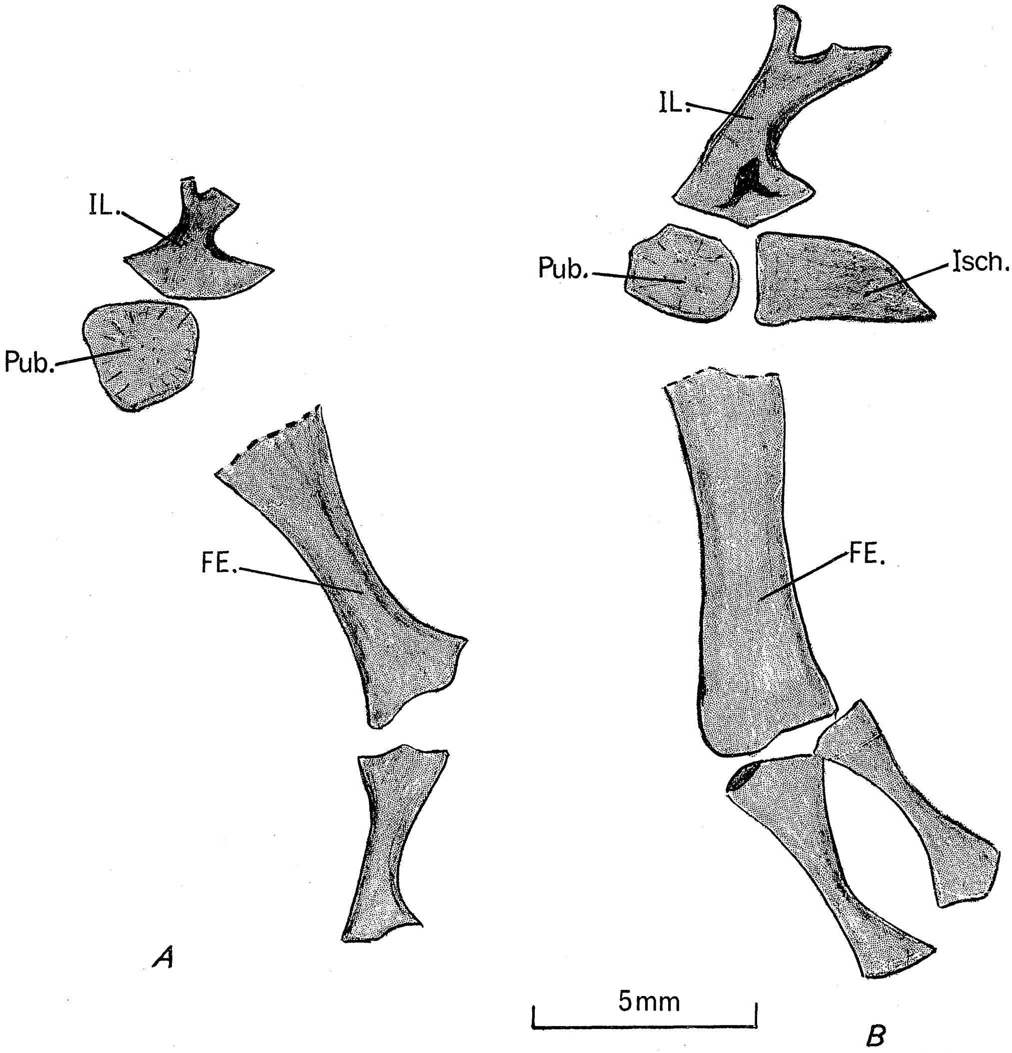

Figure 7. Pelvic girdle. *A*, *Gephyrostegus watsoni* sp.nov. *B*, *Gephyrostgus bohemicus* Jaekel, specimen I.

The pelvic girdle in specimen I (figure 7 *B*) consists of a separate ilium, pubis and ischium and is very weakly ossified at this stage in growth. In figure 7 *A* the pelvic girdle of *G. watsoni*, a slightly smaller animal is figured. A comparison of the two ilia in this figure shows an incipient division into an anterior and posterior region.

Scales

In specimen I scales are present from the shoulder girdle to the pelvic region and as the vertebrae and the ribs lie on top of the scales in both slap and counterpart, a complete body scaling was present. The scales are disturbed and scattered and not seen in regular rows as in *G. watsoni*. Two types of scales are present. One, an unornamented oat-shaped scale about 0·5 mm wide and 3 mm long with a shallow ridge along one side. The other a shorter rhomboidal scale about 0·5 mm wide, 2 mm long. Broili (1924, Pl. 1) figures oat-shaped scales behind the shoulder girdle and Jaekel (1902) states that numerous scattered small scales, rhomboidal in shape, are present in his specimen.

The reconstruction of *G. bohemicus* (figure 10 *D*) shows a slenderly built animal, the limbs well developed, the hind limb a little larger than the forelimb.

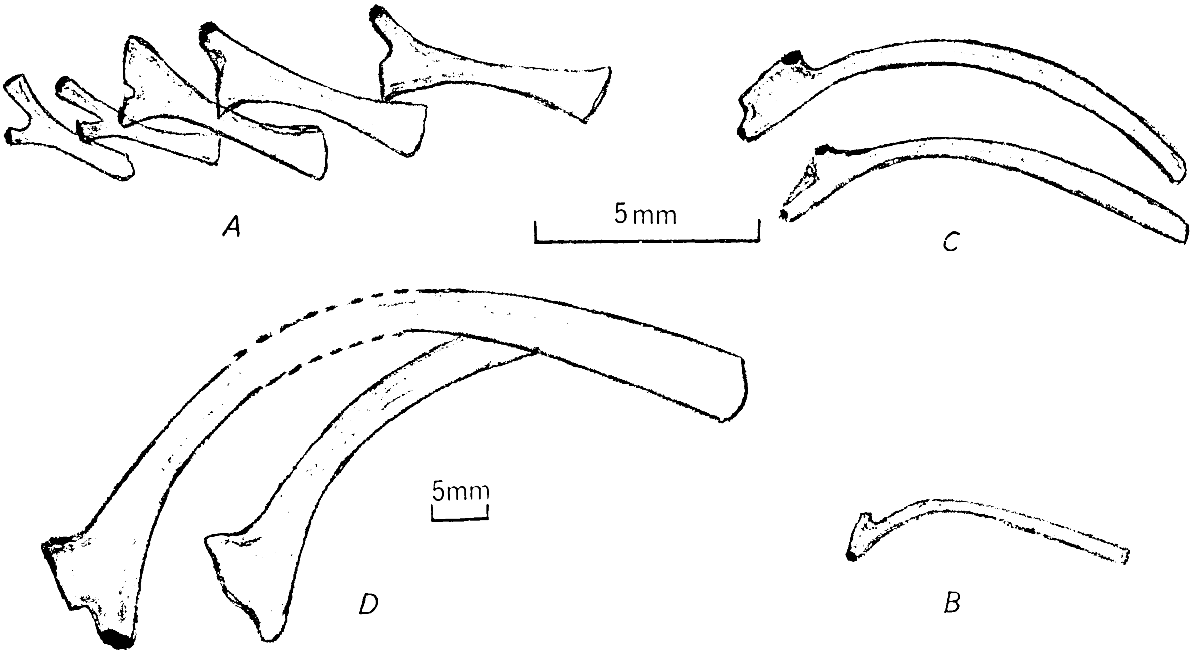

FIGURE 8. Ribs *Gephyrostegus bohemicus* Jaekel. *A*, cervical ribs from specimen II. *B* to *D*, Dorsal ribs from I, II and Broili's specimen.

Gephyrostegus watsoni **sp.nov.**

Watson (1926, pp. 238–241, text-figs. 29–31).

Type and only known material a single specimen from Nyran, D.M.S.W. B. 65 from Professor Watson's private collection now in the Museum of Zoology, Cambridge. (Figures 2 *D*; 6 *A*; 7 *A*, 9.)

Watson associated B 65 with Jaekel's type of *Gephyrostegus bohemicus* pointing out that while agreeing with Jaekel's type in general structure, it differs from it in shape and proportions.

The skull of this species is different in shape and proportion of the bones from those of *G. bohemicus*. These differences are not due to immaturity since it differs equally from specimen I, which is of comparable size, as it does from the larger specimens.

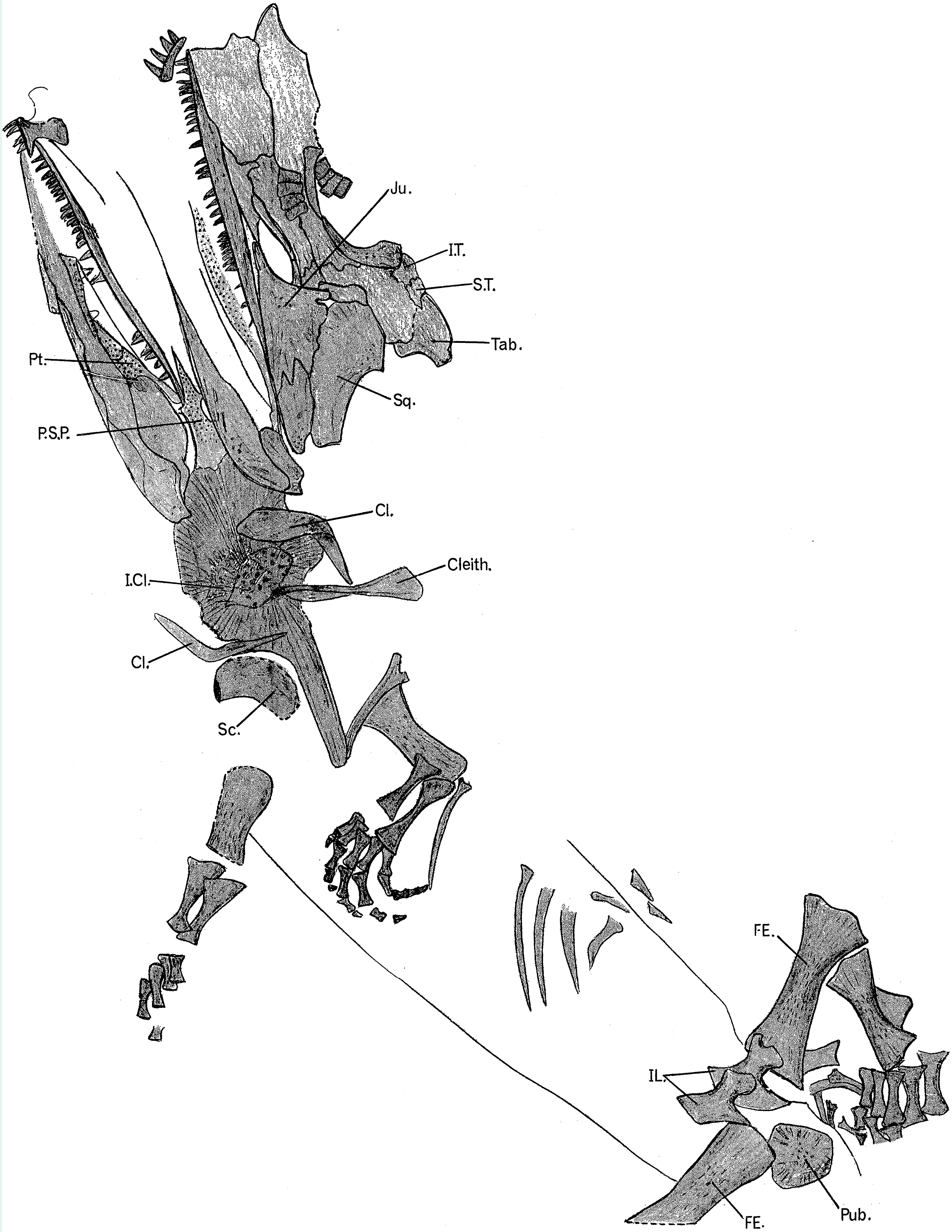

FIGURE 9. *Gephyrostegus watsoni* sp.nov. type.

Skull

The proportional differences of the skull table in the two species of *Gephyrostegus* is illustrated in figure 2. In *G. watsoni* the interorbital width is narrower and the post-orbital length of the skull shorter.

The palate (figure 9) has a long narrow parasphenoid plate in sutural contact with the basioccipital. Although the remaining palatal bones are incompletely displayed, the inter-pterygoid vacuities as in *G. bohemicus* are small.

Vertebral column and ribs

These are represented only by some faint impressions in the mid body region.

Limbs and girdles

The shoulder girdle (figure 6 *A*) is different in shape and proportions from that of *G. bohemicus*, the parasternal process shorter and wider.

The pelvic girdle is represented by an ilium and a pubis, the dorsal blade of the ilium showing an incipient division into anterior and posterior dorsal processes.

The hind limb (figure 9), as in *G. bohemicus*, is larger than the forelimb. In both fore- and hind limbs five digits are present. In the hand the first digit is reduced in size and the pigital formula 2 3 3 3 4 is unique.

Scales

There is a ventral plastron of scales as described by Watson between the shoulder girdle and the pelvis. They are better ossified than the scales of *G. bohemicus*.

DISCUSSION

The position of Gephyrostegus

The extended description given of this form confirms its placing in the Seymouriamorpha. It is in agreement with seymouriamorph structure in having a skull with a full temporal row, intertemporal and supratemporal and a reptilian type palate in which the moveable articulation of pterygoid and parasphenoid is retained, the inter-pytergoid vacuities are small and slit-like, the palatal ramus of the pterygoid is broad. The stapes is poorly ossified and consists of a short columella and a footplate without a stapedial foramen. In the post-cranial skeleton the vertebra consists of a neural arch, pleurocentrum and small inter-centrum. The neural arch with low neural spines, swollen zygapophyses and horizontal zygapophysical articulations. Cervical and sacral ribs are distinctly developed. Interclavicle with a parasternal process and ilium with an expanded dorsal blade showing a division into an anterior and posterior part but without a long posterior process. Five digits in both fore- and hind limbs.

Gephyrostegus is of special importance since it is the oldest known member of the Seymouriamorpha and its relationships to the younger members of the group should be considered. It is more primitive in the following respects.

1. *Otic notch.* In *Gephyrostegus* the dorsal border of the squamosal articulates with inter-temporal and supratemporal and touches the tabular, the squamosal embayment being

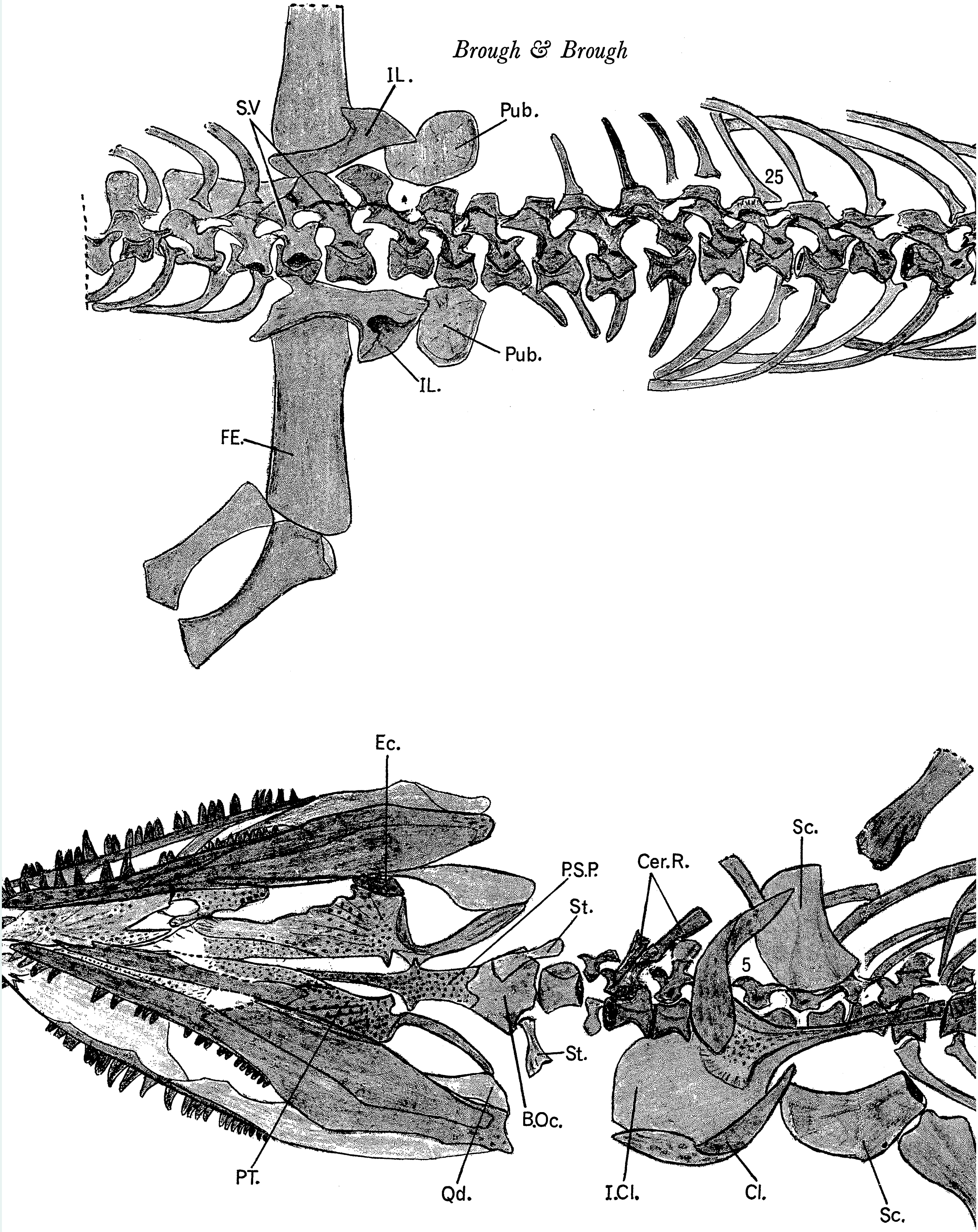

Figure 10. *A*, *Gephyrostegus bohemicus* Jaekel specimen I, Č.G.H. III B 21 C 587.
(Magn. × 2·6 approx.)

B, ,, ,, ,, ,, I, M.P. 451.
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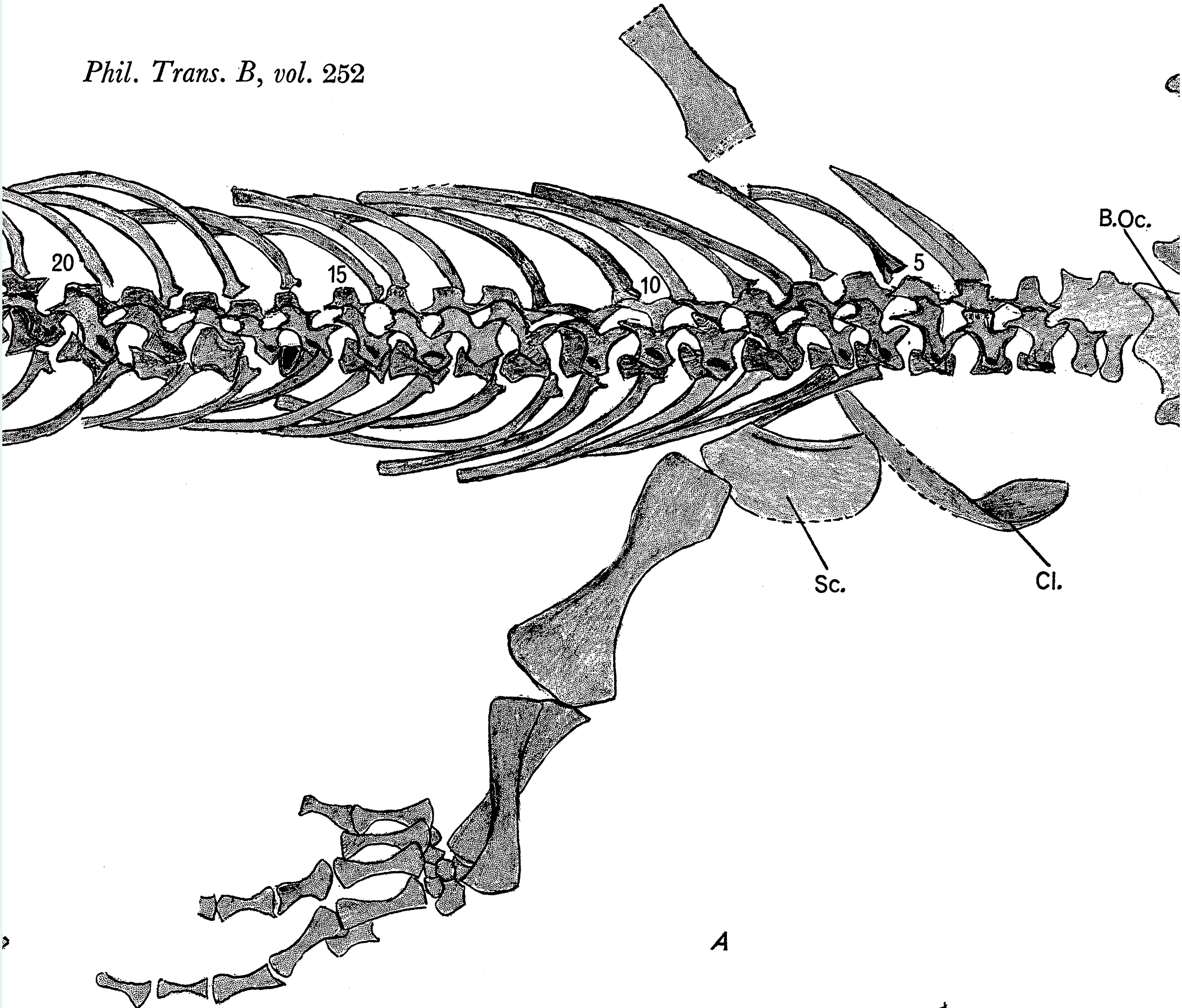

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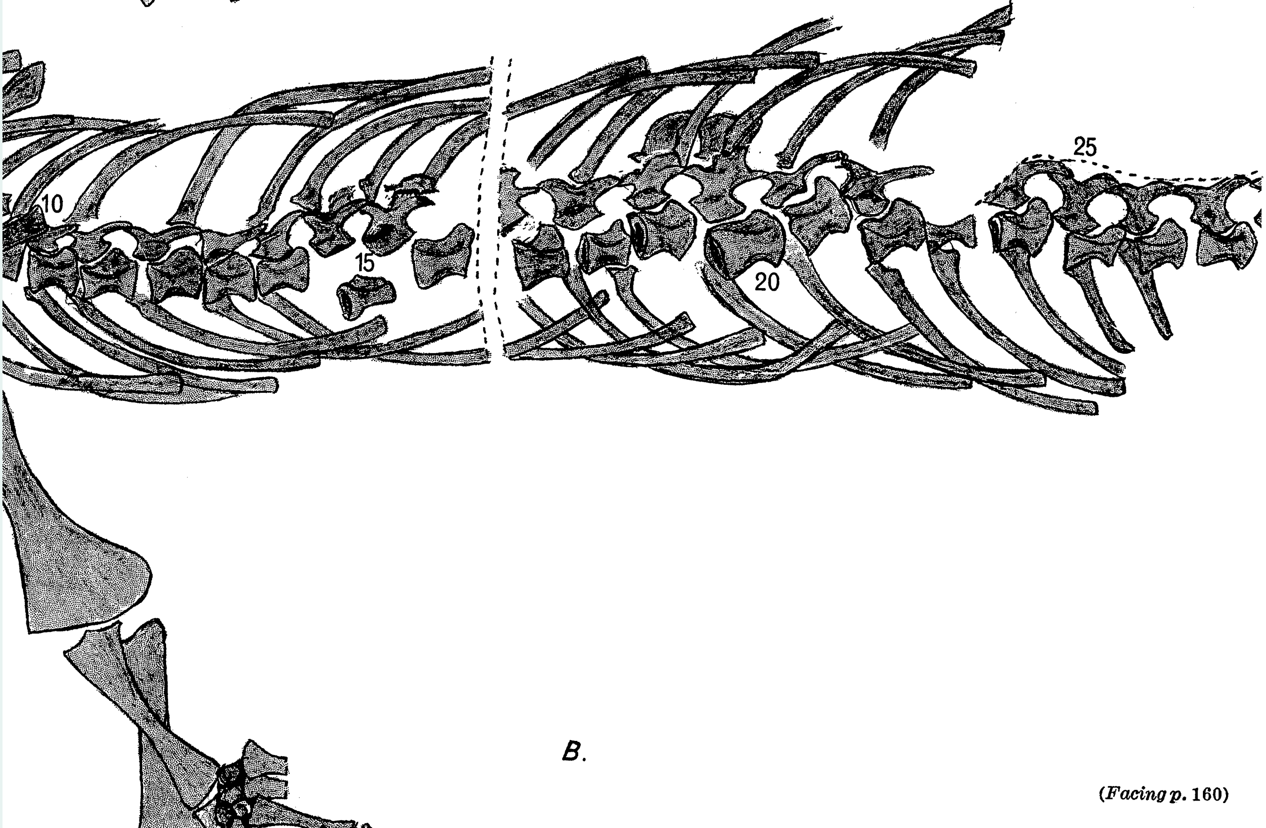

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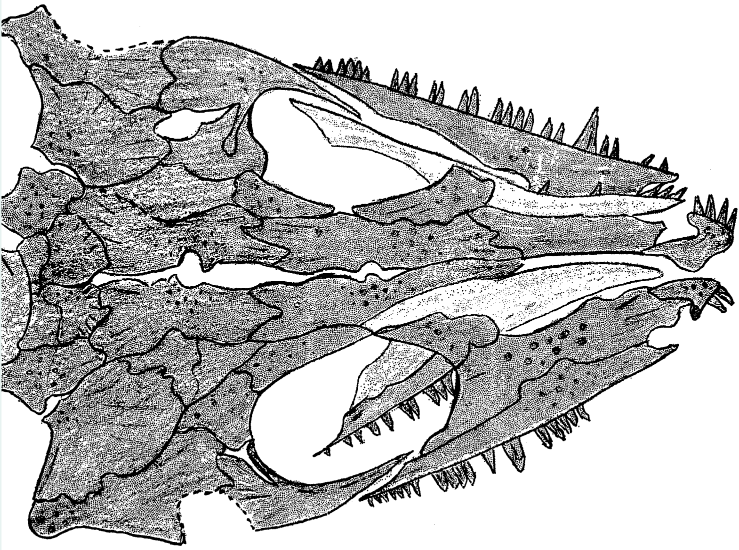

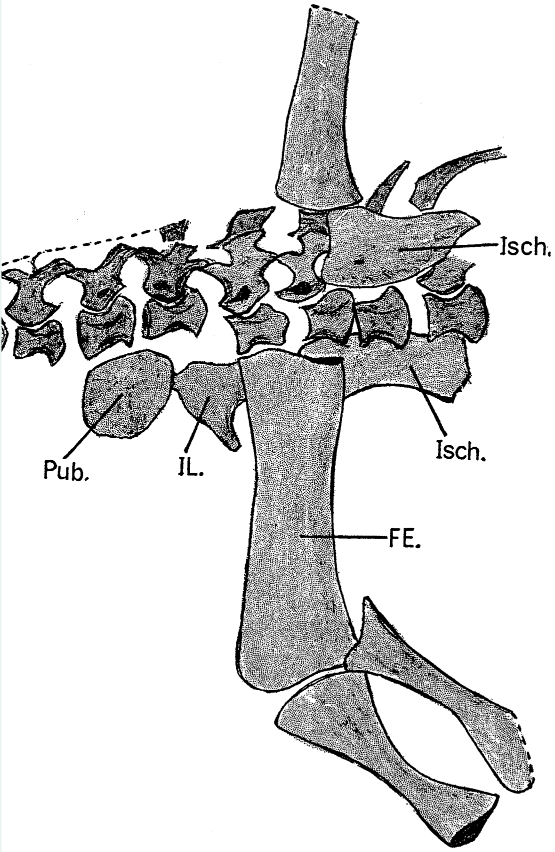
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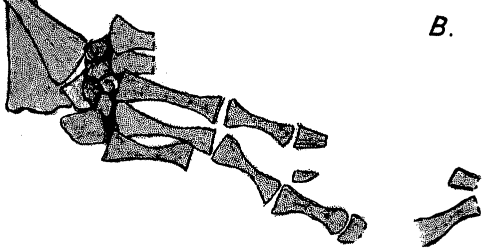

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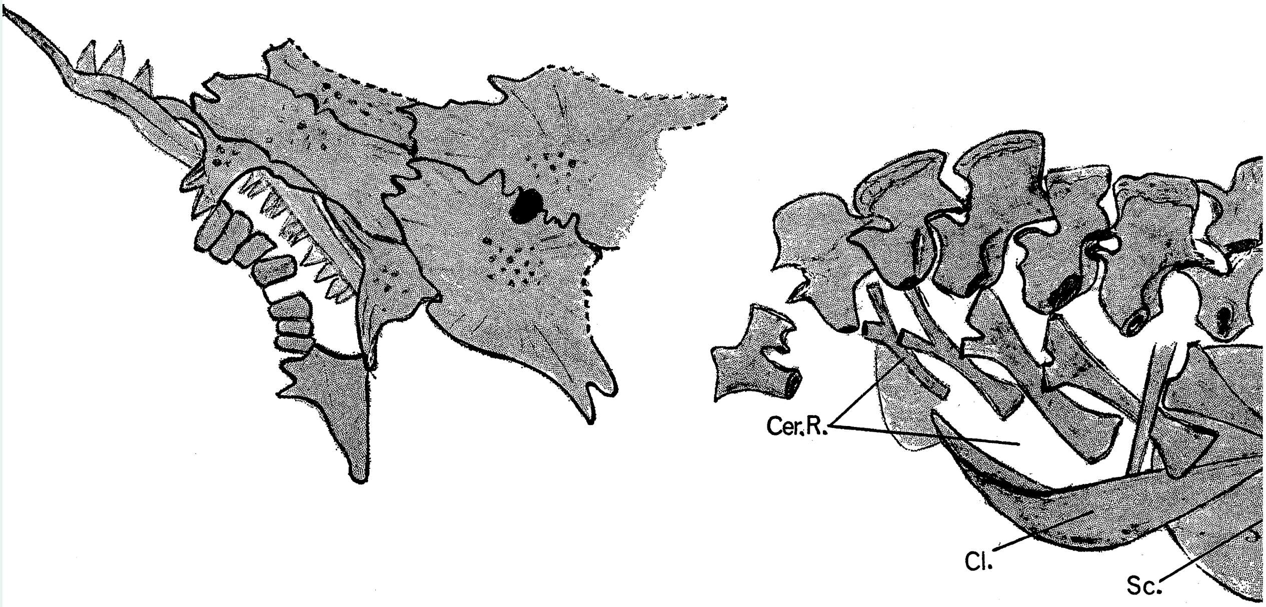
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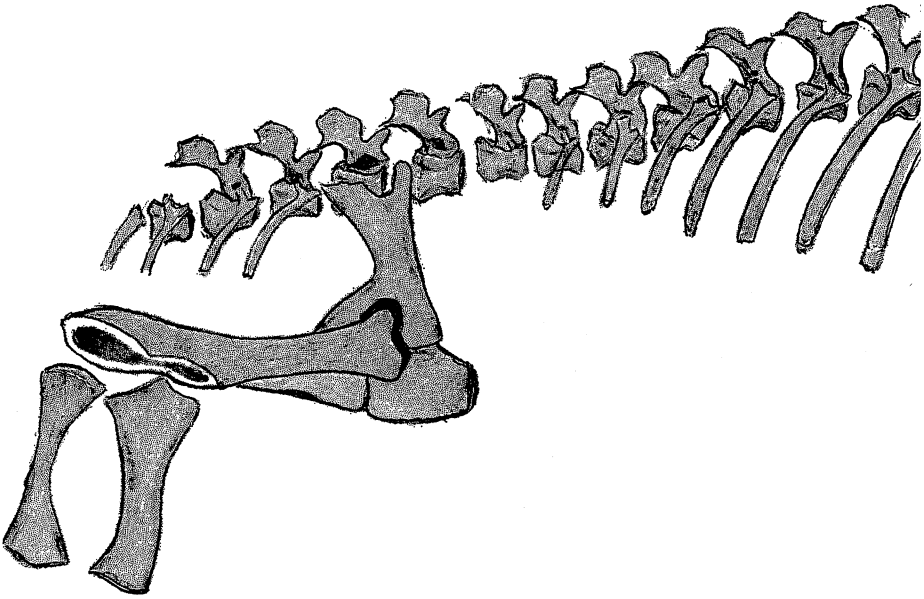

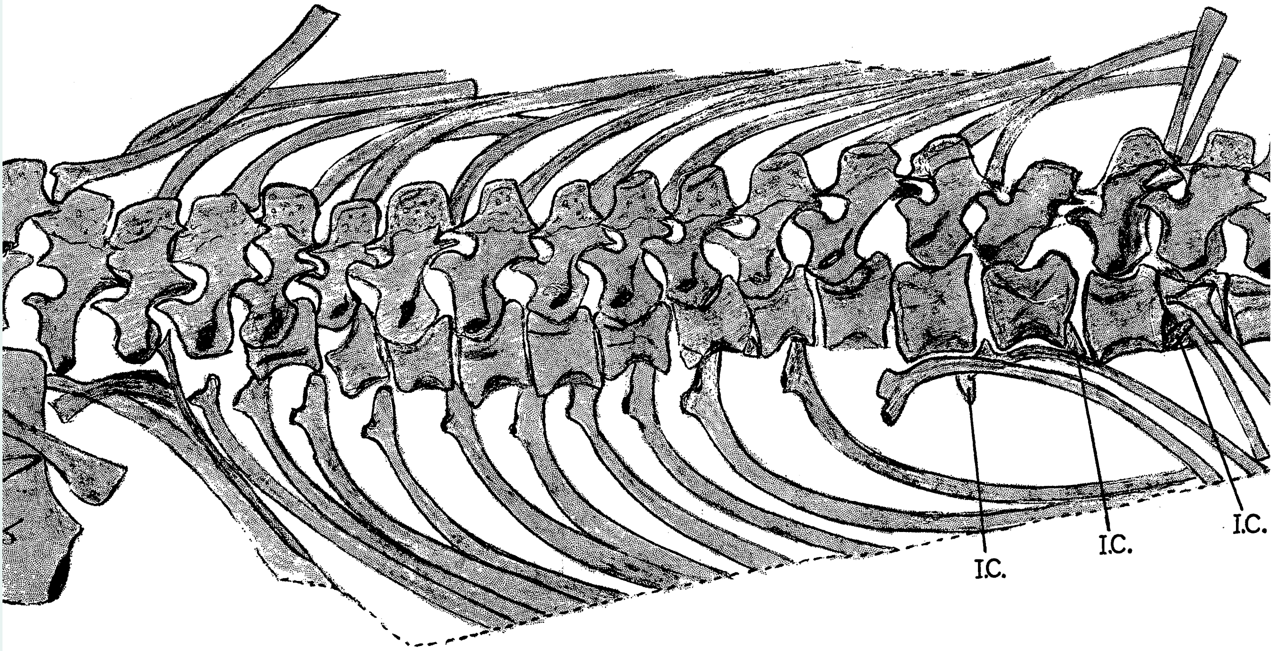

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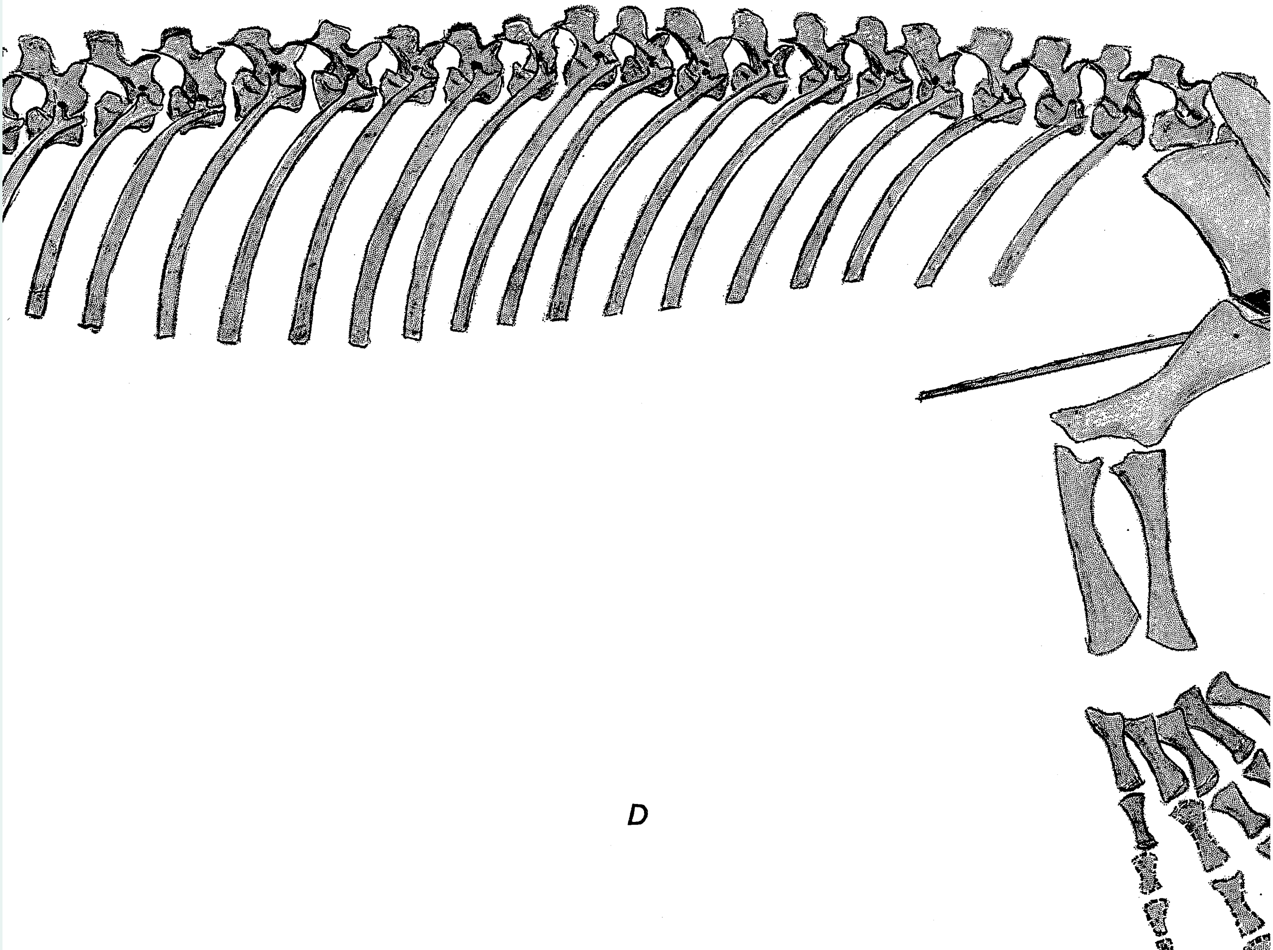

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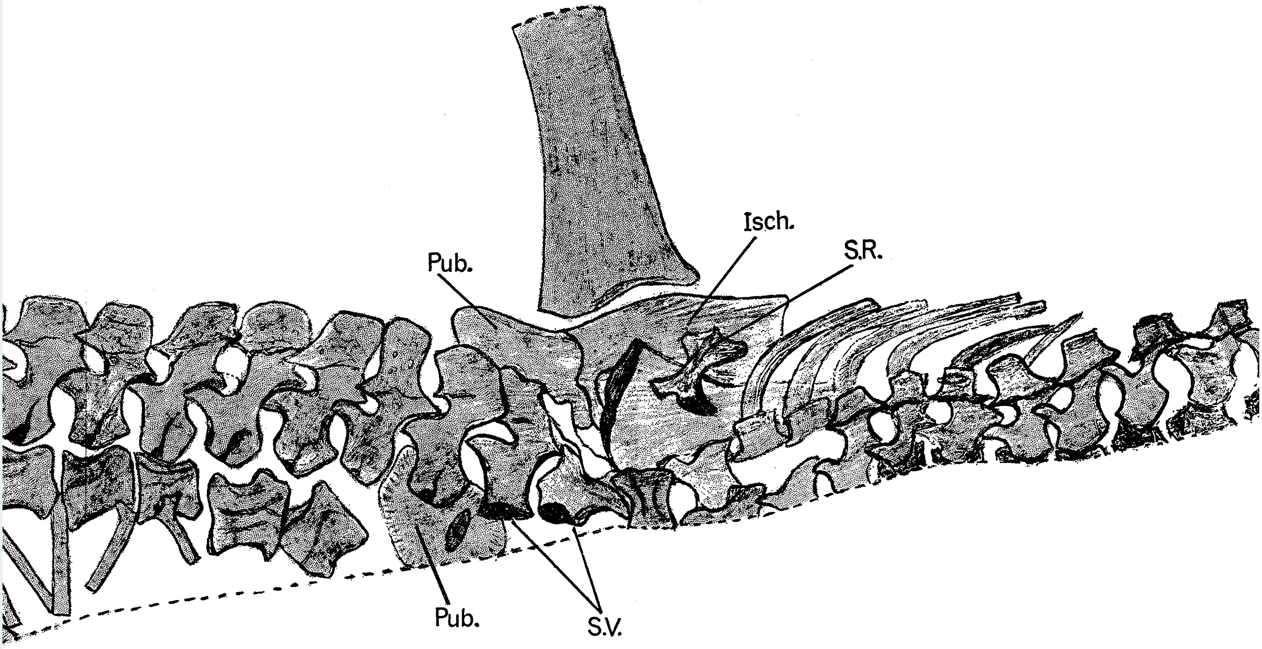

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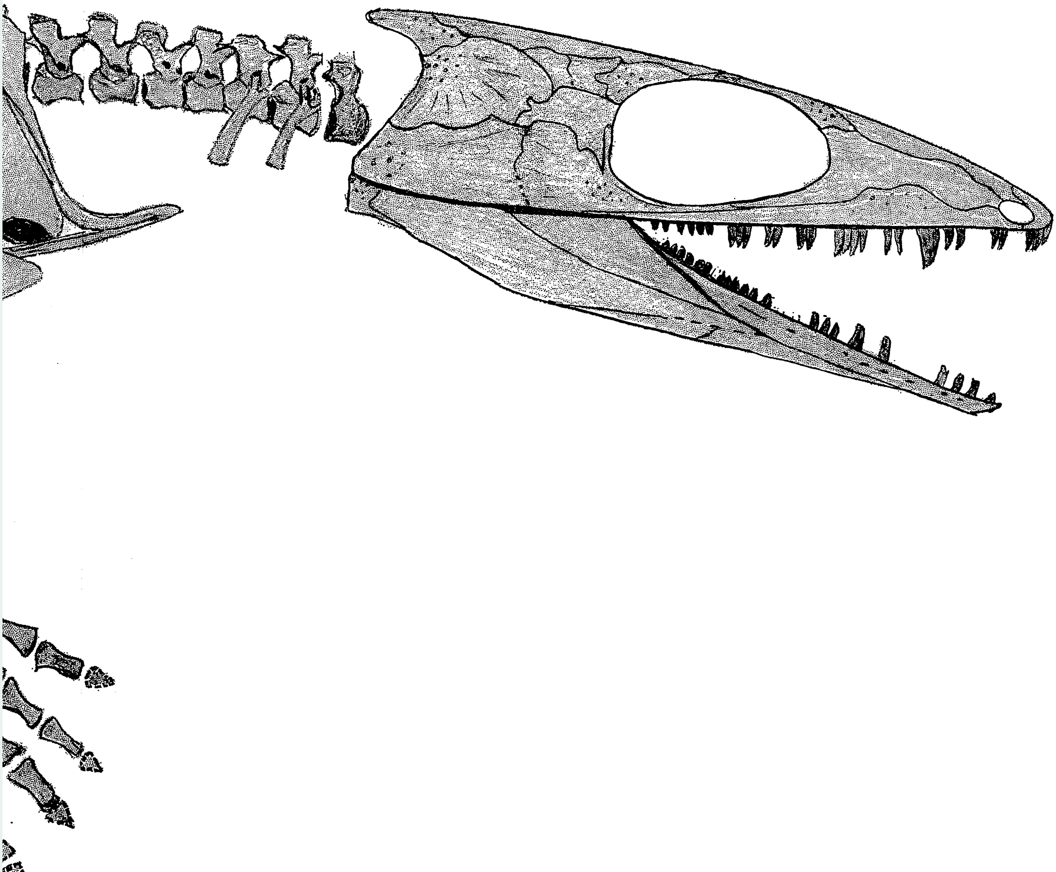

FIGU

GURE 10. *C*, *Gephyhostegus bohemicus* Jaekel specimen II, C.G.H. 3027 (Magn. × 1·9).
D, ,, ,, ,, Reconstruction based mainly on specimen I. Dotted phalange

ges from *G. watsoni* (Magn. × 2·6 approx.).

a shallow recess. In *Seymouria* and *Kotlassia* the notch is more conspicuous and extends further forward, the squamosal articulating only with the intertemporal and supratemporal.

2. *Palate.* The forward extension of the subtemporal fossa which is seen in *Seymouria* and *Kotlassia* does not appear to occur in *Gephyrostegus*.

3. *Neural cranium.* The neural cranium is narrow posteriorly unlike the later forms.

4. *Vertebrae. Gephyrostegus* has a long back with 32 pre-sacral vertebrae. *Seymouria* has 24 (White 1939) and *Kotlassia* 26 (Bystrow 1944). In these later forms the neural arches are swollen and overshadow the centra. This is not so in *Gephyrostegus* where the centra are relatively large and the lateral extension of the arches does not occur to such an extent.

5. *Scales. Gephyrostegus* is also primitive in possessing a complete body scaling of both dorsal and ventral scales.

Relationships of the Seymouriamorpha

The seymouriamorphs, microsaurs and captorhinomorphs have a broadly similar reptilian-type post-cranial skeleton. If this has been 'invented' only once as Gregory (1965) suggests, it implies a relationship between these three groups. In microsaurs and captorhinomorphs the position of the stapes, which runs from the fenestra ovalis towards the quadrate, is primitive and could be a direct inheritance from fish ancestors. This suggests that neither microsaurs nor captorhinomorphs nor their possible common ancestor had a dorsal otic notch in the skull.

The position in seymouriamorphs appears to be different, indeed in *Kotlassia* and *Seymouria* a notch involving the posterior border of the squamosal is conspicuous and the stapes runs dorsally to it from the fenestra ovalis in *Kotlassia*. In the earlier *Gephyrostegus*, however, the notch is much less well developed and is merely a rather shallow indentation on the posterior border of the squamosal; the direction of the stapes cannot be ascertained. This would support the suggestion already made by Parrington (1958) that the otic notch in seymouriamorphs is a secondary structure.

If this view is accepted the Seymouriamorpha can be regarded as a group which diverged from the proto-reptilian stem at an early stage, retaining many primitive features but showing a progressive evolution in the ear region.

Whether the Seymouriamorpha represent a blind end in evolution or give rise to forms such as the diadectomorphs as has been suggested (Olson 1965) is a matter beyond the scope of this paper.

The link between the Seymouriamorphs and Anthracosauria (= Embolomeri, Romer) depends mainly on the structure of the skull roof (Panchen 1964). The anthracosaurs have a ligamentous attachment between the cheek and skull table, an 'otic' notch in the same position as in late Seymouriamorpha and a reptiliomorph skull table pattern. The latter is regarded as a basic character and sufficient to indicate an evolutionary connection between the two groups.

The difficulty in trying to make precise and significant comment on the evolutionary relationships of these early tetrapods is due mainly of course to the extremely scanty and imperfect sample which is available for study. The nature of their evolutionary pattern, however, provides a further difficulty. The pattern is complex, groups such as the microsaurs seem to consist of a number of closely related but independent phyletic lines, each undergoing its own evolution, and in each with various parts evolving at different speeds and some not at all. This means that although we can use the words primitive and specialized for separate parts it is difficult to do so for the whole animal. If such a pattern of evolution is general, and increasing knowledge seems to indicate that it is, and considering the nature of the sample, it is not surprising that search for actual 'ancestors' has yielded almost totally negative results. Until much more material is available probably the best we can do is to consider the closeness of the larger groupings and make what we can of that.

Conclusion

The question of the classification of early tetrapods, as has been mournfully stated by a number of authors, is a difficult one, but it cannot be evaded. Our information is very incomplete due to the scanty and often fragmentary nature of the material available for study. Nevertheless, progress is being made, and while any classification must be tentative and liable to modification we fell impelled to make certain suggestions based on the studies in this and previous papers.

Two main points have impressed us. The first is that structures generally accepted as of reptilian nature are fairly widespread among Carboniferous tetrapods, often showing in forms which are demonstrably not reptiles in the full sense. These as we have demonstrated, are not necessarily of late occurrence, but are present in Lower Carboniferous forms such as *Palaeomolgophis* and *Adelogyrinus*.

The second point is that there are two elements to be recognized in the evolution of a reptile. One is structural modification to what is accepted as reptilian form, the other is the modification of life-history to the amniote type with cleidoic egg. Although not generally stated there has been a tendency to assume that these events were simultaneous, that when full reptilian structure was reached the change in life history from the amphibian to the amniote type took place. This is based on the general assumption that reptilian characters are adaptations to land life and if such a view is accepted is not unreasonable. We feel that this is far from the truth and that these two important evolutionary events proceeded more or less independently. The presence of reptilian structural characters in lower carboniferous forms such as *Palaeomolgophis*, *Adelogyrinus* and *Dolichopareias* which were probably aquatic, not only in the larval stage, but throughout life, should dispose of this view. We see the early initiation of reptilian structure in a large element of the early tetrapod fauna and the modification of life-history occurring in only some of these at a later date. The fate of the others may be interesting and will be discussed later.

The idea of an early and deep structural cleavage in tetrapods giving batrachomorph and reptiliomorph lines was advanced by Säve-Söderbergh in 1934, 1935. His main evidence was the pattern of the posterior bones of the skull table and unfortunately he did not live to carry this investigation further. Our studies have shown that this inconsequential-looking character is indeed meaningful. Where a post-cranial skeleton is known with the reptiliomorph skull pattern, there is to a greater or less extent the development of the pleurocentrum as the main central body, the presence of cervical ribs and a stalked interclavicle.

The batrachomorphs were clearly quite independent of this line from an early stage and underwent their own separate and different evolution.

The evolutionary pattern must have been very complex with, probably after an early evolutionary burst, several independent lines of batrachomorphs and reptiliomorphs undergoing their own evolution often parallel within the two great groups but quite independent. Of the reptiliomorphs some, but only some, added the modification of life-history to that of structure and became true reptiles. Of the rest, many died out, as did the seymouriamorphs, but several authors have speculated on the possibility of certain groups recognized here as reptiliomorph being ancestral to the Apoda and Urodela.

A broad classification of these creatures is necessary, for the old, based on characters of the vertebral column has had its inadequacies exposed, has been modified and is further eroded in the present series of papers.

We put forward the following suggestions for a classification which would be tidy and workable and would to some extent express the evolutionary realities of the situation. It would involve the recognition of four major groups, classes or subclasses. The former is preferable because of the anomalous nature of present day amphibia in this scheme.

Class **Eobatrachia**. Forms retaining the heavily ossified early tetrapod skull substantially unchanged, with a batrachomorph skull pattern and amphibian type life-history. This would include the Ichthyostegalia, Rachitomi and Stereospondyli.

Class **Eoreptilia**. With a reptiliomorph skull pattern and with reptilian characters more or less developed in the post-cranial skeleton, and often with evidences of an amphibian type of life-history. This would include the Microsauria and Seymouriamorpha, and the Anthracosauria should be included here, although their post-cranial skeleton is not well known. It is likely that the Aïstopoda and Nectridea belong here but are rather widely separated from the above groups. The skulls where sufficiently unmodified to show this character are of reptiliomorph type (Urocordylidae) and reptilian characters such as cervical ribs occur in the Aïstopoda. The vertebrae are peculiar and specialized, and while they will always be difficult to interpret it is possible that they are basically of the microsaur-seymouriamorph type (Brough & Brough 1967*a*).

Class **Amphibia**. Forms with a skull much modified from the early tetrapod type and with an amphibian type of life-history. This would include the Anura, Urodela and Apoda.

Class **Reptilia**. Forms with reptilian structural characters fully developed and with an amniote type of life-history.

Such a classification can no doubt be criticized in many ways and using the life-history of fossil form may be thought a weakness. In fact, the evidence of aquatic life in the eoreptilian groups is fairly substantial though far from complete. Such a classification could end the bickering about the status of seymouriamorphs. Members of this group have been placed alternately by several authors in the Reptilia and Amphibia. This is due to the real difficulty of dealing with an animal which is structurally a reptile, but which at the same time shows undoubted evidence of aquatic life inducing the strong and justifiable suspicion that in life-history it was an amphibian. The recognition of an eoreptilian class would allow the placing of these animals in such a way that all their characters are recognized without anomaly.

It may be objected that the separation and isolation of the present day Amphibia from the ancient batrachomorph forms is a rather extreme step. If the general evolutionary thesis behind this classification is accepted it must be done and is indeed useful. Watson (1940) derives the Anura from batrachomorph sources while other authors put forward arguments for a derivation of the Urodela and Apoda from what we regard as reptiliomorph groups. If these views are correct, and they may well be, there is a situation of considerable interest. We see the present day Amphibia as a series of much modified relics from widely different Palaeozoic lines but united in the fact that none of them have taken the final step, the evolution of the cleidoic egg in their adaptation to land life. Their isolation in the classification recognizes their common bond as well as their widely separate origins.

A re-classification of the early tetrapods is obviously necessary and whatever classification is adopted the community of structure of the Anthracosauria, Microsauria and Seymouriamorpha, and their position in the basic reptilian stock should be recognized.

We have tried in these studies to take account of the whole animal as far as that is possible without over-concentrating on any of its parts. It used to be thought possible and attempts have been made to find a single character that would indicate membership of a major group. It would be convenient if we could say on a single character such as an entepicondylar foramen or a pterygoid flange that this animal is a reptile. This does not work out well in practice and with our growing knowledge of the evolutionary process this is not surprising.

Some of the ideas put forward in these papers have been canvassed in some form or another before, for example, Westoll (1942*a*, *b*, 1943) remarked on microsaur-captorhinomorph affinities. No discourtesy is meant to these authors in not stating their views. To have done so a lengthy historical survey would have been necessary which would have been out of place here and which can be found elsewhere (as Gregory 1965; Parrington 1958). All we have attempted to do is to put forward some suggestions as briefly as possible in the light of the new material we have been able to describe.

Abbreviations used in the figures

Art.	articular facet for capitulum of rib	*P.P.*	post-parietal
B.Oc.	basioccipital	*P.V.*	prevomar
C.R.	cervical ribs	*P.S.P.*	parasphenoid
Cl.	clavicle	*Pt.*	pterygoid
Cleith.	cleithrum	*Pub.*	pubis
EC.	ectopterygoid	*Qd.*	quadrate
FE.	femur	*S.R.*	sacral rib
I.C.	intercentrum	*S.T.*	supratemporal
I.Cl.	interclavicle	*S.V.*	sacral vertebrae
I.T.	intertemporal	*Sc.*	scapulo-coracoid
IL.	ilium	*Sq.*	squamosal
Isch.	ischium	*St.*	stapes
Ju.	jugal	*T.P.*	transverse process
Oc.F.P.P.	occipital flange of post-parietal	*Tab.*	tabular
P.C.	pleurocentrum		

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ADDENDUM

Added in proof 7 *March* 1967

Since the above was written our attention has been drawn to a paper by E. E. Williams (1959, *Quart. Rev. Biol.* **34**, 1–32) which is an exhaustive review of the nature and relationships of tetrapod vertebrae looked at mainly from the point of view of embryological development. He comes to the interesting conclusion, for which he makes out a good case, that the vertebral centra of living lepospondyls are pleurocentra and that by analogy those of microsaurs also. This fits well with our view since we have presented abundant palaeontological evidence to show that the microsaur centrum is a pleurocentrum and that when this is the only central element present it is so due to the loss of the intercentrum. His work, as well as a recent paper by Panchen (1966, *J. Zool. Lond.* **150**, 199–222), on the vertebral column of the anthracosaur *Eogyrinus attheyi* lends support to our view of the closeness of relationship between the anthracosaur, seymouriamorph and microsaur groups and, if anything, strengthens the case for the systematic recognition of this assemblage which we have suggested above.

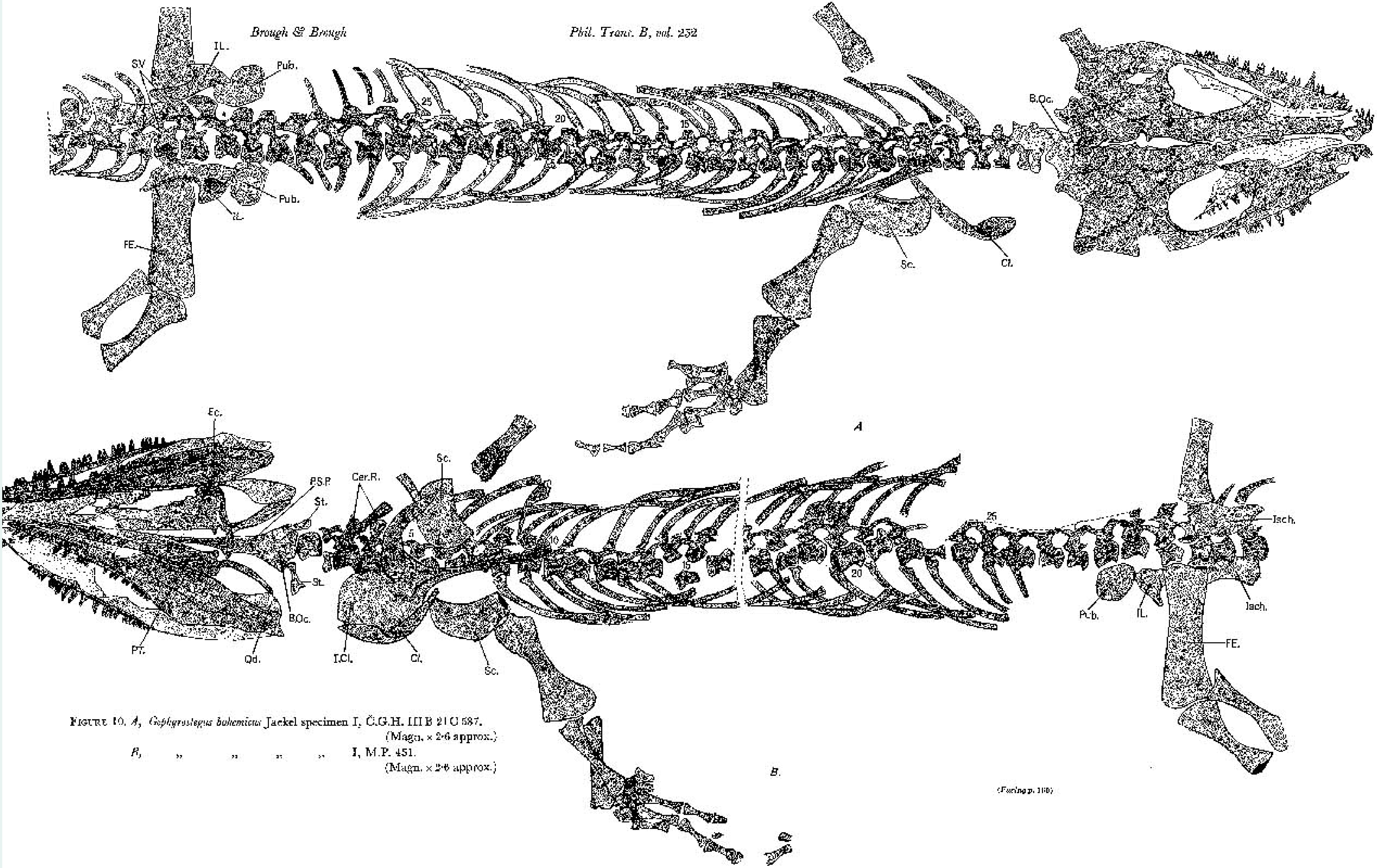

FIGURE 10. *A*, *Gephyrostegus bohemicus* Jaekel specimen I, Č.G.H. III B 21 C 587. (Magn. × 2·6 approx.)
B, „ „ „ „ I, M.P. 451. (Magn. × 2·6 approx.)

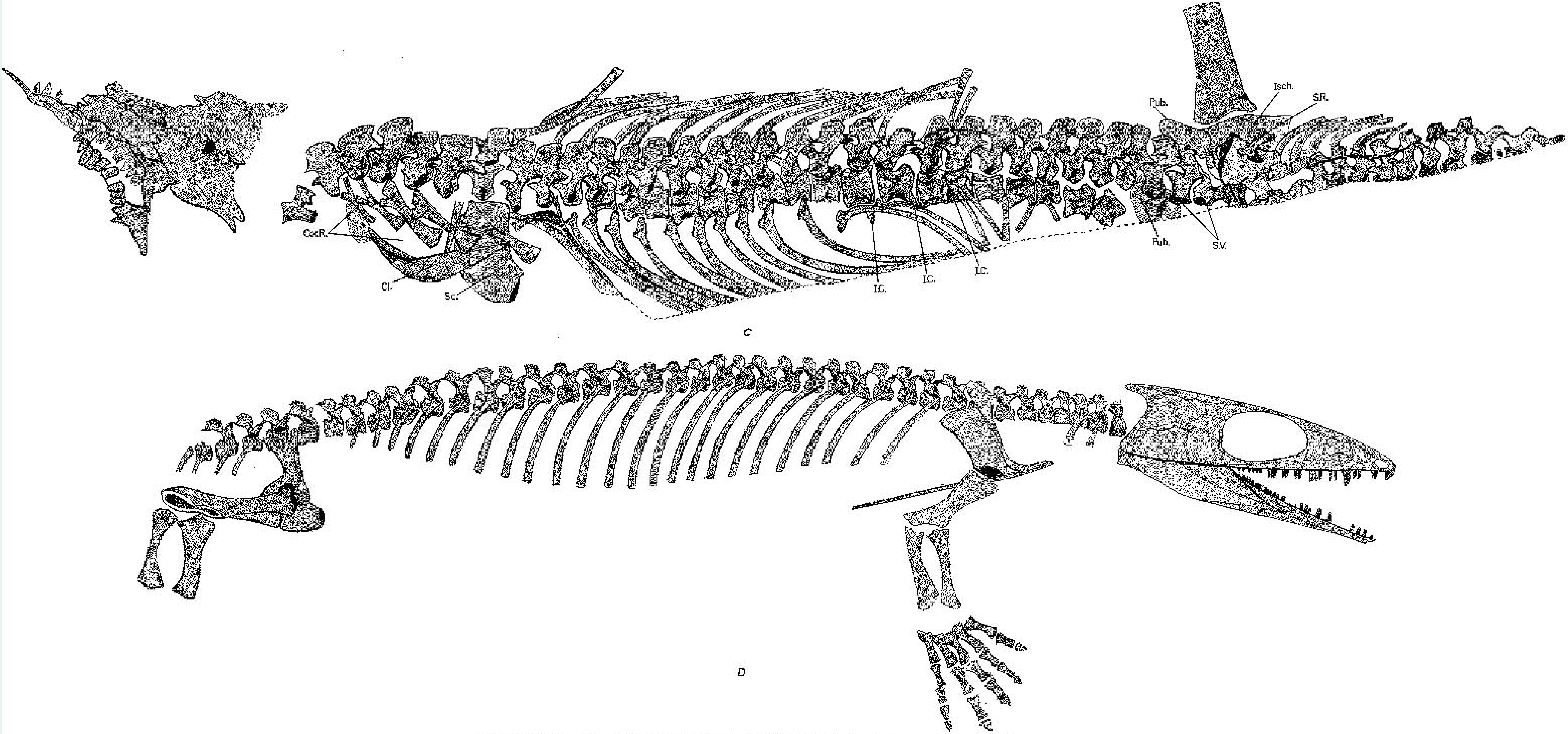

FIGURE 10. C, *Gephyrostegus bohemicus* Jaekel specimen II, C.G.H. 3027 (Magn. × 1·9),
D, „ „ „ Reconstruction based mainly on specimen I. Dotted phalanges from *G. watsoni* (Magn. × 2·6 approx.).