The Devonian Fish Palaeospondylus gunni Traquair

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THE DEVONIAN FISH *PALAEOSPONDYLUS GUNNI* TRAQUAIR

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[Plates 22–25]

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The anatomy of *Palaeospondylus* is redescribed with a new interpretation of the skull. Paired fins are present. The vertebral column and tail are now correctly orientated. A new order Palaeospondyloidea is established and its affinities discussed.

1. Introduction

The little fish, *Palaeospondylus gunni*, from the Middle Devonian of Achanarras, Caithness, is perhaps the most widely known of all problematical fossils. Ever since it was first described by Traquair in 1890, it has attracted the attention of a very large number of workers. Nevertheless, its affinities have not yet been convincingly demonstrated. Traquair (1890, 1893 *a*, 1893 *b*, 1894, 1897) and the majority of writers, including Ayers (1933), Bulman (1931), Deruiguin (1921), Gill (1896), Howes (1891), Stensiö (1927), White (1935), and Woodward (1892, 1898), have considered *Palaeospondylus* to be related to the Cyclostomes. However, other workers have interpreted *Palaeospondylus* in a very different manner. Graham Kerr (1900) and Miller (1930) have ingeniously urged its Dipnoan affinities; Sollas and Sollas (1903) have suggested Elasmobranch relationships; it is said that T. H. Huxley believed it to be a larval *Coccosteus*; Dawson (1893) suggested it was a larval amphibian; and Bashford Dean (1895) originally considered it to be a Cyclostome, but later after examining some specimens (1896, 1898, 1900) he found this view untenable, believing that *Palaeospondylus* was more probably a larval form, possibly related to the Arthrodira, a view also held by Abel (1912). Finally, Dean (1904), after reading the work of the Sollases, suggested almost by way of a joke that it was a Holocephalan. The least probable solution is that of Kyle (1926), who believed *Palaeospondylus* to be a larval herring!

Very few authors appear to have felt satisfied that the problem of the affinities of *Palaeospondylus* was finally settled, and some writers, such as Goodrich (1909), Forster-Cooper (1930), and Dean (1904), have expressed this point of view. Dean remarks

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'what is especially needed in our future dealings with *Palaeospondylus* is less memoir and more material'. This sentiment was strongly endorsed by Dr C. Forster-Cooper, and he made it a special aim to collect further material of the little fish during the five summers, 1931–5, in which he worked the quarry at Achanarras. He was amply rewarded for his labours not only by the large number of new specimens he collected, but by the excellent preservation of some of them. On being appointed Director of the British Museum (Natural History), Dr Forster-Cooper felt that his new duties would prevent his working out this material, and he very generously invited me to do so for him.

I find it difficult adequately to express my thanks to Dr Forster-Cooper not only for allowing me to describe *Palaeospondylus*, and for pointing out to me certain of the new features of its anatomy, on which my views as to its affinity are largely based, but also for preparing most of the material himself. I am also greatly indebted to Sir Arthur Smith Woodward, Professor E. S. Goodrich, Professor D. M. S. Watson, Professor E. A. Stensiö and Dr O. M. B. Bulman for discussing this work during its progress and for much helpful advice and criticism, and especially to Professor Goodrich for reading the manuscript. I would also like to take this opportunity of thanking Dr E. I. White of the British Museum (Natural History), Mr F. R. Parrington of the Museum of Zoology, Cambridge, Dr A. C. Stephen of the Royal Scottish Museum, Edinburgh, Dr H. R. Hewer of the Imperial College of Science, London, and Dr C. J. Stubblefield of the Geological Survey, for the loan of specimens in the collections in their care. I have already published a brief account of the results of these researches (Moy-Thomas 1939), but this paper represents the data on which these views were based and a discussion of the evidence.

2. Material and methods

Palaeospondylus has been subjected to two ingenious techniques in the past, both of which added largely to our knowledge of its anatomy. Sollas and Sollas (1903) studied the structure of the head by means of serial sections, and Bulman (1931) by the method of 'transfer preparations'. In this work the material was only prepared by removing the overlying matrix from the fossil by carefully dissolving it away with hydrofluoric acid, a difficult, but in the majority of cases a very successful technique. Otherwise, little was done to the specimens except to examine them with a low-powered binocular microscope under various liquids, of which xylol gave the best results.

In all I examined nearly five hundred specimens of *Palaeospondylus*. This material consisted of the big collection in the Museum of Zoology, Cambridge, made by Dr Forster-Cooper, the specimens, on which Traquair based his description, in the Royal Scottish Museum, Edinburgh, the specimens in the Imperial College of Science, the Geological Survey and the British Museum (Natural History). Among the specimens in the British Museum (Natural History) some of those collected by Dr Forster-Cooper are the most excellent in existence, and without them it would not have been possible to write this paper.

3. General body form

Bulman (1931) was the first to draw attention to the carbonaceous film, which indicates the outline of the body, and is visible in many specimens of *Palaeospondylus* when wetted. It is clear that Dean (1896, 1900) also observed this film, when he described oblique markings as the remains of fin-rays. From this, and the manner in which the fossils are preserved, Bulman concluded, in my opinion correctly, that the body was evidently much compressed dorso-ventrally at the anterior end, but was laterally compressed posteriorly in the caudal region, and 'probably for some distance forwards from this in front of the anus'. He also concluded that the body although dorso-ventrally compressed anteriorly was narrow and not laterally expanded nor ray-like. It seems to me that this dark film not only represents the remains of the body, but in many cases also that of the paired fins. This film is quite well shown in figure specimens B.M.N.H.,* P 22404 (*B.C.F.*, figure 16, plate 24) and B.M.N.H. P 22392 A (*C.CF.* figure 17, plate 24).

In some especially well-preserved specimens the dark film appears granular, which suggests it to be in part formed by a shagreen of very small scales or denticles, similar to that found in rare cases on the body of the Arthrodire *Coccosteus* from the same rocks (Heintz 1938).

One of the most important facts still to be discovered about *Palaeospondylus* is the nature of the microscopic structure of the skeleton. The question was discussed in detail but with little positive result by the Sollases, who concluded that it must have been bone or calcified cartilage. The state of preservation of the material makes it impossible to add to their work, but as there is so great a similarity between the appearance of the skeleton of *Palaeospondylus* and the bone of other fishes like *Coccosteus* in the same rocks, the skeleton of *Palaeospondylus* will here be referred to as bone. In some specimens peculiar denticle-like protuberances are present on some of the skeletal elements. They can be seen on the skull of B.M.N.H. P 22401 on the bone labelled *CH* (figure 9, plate 22), and directly anterior to it. At first their presence led me to believe that they might indicate the dermal origin of some of the bones. However, as they are present in some specimens on such obviously endoskeletal structures as centra and neural and haemal arches, and as they are extremely irregular in their arrangement and vary much in size, it seems more probable that they are caused by post-mortem changes during fossilization. There seems therefore little doubt that the skeleton preserved is entirely endoskeleton.

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* In this work the letters B.M.N.H., M.Z.C., R.S.M., I.C.S., refer respectively to specimens belonging to the British Museum (Natural History), Museum of Zoology, Cambridge, the Royal Scottish Museum, Edinburgh, and the Imperial College of Science, London.

The smallest specimen examined which was complete enough to estimate the size with any degree of accuracy was R.S.M. 1898–59–5, measuring about 13 mm. in total length, and the largest M.Z.C. 159 measuring about 43 mm. Dean (1900), however, records a specimen of 52 mm., and one as small as 6 mm.; but the latter specimen is undoubtedly incomplete. Although several hundred specimens were measured no change in proportion between the head and body length could be detected with increase in size, nor were there any structural differences between the largest and smallest specimens. The length of the head in all cases was contained about six times in the total body length.

4. The skull

The skull of *Palaeospondylus* is invariably preserved so that the ventral or more rarely the dorsal surface is uppermost on the rock: a specimen preserved in lateral view has never been found. This provides very strong evidence that the skull was dorso-ventrally compressed in life. In the majority of specimens very little displacement of the individual elements of the skull is found; in fact so rare is displacement that great difficulty is usually experienced in determining whether certain structures are fused or merely articulated with one another. However, in three instances considerable dislocation has taken place, and these specimens, R.S.M. 1893–68–3 (figure 10, plate 22), R.S.M. A. (unnumbered), (figure 12, plate 23), I.C.S. 1171, proved invaluable for interpreting the morphology of the skull. Dean (1900) also figures a dislocated skull (his figure 4, plate 1). Elucidating the cranial anatomy is by no means easy, and although about five hundred specimens were examined only a very few were sufficiently well preserved to determine the details of the anatomy of the head. The dorsal surface is best preserved in the following specimens: B.M.N.H. P 22394 (figure 11, plate 22), B.M.N.H. P 22400 (figure 13, plate 23), B.M.N.H. P 22397 and M.Z.C. 230 (all collected by Dr Forster-Cooper); and the ventral surface in the following specimens: B.M.N.H. P 22401 (figure 9, plate 22), B.M.N.H. P 22396 (figure 8, plate 22), B.M.N.H. P 22392 (figure 17, plate 24) (collected by Dr Forster-Cooper) and R.S.M. 1936–38–3, R.S.M. 1936–38–8; the following description is based on these specimens unless others are specifically referred to.

(*a*) *Neurocranium*

In the following account of the head reference will only be made to the accounts of Bulman (1931) and the Sollases (1903), as observations in other accounts such as those of Dean and Traquair are very unreliable. From the disarticulated specimens mentioned above (figure 10, plate 22, figure 12, plate 23, and figure 3), and from other well preserved specimens with the visceral arches in place (figures 1 and 2, and figures 8, 9, and 11, plate 22), the neurocranium can be seen to consist of a pair of auditory capsules connected by a well ossified floor and lateral walls to the anterior processes known as the 'rostralia'. No occipital region is developed behind the auditory capsules. The auditory capsules (*AC*) are much dorso-ventrally flattened, and are relatively large and well developed in relation to the rest of the skull. Their size is particularly significant, as it provides the best evidence that *Palaeospondylus* must have possessed more than two semicircular canals as suggested by Bulman (1931).

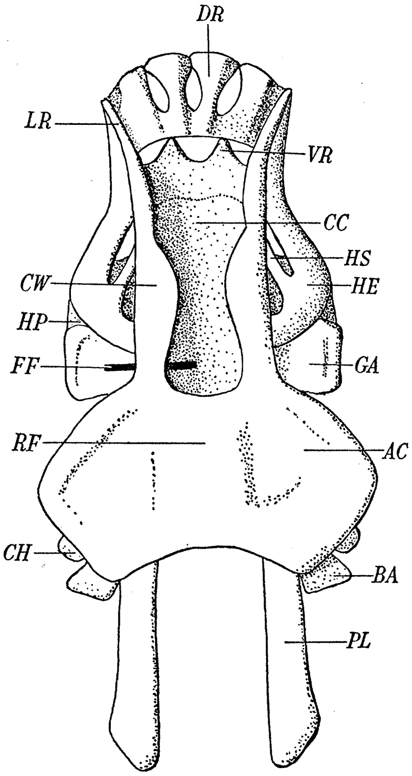

FIGURE 1. *Palaeospondylus gunni* Tr. Restoration of skull in dorsal view.

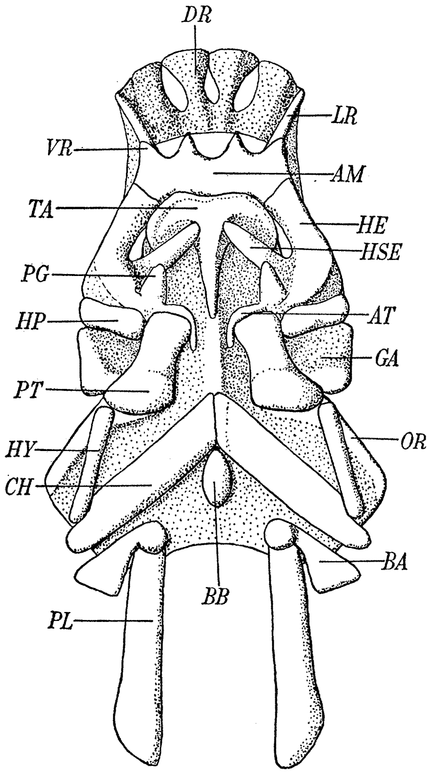

FIGURE 2. *Palaeospondylus gunni* Tr. Restoration of skull in ventral view.

He admits, however, that the suggestion is based 'on somewhat imperfect evidence'. Unfortunately, the crushed state of the material makes it impossible to describe the auditory labyrinth in any detail. Nevertheless, from the evidence of serial sections the Sollases (1903) demonstrated that the auditory capsules are not well ossified on their inner surface, and a communication exists between the cavity of the auditory capsules and the brain cavity. The outer edges of the otic capsules are well defined, the anterior being greatly thickened ventrally (*OR*). The Sollases interpreted this anterior thickening as a branchial arch, but I am fully in agreement with Bulman that it is really part of the auditory capsule. These anterior thickenings are slightly enlarged at the front end and hollowed out ventrally into an articular surface (*AS*).

The floor of the neurocranium is complete from the occiput to the anterior transverse bar, named by the Sollases the 'ampyx' (*AM*) from which the ventral rostralia

(*VR*) arise. Anteriorly the floor is formed of a well defined T-shaped structure, the 'tauidion' (*TA*) of the Sollases. The median arm of the *T* of the 'tauidion' lies along the anterior mid-ventral part of the skull which, anteriorly to the auditory capsules, is produced downwards into a keel, whereas the cross-bar abuts against and slightly overlaps the 'ampyx' (*AM*) and is continued upwards with the floor of the brain-case with which it possibly fuses. I have been quite unable to confirm the presence of a median foramen described by the Sollases opening ventrally on either side of the longitudinal arm of the 'tauidion'. Bulman, who also figures this foramen in his reconstruction, does not convincingly demonstrate its presence in any of his figures of actual specimens. In the material I have examined, in which this region is especially well preserved in both dorsal and ventral views, I could not find any traces of it.

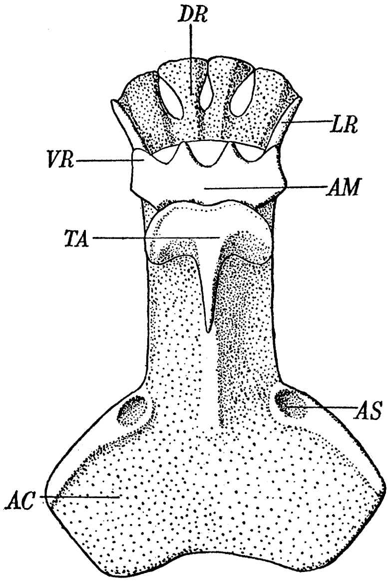

FIGURE 3. *Palaeospondylus gunni* Tr. Restoration of neurocranium in ventral view.

The Sollases observed that the floor of the skull in the region of the auditory capsules is usually at a higher level than the floor more anteriorly, the change in levels being quite sudden. The deeper anterior part directly in front of the auditory capsule was interpreted by the Sollases, Bulman and Stensiö (1927) as the *fossa hypophyseos*. I am inclined to believe, however, that the change in level is not entirely due to this fossa, but is caused mainly by the thin roof between the two capsules collapsing under pressure. If this is the correct interpretation, the brain cavity was completely roofed over in the otic region (*RF*). Anteriorly to the auditory capsules the walls of the neurocranium are well calcified, and are expanded dorsally towards the middle line roofing over part of the brain cavity. This roofing is by no means complete, and a considerable area is left unroofed from the auditory capsules to the rostralia. The cranial walls in life cannot have been very high, but in a dorso-ventrally compressed fossil it is difficult to be certain to what extent the skull has been crushed. Nevertheless, the evidence of serial sections and transfer preparations shows that at their highest point the maximum height of the skull walls was equal in height to about a sixth of its total length. Anteriorly the walls of the neurocranium diverge, are not so high as posteriorly and are continued at the front end into the rod-like structures, named by previous authors the 'lateral rostralia' (*LR*). Directly in front of the auditory capsules the side walls are interrupted by a large foramen (*FF*), which Bulman and the Sollases interpreted as the foramen for the optic nerve. However, the position of the orbits can only be speculation, and it is equally probable that it is the foramen for the facial and trigeminal nerves. The evidence of serial sections demonstrated the presence of other more anterior and smaller foramina; but, as is to be expected in a crushed fossil, these foramina were not found to be sufficiently constantly present to warrant any interpretation. Notwithstanding this, some of them must clearly represent nerve foramina.

As has been already mentioned, the anterior end of the floor of the neurocranium is bounded by a very strongly calcified transverse bar, the 'ampyx' (*AM*) from which arise four forwardly directed, pointed but short processes, the 'ventral rostralia' (*VR*). Two of these processes are situated at the outside ends of the bar, and the other two lie on either side of the middle line. Dorsally and anteriorly to the 'ventral rostralia' lie the 'dorsal rostralia' (*DR*). The majority of writers have considered these to be five forwardly-directed pointed processes similar to the 'ventral rostralia', forming a ring with them and the lateral rostralia, and according to Bulman arising on a separate transverse bar. However, there can be no doubt from the evidence of well preserved material, especially specimen B.M.N.H. P 22394 (figure 11, plate 22), that this is not the correct interpretation. In this specimen there appear to be only four of these 'rostralia', each having a widely expanded distal end, which touches or may even be confluent with its neighbour. In specimen B.M.N.H. P 22401 (figure 9, plate 22) there appear to be six such processes, whereas in R.S.M. 1936–38–3 (figured by Traquair) five processes are present. These discrepancies are not at first sight very easy to explain, but the state of preservation of B.M.N.H. P 22394 (figure 11, plate 22) is very good, and makes it seem possible that the spaces between each process may be artifacts. If this is so, it would seem that the 'dorsal rostralia' may be formed of a continuous transverse plate thickened at intervals; in the majority of specimens only these thickenings are preserved which give the appearance of 'rostralia'. There can, however, be no doubt, whatever the true structure of the region may be, that it is separate from the 'ampyx' and apparently attached to the 'lateral rostralia' at the sides.

(*b*) *Visceral skeleton*

Although much doubt has existed as to the nature of the parts of the cranium not yet described above, I agree with Bulman (1931) and Stensiö (1927) that they are of visceral origin. Laterally to the front part of the neurocranium lie the 'hemidomes'

(*HE*) of the Sollases. These are curved structures, the anterior ends of which articulate ventrally with the 'ampyx', but dorsally appear to be continued forward into a process outside the 'lateral rostralia'. Posteriorly the 'hemidomes' apparently articulate with side walls of the neurocranium, anteriorly to the large nerve foramen. The space between the neurocranium and the curved 'hemidome' is subdivided by a process named by the Sollases the 'hemidome septum' (*HSE*). This is a forwardly directed bar running under the side wall of the brain case, and being continued ventrally as a process, lying in the angle of the T-shaped 'tauidion' and partially overlapping it. The 'hemidome' in disarticulated specimens is, therefore, found to be a triradiate structure. The outer wall of the 'hemidome' is nearly as high as the lateral wall of the brain case, and its outer side slopes towards the middle line. In very crushed specimens the anterior chamber appears to be roofed over as described by Bulman and the Sollases, but I do not believe that this was really the condition in life. Posteriorly and ventrally the 'hemidome' is thickened into a well marked ridge, which lies almost at right angles to the long axis of the skull. Laterally this ridge projects a short way behind the curve of the 'hemidome', giving rise to a process which has been termed the 'hemidome process' (*HP*). I am not absolutely convinced that this structure is actually fused with the 'hemidome'; it may possibly be independent.

Posteriorly to the 'hemidomes' and directly in front of the auditory capsules at the level of the large foramen, the 'gammation' (*GA*) of the Sollases is situated. Dorsally the 'gammation' appears as a somewhat square flattened structure, but ventrally it is much thickened along its posterior margin. This thickened posterior part lies very close to the articular surface on the anterior end of the auditory capsules, but ventrally, however, it is covered by the 'posterior trapezial bar' (*PT*) of the Sollases; but in some specimens where the latter is broken away it can actually be seen to be articulating with the auditory capsules (figure 17, plate 3 and figure 4). The Sollases identified a pair of structures pointing forwards towards the middle line, but separated from one another by the median ventral keel-like part of the skull. Each of these structures appeared to have somewhat the shape of a trapezium, and to bear a transverse bar at its anterior and posterior ends. These bars were called by the Sollases, the 'anterior (*AT*) and posterior trapezial bars' (*PT*). This interpretation is, however, not entirely correct, for whereas the 'anterior trapezial bar' is completely separate from the main bar and is actually bent round it towards the middle line, the 'posterior trapezial bar' is merely a swelling at the posterior end of the 'trapezium'. From specimens broken in this region there is every reason to believe that the 'posterior trapezial bar' actually articulates with a downward extension of the 'gammation'. In this region the 'gammation' thus articulates dorsally with the auditory capsule and ventrally with the 'posterior trapezial bar'. Slightly to the side of and in front of the 'anterior trapezial bars' lie two pointed structures which appear to be the same as those identified by the Sollases as the 'pregammation' (*PG*). The exact attachment of these is not clear, and it is very possible that they are continuous with the 'anterior trapezial bars'. Lying beneath the auditory capsules are two pairs of rod-like structures, which I interpret, for reasons given below, as the hyomandibulars (*HY*) and ceratohyals (*CH*). The former are the shorter and lie more or less antero-posteriorly along the outer sides of the auditory capsules. They articulate posteriorly with well marked articular facets on the ceratohyals, which are broad, well developed structures meeting one another in the middle line. These structures are the second and third branchial arches of the Sollases, and the first and second 'subotic rods' of Bulman. Directly posteriorly to the symphysis of the ceratohyals lies a small elliptical body, the basibranchial (*BB*), which was noticed by the Sollases, but not mentioned by Bulman. Posteriorly to the ceratohyals lies a further pair of articulating rods. The anterior of these (*BA*) consists of a median knob-like part and a lateral short expanded projection. A pair of long posterior rods (*PL*), similar in size to the ceratohyals, articulates with the knob-like portion of the anterior rods (*BA*). The latter rods (*BA*) were called by the Sollases the fourth branchial arches, and by Bulman the third subotic rods, and the former (*PL*) by all authors the 'Post-occipital lamellae'. Lying ventrally to the posterior end of these bars are two thinner and slightly curved rods, which are here considered to be the pectoral girdles (plates 22, 23, 24, *PC*). Bulman describes these as being formed of two pieces, believing them to be branchial arches. The new material, however, leaves no doubt that they are single rods.

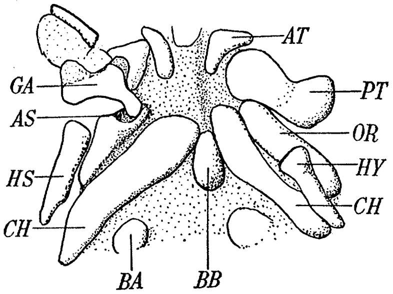

FIGURE 4. *Palaeospondylus gunni* Tr. Ventral view of part of the skull of B.M.N.H. P 22392, showing the articulation of the 'gammation' with the auditory capsules. × 16.

In interpreting the visceral skeleton, it is easiest to begin considering the rods here termed the ceratohyals (*CH*). If *Palaeospondylus* is a gnathostome there cannot be any reasonable doubt that two such large rods meeting one another in the middle line are either the ceratohyals or mandibles. If they are the mandibles their position below the auditory capsules is peculiarly far back and interpretation of the more anterior visceral elements would be well nigh impossible. If on the other hand these rods are considered to be the ceratohyals, then the lateral rods which articulate with their posterior ends are the hyomandibulars (*HY*) and the small median element, directly behind their junction, the basibranchial (*BB*). On this interpretation all the anterior visceral elements must belong to the mandibular arch.

At first sight the anterior elements appear to be in a very specialized condition, and not to resemble closely the elements of the mandibular arch of any other gnathostome. There is no doubt that they do represent a specialized condition and that they are specialized for some purpose which is not exactly clear, but nevertheless they do not defy interpretation. First, since there is no doubt that the 'posterior trapezial bars' articulate with a downwardly projecting part of the 'gammations' and that the 'gammations' also articulate with the anterior ventral corners of the auditory capsules, it is probable that these represent the posterior part of the lower jaw and the palatoquadrate respectively. Now since the 'hemidome' parts of the skull and the 'gammations' lie in just the position one would expect to find the palatoquadrate, and since the 'gammations' do actually articulate with the auditory capsules, it seems very reasonable to interpret them as the anterior and posterior parts of the palatoquadrate. This would mean that the articulation would be the 'basal' one, very similar in all respects to that found in some Urodeles e.g. *Hynobius* (Edgeworth 1923) (figure 5 *BP*) between the posterior part of the palatoquadrate and the auditory capsule. If the interpretation is correct the palatoquadrate must be pretty firmly articulated to the neurocranium, attached anteriorly by an ethmoid articulation and medially by the posterior end of the 'hemidome', and since it receives no support from the hyomandibular the type of jaw suspension would be auto-stylic. The 'hemidome septum' still requires explanation, and it seems possible that it is a palatal tooth-bearing process. It is very difficult to offer a convincing explanation of the 'anterior trapezial bar' and the pregammation, but since neither structure appears to be closely connected to the neurocranium nor to the palatoquadrate it seems possible that they may represent more anterior ossifications of Meckel's cartilage, or possibly tooth plates or again ossifications bearing teeth, a view which is supported by the fact that the palatoquadrate in all specimens is found overlapping the 'hemidome septum'. Since the palatoquadrate is so closely connected to the neurocranium it seems probable that some kind of crushing dentition must have been present. If this interpretation is correct, the opening of the mouth would lie a short distance behind the 'ampyx',

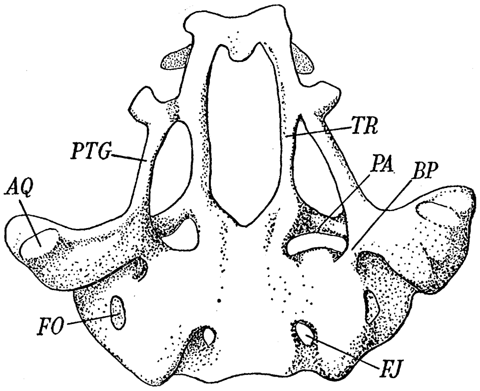

FIGURE 5. *Hynobius* larva 20 mm. Ventral view of chondrocranium (after Edgeworth).

leaving the skull with a long rostral region. The only structures left to be explained are the post-occipital lamellae, and the two small structures to which they articulate. Although the possibility always remains that they may be connected with the shoulder girdle, I have rejected this explanation on the grounds of their large size, and that other structures which are probably the girdles lie ventrally to them. I prefer to consider them as branchial arches. Why they are so much enlarged is still a mystery. The remaining branchial arches were, however, probably cartilaginous, and were their position known the post-occipital lamellae would probably appear less isolated and of more branchial arch-like appearance. It must be remembered that it is by no means unusual in Elasmobranchs for the pharyngobranchial of the fifth arch to be a great deal larger than the more anterior ones. Many previous writers have provided theories of their nature and the opinion given above agrees with that of the Sollases. Jaekel (1927) supposed them to be parachordals, Stensiö (1927) compared them with the pronephric lamella of a Cephalaspid, Bulman (1931) considered them to be part of a rasping tongue apparatus and Graham Kerr interpreted them as cranial ribs. However attractive at first sight these speculations may be, on examination of the evidence it still seems most likely that they are modified parts of a branchial arch.

5. The paired fins

As has already been pointed out, it is my belief that the slightly curved rods (plates 22, 23, 24 and figure 4, *PC*) lying ventrally to the 'post-occipital lamellae' are the pectoral girdles. Dean (1896) described and figured pectoral fins, but after severe criticism from Traquair (1897) he seemed (1900) slightly less sure that these 'parallel nearly transverse markings in the region where the pectoral fins would appear' were really the remains of fins. The markings are part of the carbonaceous film described above (p. 393) and although it seems highly probable that they are not entirely due to the presence of paired fins, it is also quite possible that they are in part due to the internal skeleton of the pectoral fins. They are quite well shown in several specimens, notably B.M.N.H. P 22400 (figure 16, plate 24, *CF*), although Dean greatly exaggerated the clarity of their appearance.

In about 40% of the specimens examined at the level of the sixth or seventh vertebra behind the 'post-occipital lamellae' lies a pair of structures, which although frequently varying in shape are usually triradiate (figures 13, 14, plate 23, figures 15–17, plate 24, *PV*). Two of the radii point towards the vertebral column and the third outwards and backwards. These structures frequently, but by no means invariably, lie close to the edge of the dark carbonaceous body film. There can be little doubt that they are part of the pelvic fin skeleton, and from their shape it is very probable that they are the skeleton of the pelvic girdles. No definite radials have been observed in connexion with them, but as in the case of the pectoral fins these are probably represented to a certain extent by the carbonaceous film. If these skeletons have been correctly identified as the pelvic girdles, the pelvic fins lie relatively rather far forward in the body.

These structures were almost certainly observed by Dean and figured by him, but their significance was lost, owing to the exaggerated way in which he figured the other 'transverse markings' in the carbonaceous film. There can be no doubt that the Sollases also observed at least one of them, which they figured as a displaced neural arch (their figure 1, plate 16, *vna*).

The presence of paired fins in *Palaeospondylus* is very important in connexion with its affinities, since their absence was considered to be one of the main pieces of evidence supporting their Cyclostome affinities: it is a significant fact that among contemporaneous Devonian fishes the Placoderms have the pelvic girdle situated very far anteriorly, e.g. *Rhamphodopsis* (Watson 1934, 1938) and *Pseudopetalichthys* (Broili 1933*b*; Moy-Thomas 1939).

6. The unpaired fins

No traces of dorsal nor anal fins could be found in any of the material examined.

The tail (figure 6; figures 19, 20, plate 25) is heterocercal, and the caudal fin is formed by the haemal spines (*HS*) and a single row of radials (*RA*). Although the caudal region is nearly always preserved, only very occasionally can this row of radials be seen. The tail is best preserved in R.S.M. 1893–145–6 (figure 20, plate 4), which was figured by Traquair (1893*b*), but another specimen B.M.N.H. P 22401 (figure 19, plate 25) is very interesting for comparison as it has the radials displaced. There appear to be about twenty-five radials in all, although their exact number is difficult to determine, as they become very small posteriorly. They are all expanded proximally into a knob-like protuberance for articulation with the similarly expanded distal end of the haemal spines. Distally from a point at about half their length they dichotomize into five pointed processes, which very rarely can be seen to dichotomize again. The radials increase in length from before backwards to about the tenth, and then gradually decrease in proportion to a similar decrease in the length of the haemal spines.

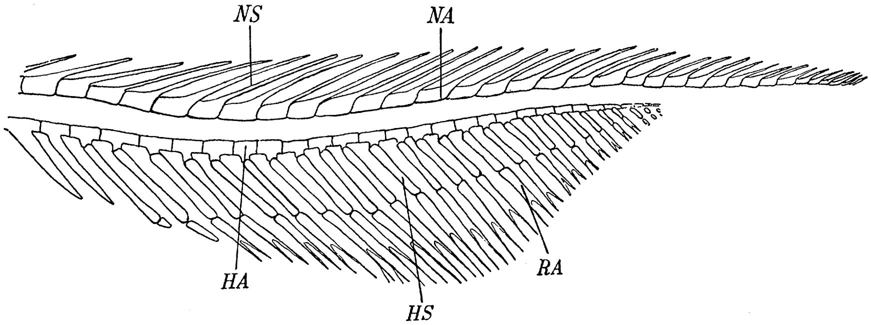

Figure 6. *Palaeospondylus gunni* Tr. Restoration of tail.

Perhaps the most interesting new features in the structure of the tail described here are, firstly that it is heterocercal, and secondly that the dorsal and ventral lobes are correctly orientated. Traquair (1890, 1893 *a*, *b*) described the ventral as the dorsal lobe, and his descriptions influenced all other writers, although Dean (1896, 1900) believed the tail to be possibly heterocercal. In several specimens particularly B.M.N.H. P 22400 (figure 13, plate 23) it was possible to trace the neural arches serially backwards from behind the head to the tip of the tail, thus providing the evidence for the interpretation of the tail. The presence of radials distinct from the haemal spines in the tail is also demonstrated for the first time.

These two points are especially important, as the nature of the tail of *Palaeospondylus* was considered to be one of the strongest reasons for believing it had Cyclostome affinities, a resemblance between the tail of *Petromyzon*, with its dorsally bifurcating fin rays being claimed. Dean (1900) suggested that the fin rays, since they dichotomize, must be exoskeletal structures, but this does not necessarily follow as dichotomized endoskeletal fin-rays are by no means uncommon in living Elasmobranchs.

7. The axial skeleton

It has been possible to throw much new light on the structure of the axial skeleton; nevertheless, the poor state of its preservation leaves several points of interest still in doubt. Fortunately none of these points is of great importance from a phylogenetic aspect.

One of the most striking features of *Palaeospondylus*, responsible even for its name, is the presence in the vertebral column of centra, which extend throughout its length except in the caudal region (figure 7, *CE*; figures 13, 14, plate 23, figures 15–17, plate 24, figure 18, plate 25, *CE*). Usually about forty centra are present. They are ring-like and do not constrict the notochord; anteriorly the rings are complete, but, although it is difficult to be certain, they appear not to be complete ventrally throughout the greater part of the column. The most anterior vertebra is usually found in close association with the occiput, and unlike the two succeeding centra, seldom becomes displaced. All three anterior vertebrae are relatively narrower antero-posteriorly than the remainder, and do not appear to articulate with one another. This separation led Bulman (1931) to suggest that possibly only the anterior half of the sclerotome is ossified. The neural arches (*NA*) are low and without prominent spines on about the first twenty-five vertebrae; the arch of the most anterior vertebra is rather broader than any of the others. Posteriorly neural spines (*NS*) are developed, which are at first broad and blunt, but gradually become more pointed farther back, until in the caudal region they are long spine-like processes. However, the length of the neural spines decreases again towards the end of the tail.

Ventrally to the centra throughout the entire length of the vertebral column, except perhaps in the region of the most anterior centra and at the extreme posterior end, haemal processes (*HA*) are situated. These processes are presumably formed by the combined basiventrals and interventrals, but their precise structure cannot be determined. However, they must be short and rib-like anteriorly, but posteriorly form a haemal canal, as in many living Elasmobranchs. Unfortunately the exact point at which they change from lateral rib-like structure to form a haemal canal cannot be identified, but it probably lay a short distance behind the pelvic fins. On about the eighth vertebra in front of the caudal fin haemal spines (*HS*) are developed, which appear to be distinct from the arches. Anteriorly they are short and blunt, but they soon become thin and pointed farther back. However, at the point where the caudal fin arises they become blunt and knob-like distally, and articulate with the row of radials. The haemal spines gradually decrease in length posteriorly, and finally disappear altogether.

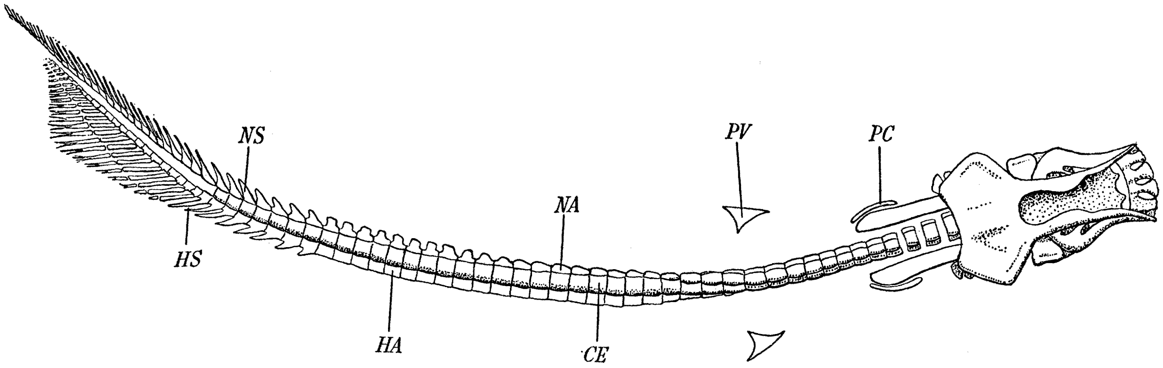

FIGURE 7. *Palaeospondylus gunni* Tr. Restoration of entire fish.

The haemal arches and spines in the tail region (figures 6, 7; figures 19, 20, plate 25) lose their segmental arrangement and become more numerous than the neural arches, the tail being formed of about twenty-five haemal arches, which correspond only to about twenty neural arches. At the extreme posterior end the haemal arches are not present, and there are about a dozen neural arches with no ventral elements corresponding to them.

The above description of the axial skeleton of *Palaeospondylus* differs mainly from previous accounts in that the dorsal and ventral surfaces are correctly distinguished throughout. Confusion has arisen in the past over the belief that the tail had a larger dorsal than a ventral lobe, which in its turn led to the identification of haemal elements as neural. Traquair (1890, 1893 *a*, *b*) made this mistake throughout his observations, and although Dean (1900) appears to have in some cases correctly identified the neural arches he was much influenced by Traquair's observations in his restoration. As has already been stated in connexion with the anatomy of the caudal fin, there can be no reasonable doubt that the neural and haemal arches have now been rightly identified. They can be traced from the skull to the tip of the tail without interruption in several specimens, especially B.M.N.H. P 22400 (figure 13, plate 23).

8. AFFINITIES OF *PALAEOSPONDYLUS*

Since different writers in turn have claimed that *Palaeospondylus* is related to nearly every group of fishes and also the Amphibia, each group will be considered in detail. It is first, however, necessary to decide the issue whether or not *Palaeospondylus* is an adult or a larval form. It is said that before Traquair's original description of *Palaeospondylus* T. H. Huxley pronounced it a 'baby *Coccosteus*'. Several other authors notably Dean and Graham Kerr have also held the opinion that *Palaeospondylus* was a larval form, and the former produced elaborate measurements to show that there is a proportional increase in the relative length of the vertebral column to the head with increase in size. The Sollases very rightly criticized Dean's tables of measurements and demonstrated a more or less constant proportion between the length of the head and vertebral column, a conclusion which I have been able to support after measuring several hundred specimens. The Sollases, however, did not deny the possibility of some change in proportion, and attempted to demonstrate a slightly more rapid growth of the front part of the skull, which I have not been able to confirm. It must be remembered that the entire head of *Palaeospondylus* is never very much more than 5 mm. in length and in a compressed fossil of this size considerable allowance has to be made for the different states of preservation of each specimen. Consequently conclusions based on the measurements of the Sollases in millimetres taken to three places of decimals must be looked on with great suspicion.

In addition to the absence of any demonstrable change in proportions or structural change with increase of size the state of ossification of the skull is very great for a larval form, and the ossified ring-like centra are sufficient to make it certain that *Palaeospondylus* is an adult. The absence of ossification of certain structures such as the radials of the paired fins and of dorsal and anal fins is just as likely to be found in adults as in larval forms and cannot be used as evidence on behalf of the view that *Palaeospondylus* is a larva.

(*a*) *Cyclostomes*

Traquair and other early writers on *Palaeospondylus* based their view that it was related to the Cyclostomes on the absence of jaws and paired fins, the dichotomy of the dorsal fin rays, and the presence of rostralia around the supposed narial opening. Since it seems improbable that any such rostral ring of processes existed, since paired fins are undoubtedly present and since Traquair omitted the presence of radials and described the tail upside down, only the absence of jaws is left for consideration. On the interpretation given here it seems as though jaws were almost certainly present, and, as ring-like centra are unknown in Cyclostomes, there would seem to be no justification for this view on the evidence put forward by Traquair.

Stensiö (1927) and Bulman (1931) have attempted to show that *Palaeospondylus* is related to *Myxine*. Stensiö's ideas are based on insufficient knowledge of the skull, and need not be discussed in detail. Bulman, however, who gave an excellent description of the skull and made most valuable observations, concludes that there were possibly only two semicircular canals in each auditory capsule, that the rostralia represented a ring of spike-like process round the nasal opening, and that the skeleton interpreted above by me as the hyomandibular and ceratohyal, and the post-occipital lamellae, were all part of a rasping tongue apparatus. The relatively large size of the auditory capsules makes it seem to me extremely unlikely that there were only two semicircular canals; the dorsal rostralia are shown not to be spike-like processes in well preserved specimens, and although the rasping tongue explanation is ingenious, in the absence of any other obviously Cyclostome characters it becomes extremely improbable.

It may therefore be safely concluded that there is no evidence at all to support the theory that *Palaeospondylus* is related to the Agnatha.

(*b*) *Dipnoi*

Graham Kerr (1900) and Miller (1930) have demonstrated several points of apparent resemblance between Traquair's figures of the skull (Traquair 1894, figures 2, 5, plate IX) and that of young semimacerated specimens of *Lepidosiren*. They compared the 'post-occipital lamellae' with cranial ribs, and the rods called by me ceratohyals with those of the young Dipnoan. In Traquair's figure 5 they also identify a median parasphenoid and lateral tooth-plates. Unfortunately this is a figure of the *dorsal* not the ventral surface, and the median 'parasphenoid' is only the roof of the brain-case, and the tooth-plates are part of the hemidomes. The Sollases (1903) have already pointed out the difficulty in considering the post-occipital lamellae to be cranial ribs, since they are not attached to the skull.

Miller, in an attempt to overcome a further objection, the presence of centra, against *Palaeospondylus* being a Dipnoan, stresses the importance of a small string of cartilaginous blocks in the tip of the tail of *Lepidosiren*, which she believes may indicate that the notochord was segmented in early Dipnoans. Although this does not seem to have been generally the case in early lung fishes, some at least like the Upper Devonian *Rhynchodipterus* (Säve-Söderbergh 1937) undoubtedly had ossified centra.

The Sollases although abandoning the view that *Palaeospondylus* is related to the Dipnoi, recognize certain similarities between their skulls, especially the large size of the auditory capsule, the unroofed cranial cavity and the foramen in front of the auditory capsules in larval Dipnoans. To these might be added the strong resemblance of the palatoquadrates in the two groups and the probable crushing type of dentition. The hemidome's anterior articulation can be compared with the ethmoid articulation, probably present in early Dipnoan larvae as in some Amphibia (figure 5), and the posterior as the ascending process. Similarly the gammation can be compared with the quadrate region and possibly the otic process of a Dipnoan. Further, as Graham Kerr and Miller have pointed out, the 'rostralia' may be comparable to the structure in Dipnoan larvae that houses the nasal sacs.

However, there are many objections other than those already stated to this view. Most important perhaps of these is the exceedingly improbable assumption that *Palaeospondylus* is a larva at all. No adult Dipnoan is known without any dermal bones or scales. The tail is not particularly Dipnoan, and the nature of the ribs and vertebral column and the position of the fins are against this view. A fully developed hyomandibular is decidedly not a Dipnoan characteristic, nor is the median T-shaped anterior bone like the 'tauidion'. Also, if the 'post-occipital lamellae' are not cranial ribs, they are as unlike anything known in the Dipnoi as in other groups, and it must be remembered that there is always a certain degree of resemblance of the development of the palatoquadrates in forms with crushing dentitions and autostylic skulls. For these reasons I find myself unable to adopt the point of view that the resemblances between *Palaeospondylus* and a larval Dipnoan are of any significance.

(*c*) *Amphibia*

Although many of the similarities between the skull of *Palaeospondylus* and a young Dipnoan apply equally to the Amphibia, the nature of the tail and vertebral column are so fundamentally unlike anything known in the Amphibia that the possibility of relationship cannot be considered.

(*d*) *Osteolepidoti*

There is a certain general resemblance between the ring-like centra in the vertebral column of *Palaeospondylus* and those of some Osteolepids, but here the similarity stops. The complete absence of dermal bones and scales, and the nature of the visceral arch skeleton are sufficient grounds for believing that no close affinity exists.

(*e*) *Actinopterygii*

It is hardly necessary to refute the views of Kyle (1926) that *Palaeospondylus* is a larval herring, since Teleosts are not found till the Mesozoic. However, Palaeoniscids are known in the Devonian and the general shape of their neurocrania is not unlike that of *Palaeospondylus*, but the absence of dermal bones is unknown in Palaeoniscids, and even in those forms without body scales a patch of scales is usually found on the caudal lobe. The form of the vertebral column, the tail with radials and the visceral arch skeleton of *Palaeospondylus* exclude any possibility of close relationships.

(*f*) *Elasmobranchii*

The Elasmobranch affinities of *Palaeospondylus* have been chiefly argued by the Sollases (1903), although their reasons for doing so are to a great extent based on very unsatisfactory data. They quite rightly emphasize the general similarity of the shape of the cranium, but believe the 'hemidomes' to be the nasal capsules; this cannot be true as they are only articulated to the skull. The 'rostralia' are directly compared with those of Elasmobranchs, and the 'gammation' is believed to be the hyomandibular, the 'pregammation' the palatoquadrate, the 'posterior trapezial bar' the hyoid, and the anterior the mandible. The remaining posterior visceral arches were considered to be branchial arches. The more recent observations of Bulman and myself, however, make such comparisons as these impossible, as it would be very strange if the hyomandibular articulated with the base of the auditory capsules and the mandible bent round the front of the hyoids.

Dean (1904) suggested relationship with the Holocephali on the grounds that both they and *Palaeospondylus* had continuous dorsal fins, protocercal tails, ring centra, elaborate nasal cartilages and huge heads. There is, however, no direct evidence that the dorsal fin of *Palaeospondylus* was continuous, its tail is not protocercal but heterocercal, and the remaining characters alone are of little significance.

Although these arguments of Dean and the Sollases amount to very little, there are certain very striking Elasmobranch features in *Palaeospondylus*. The shape of the tail is not unlike that of certain living sharks, and distally bifurcating radials are also not uncommon in this group (e.g. *Lamna*). Furthermore, the tail fins of many early Selachians e.g. *Ctenacanthus* (Moy-Thomas 1938) are supported by radials. Hollow ring-like centra are found as early as the Lower Carboniferous, e.g. *Chondrenchelys* (Moy-Thomas 1938); the presence of haemal ribs, and neural arches which start low anteriorly and become pointed towards the tail, are also typical of many modern Selachians. The position of the pelvic fins is also not inconsistent with Elasmobranch affinity, neither is the general shape of the neurocranium, the large rostral elements and the dorso-ventral compression of the anterior end of the fish. To these characters may also be added the fact that the hyomandibular plays no part in the Holocephali in the suspension of the jaws, the skull being autostylic and the dentition crushing.

On the other hand it is not till the Upper Devonian that primitive Elasmobranchs appear, and it is very significant that many of the features of *Palaeospondylus* are like *modern* and not *primitive* Elasmobranchs. Also it is difficult to reconcile a structure like the 'tauidion' with any in Elasmobranchs as at present defined, and Elasmobranch cartilage when calcified presents a very characteristic appearance.

(*g*) *Placodermi*

Modern researches on fossil fishes have shown that the Placodermi are a very large and varied group, including the Acanthodii, Antiarchi, Arthrodira, Macropetalichthyda, and the very Elasmobranch-like group, the Stegoselachii in which I (Moy-Thomas 1939) include the Rhenanida. In the majority of these groups there is a strongly developed bony exoskeleton, but in the Acanthodii and Stegoselachii this is reduced to a very great extent and the endoskeleton is often well ossified.

The Stegoselachii are known throughout the Devonian and include the shark-like *Nessariostoma* and *Stensiöella* (Broili 1933 *a*) and *Pseudopetalichthys* (Broili 1933 *b*; Moy-

Thomas 1939), and the ray-like *Gemündina* (Broili 1930, 1933 *a*) and *Jagorina* (Jaekel 1927; Holmgren and Stensiö 1936), and it is with these fishes that *Palaeospondylus* can be most easily compared, but in many respects it also resembles the other Placoderm groups. In both *Gemündina* and *Pseudopetalichthys* ring-like centra are known, but in these forms the true nature of the tail and the details of the neural and haemal elements of the vertebral column are unknown. However, in the Arthrodires *Coccosteus* (Heintz 1938) and *Phyllolepis*, in the Acanthodii and the Antiarchi, the tail is heterocercal; actually the shape of the tail of the Antiarch *Bothriolepis* is exactly the same as that of *Palaeospondylus*. Radials are also described in the tail fin of Acanthodians (Watson 1937). The anterior position of the pelvic fins is found in *Pseudopetalichthys*, and also in some Arthrodires like *Rhamphodopsis* (Watson 1938). It is also a significant point that, in those Arthrodires in which the body is known, the radials of the fins are usually not preserved.

The neurocranium of Placoderms (Stensiö 1925, 1934; Watson 1937) usually has a characteristically prominent and long occipital region and in this respect is extremely unlike that of *Palaeospondylus*. In the ray-like *Jagorina* (Holmgren and Stensiö 1936), however, this region of the skull is very short. Watson (1937) has shown that in the Acanthodians and Arthrodira (1938), and probably in all Placoderms, the visceral arches are in a primitive condition. The most anterior gill-slit is not modified into a spiracle, and the hyomandibular plays no part in the suspension of the jaws, a condition which led Watson (1937) to name the group Aphetohyoidea (free hyoid). In *Palaeospondylus* the hyomandibular clearly has no supporting function in connexion with the mandibular arch, and is therefore in the Aphetohyoidean or Placoderm condition.

The ventral position of the mouth and small size of the lower jaws find several parallels among Placoderms. *Pseudopetalichthys* (Broili 1933 *b*) has a mouth in this position and has small and peculiarly shaped mandibles, which are especially interesting in that they scarcely, if at all, meet one another in a symphysis, and are in general appearance amazingly like those of *Palaeospondylus*. In *Rhamphodopsis trispinatus* (Watson 1938) the jaws were also small. They have been reconstructed by Watson as though the mouth was terminal, but it seems probable that they were situated more posteriorly and the mouth ventrally, since the hyoid arch skeleton in Watson's figure lies a considerable distance in front of the eye.

The palatoquadrate ossifications in Placoderms other than Acanthodians (Stensiö 1934) are not very well known, but it is interesting to observe that as a rule the original cartilage, as is also the case in the lower jaw, is ossified in more than one piece, a feature shared by *Palaeospondylus*. The type of the attachment of the palatoquadrate to neurocranium developed in *Palaeospondylus* is highly reminiscent of the condition in *Pholidosteus* where according to Stensiö (1934) 'since there was a rigid connexion between the rostral part of the palatoquadrate and endocranium, it follows that the whole palatoquadrate must have been rigidly attached to the endocranium. Accordingly we must have here in *Pholidosteus* a sort of autostylic suspension.'

Since it has been concluded that the so-called 'rostralia' probably did not form a circlet of cirrhi but a more solid structure, it is interesting to note that in the Stegoselachian *Nessariostoma* (Broili 1933*a*) a well-developed rostral region is present. Unfortunately the internal skeleton of this rostral region is unknown. Tooth plates and crushing dentitions are common structures in Arthrodires, so that if I am correct in believing that such plates were present in *Palaeospondylus* a further point of similarity is established.

Finally, there is no difficulty in finding a comparable structure to the 'tauidion' in Placoderms, as an anterior palatal ossification is found in some Arthrodires like *Pholidosteus* (Stensiö 1934) and Acanthodians (Watson 1937). This ossification in *Pholidosteus* is particularly striking as it is somewhat T-shaped, and its anterior margin is excavated to receive the nasal capsules. The appearance of this anterior margin reminds one so strongly of the anterior margin of the 'ampyx', that it is very tempting to suggest that the nasal sacs may have been situated in the spaces between the ventral rostralia.

Despite the many points of close resemblance between the Placoderms and *Palaeospondylus*, there are a few objections to the view that close affinity exists between them, but none of a very serious nature. The complete absence of dermal ossifications would be peculiar in a Placoderm, but does not necessarily exclude the possibility of relationship. The Stegoselachii have the dermal ossifications considerably reduced in both number and size, and in a very small fish like *Palaeospondylus* it would not be at all surprising to find it had either been reduced altogether or remained only as a shagreen of minute denticles. Moreover, since it is highly probable that fishes of the Placoderm stage of organization were the ancestors of the Elasmobranchs, there seems every reason to suppose that forms must have existed among the Placoderms without dermal armour. Similarly it is not possible to find any parallel or give any special explanation of the post-occipital lamellae, but in a group in which so little is known of the branchial arches it is still possible that something comparable may occur. As I have said above, until further evidence is forthcoming speculation is fruitless.

(*h*) *Discussion and conclusions*

From this discussion of the affinities of *Palaeospondylus* it becomes obvious that it is not a larval form, and that only with the Placodermi and Elasmobranchs can any definite points of similarity be established. It is true that the palatoquadrate of *Palaeospondylus* shows a general superficial resemblance to that of the Dipnoi and Amphibia, but this is probably only due to the autostylic jaw suspension. The weight of the evidence, however, overwhelmingly favours Placoderm affinity in general, and the absence of a heavily ossified exoskeleton suggests the Stegoselachii in particular. It is concluded that *Palaeospondylus* is probably a small Placoderm in which the exoskeleton was even further reduced than in the Stegoselachii, thus representing a hitherto unknown order, the *Palaeospondyloidea*.

One further question remains to be discussed. Is the resemblance to the Elasmobranchii fortuitous, or does it demonstrate relationship between the Placodermi and Elasmobranchii? A great deal has been written recently on the relations of these two groups with one another, chiefly by Watson and Stensiö. The former has stressed the great differences between them, whereas the latter has emphasized the many points of similarity. The most important consideration, however, seems to be that the Elasmobranchii, although they are a compact group with a definite evolutionary story of their own (Moy-Thomas 1939) which starts in the Upper Devonian, must have had ancestors among earlier fishes, and there is very little disagreement among palaeontologists that their origin was from amongst the Placoderms. It therefore seems to me highly significant that forms like the Stegoselachii should have anticipated the later development of the Elasmobranchii in so many characters, and in this respect *Palaeospondylus* may be regarded as another type of Placoderm which also foreshadows its Elasmobranch descendants in many features.

9. Summary

1. The anatomy of *Palaeospondylus* has been redescribed and its affinities discussed.

2. In the skull the 'hemidomes', 'gammations' and 'trapezial bars' are shown not to be fused to the neurocranium, but to be visceral articulating elements. The two former are interpreted as parts of the palatoquadrates, and the latter as the lower jaws. A hyomandibular and ceratohyal are identified, but the former plays no part in the jaw suspension. The 'rostralia' cannot have formed an anterior ring of cirrhi, because the 'dorsal rostralia' terminate bluntly and may even have formed a continuous plate, and it is concluded that the skull had a prominent rostral prolongation.

3. The presence of paired fins, undoubtedly pelvic and probably also pectoral, is described.

4. The vertebral column and tail previously described upside down are for the first time correctly orientated. The former is shown to have haemal elements throughout its length, and the latter to be heterocercal, the caudal fin being supported by haemal spines and a row of distally bifurcating radials.

5. The view that *Palaeospondylus* has Cyclostome affinities is abandoned on account of the presence of paired fins, centra, a heterocercal tail and jaws. *Palaeospondylus* is believed to be related to the Placoderms (Aphetohyoidea), but to represent a new order, the *Palaeospondyloidea*, which in its lack of dermal skeleton and other features suggests a closer affinity between the Placodermi and Elasmobranchii than is generally held to exist.

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EXPLANATION OF LETTERING OF TEXT-FIGURES AND PLATES

AC, auditory capsule.
AM, ampyx.
AQ, articular surface of quadrate.
AS, articular surface.
AT, anterior trapezial bar.
BA, branchial arch.
BB, basi-branchial.
BP, basal process of quadrate.
CC, cranial cavity.
CE, centrum.
CF, carbonaceous film.
CH, ceratohyal.
CW, cranial wall.
DR, dorsal rostralia.
FF, foramen for fifth nerve.
FJ, foramen for jugular vein.
FO, foramen ovale.
GA, gammation.
HA, haemal arch.
HE, hemidome.
HP, hemidome process.
HS, haemal spine.
HSE, hemidome septum.
HY, hyomandibular.
LR, lateral rostralia.
NA, neural arch.
NS, neural spine.
OR, thickened anterior edge of otic capsule.
PA, ascending process of palatoquadrate.
PC, pectoral girdle?
PG, pregammation.
PL, post-occipital lamella.
PT, posterior trapezial bar.
PTG, pterygoid.
PV, pelvic girdle.
RA, radial.
RF, skull roof.
TA, tauidion.
TR, trabecula.
VR, ventral rostralia.

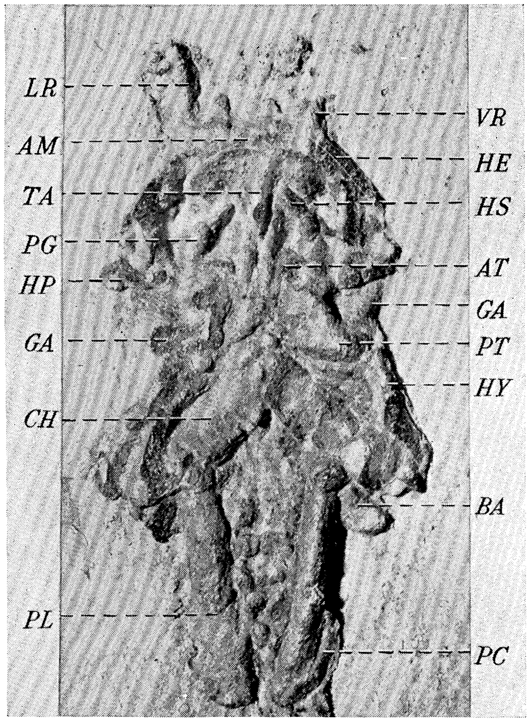


FIGURE 8. *Palaeospondylus gunni* Tr. Ventral view of the skull of B.M.N.H. P 22396. × 12.

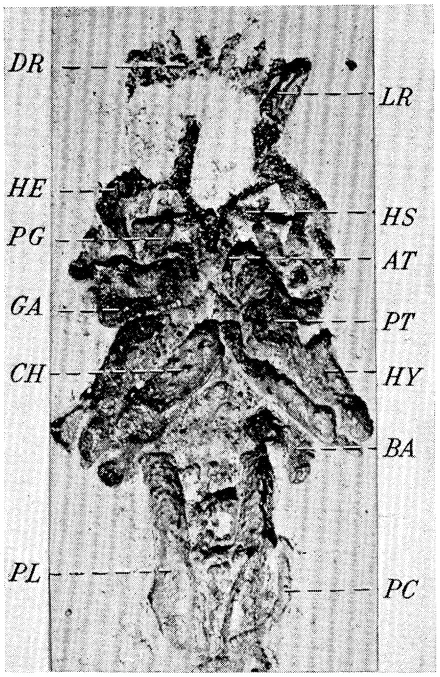


FIGURE 9. *Palaeospondylus gunni* Tr. Ventral view of the skull of B.M.N.H. P 22401. × 10.

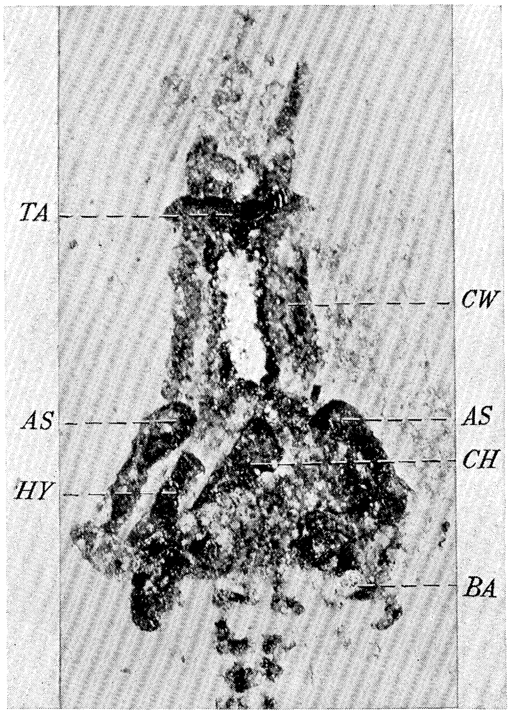


FIGURE 10. *Palaeospondylus gunni* Tr. Ventral view of the disarticulated skull of R.S.M. 1893–68–3. × 14.

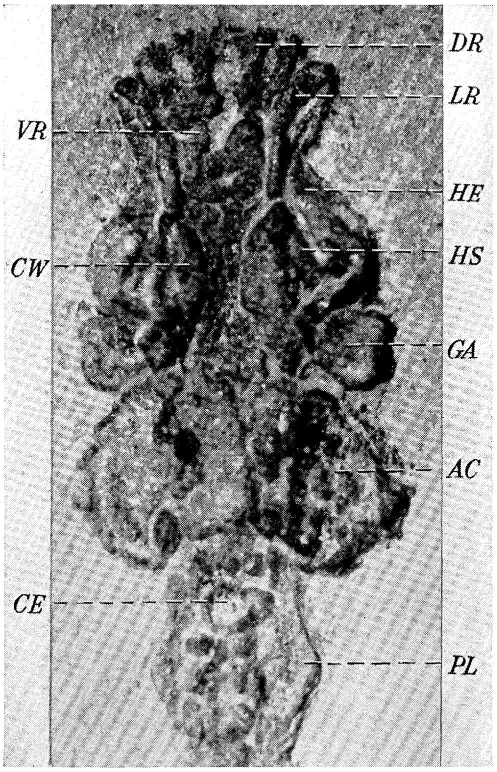
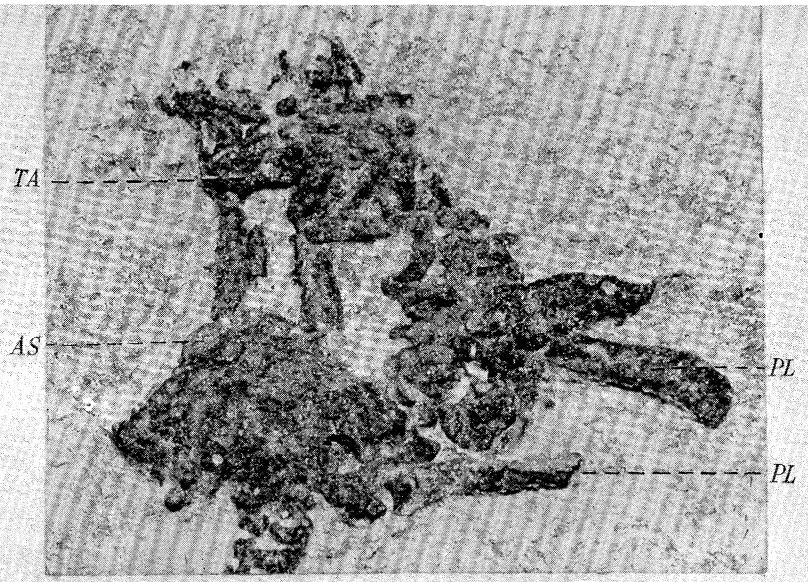


FIGURE 11. *Palaeospondylus gunni* Tr. Dorsal view of the skull of B.M.N.H. P 22394. × 14.



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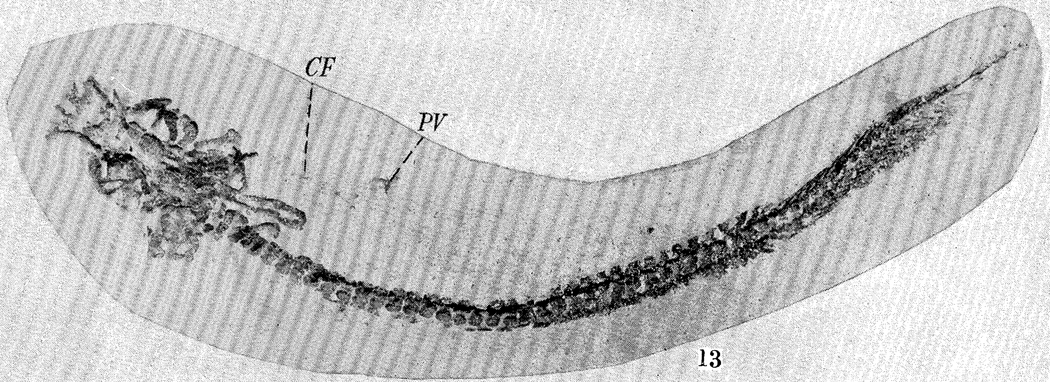

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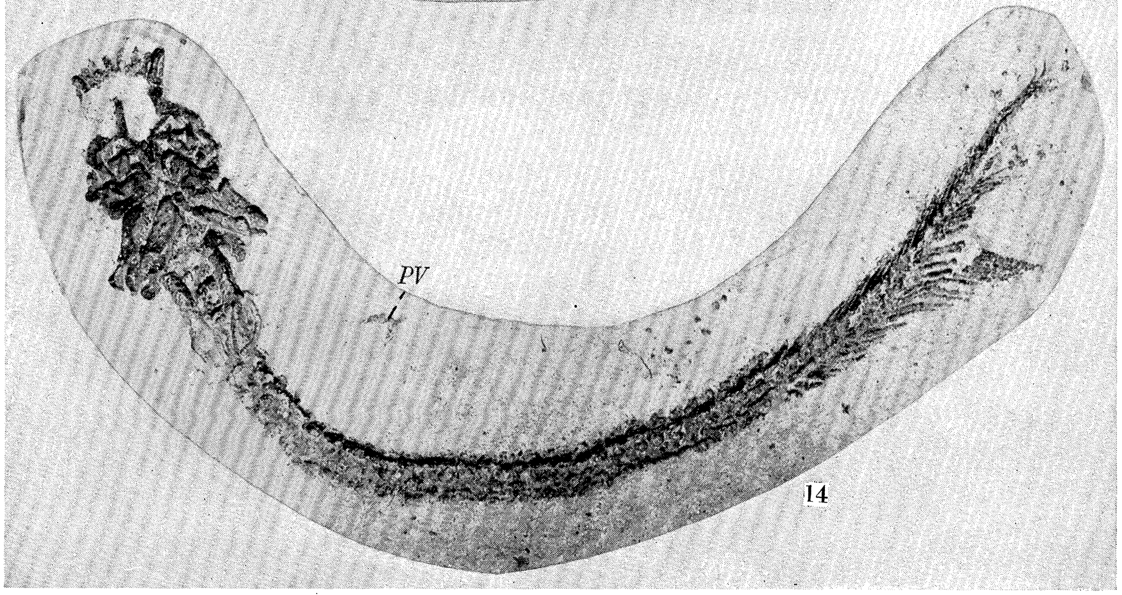

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Figure 12. *Palaeospondylus gunni* Tr. Ventral view of the disarticulated skull of R.S.M. (unnumbered). A. × 15.

Figure 13. *Palaeospondylus gunni* Tr. B.M.N.H. P 22400. × 4¾.

Figure 14. *Palaeospondylus gunni* Tr. B.M.N.H. P 22401. × 5.

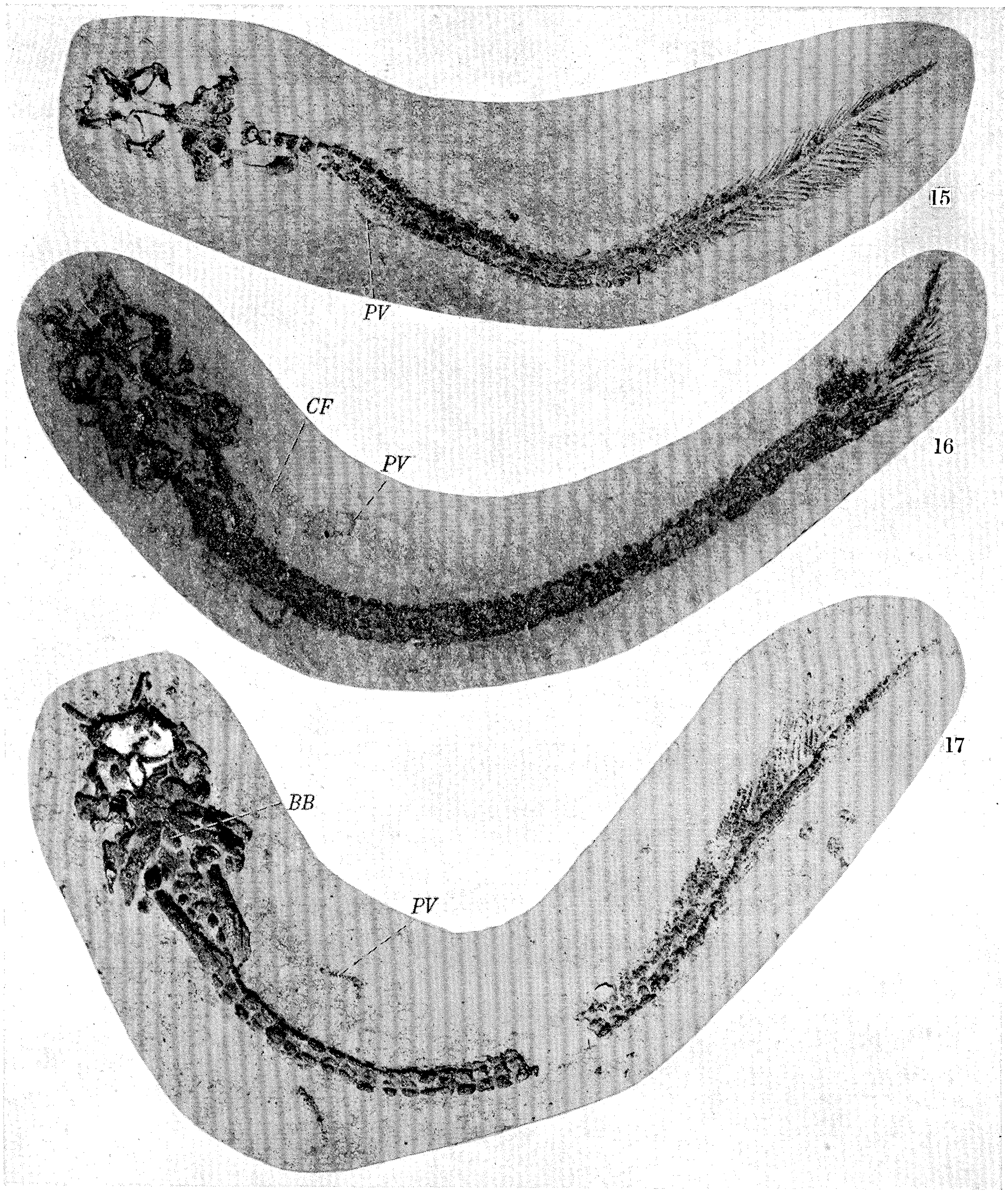


FIGURE 15. *Palaeospondylus gunni* Tr. R.S.M. 1893–145–6. × 4.
FIGURE 16. *Palaeospondylus gunni* Tr. B.M.N.H. P 22404. × 5½.
FIGURE 17. *Palaeospondylus gunni* Tr. B.M.N.H. P 22392 A. × 8½.

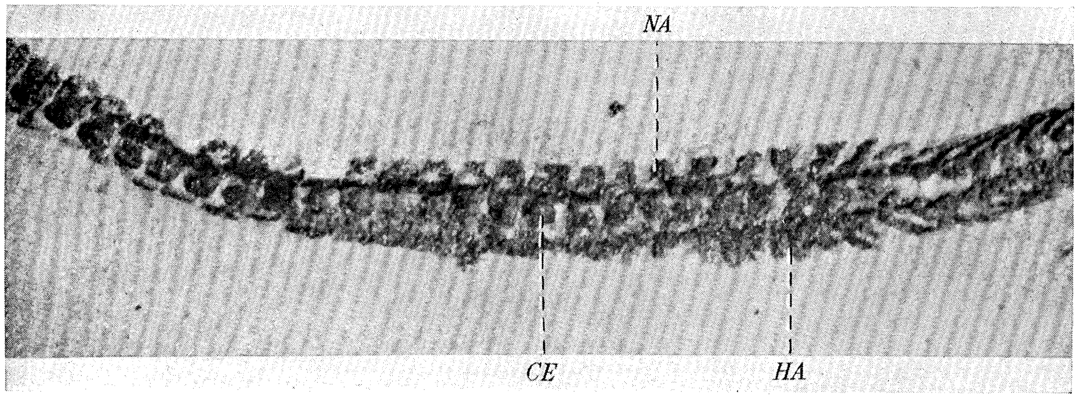


Figure 18. *Palaeospondylus gunni* Tr. Part of the vertebral column of B.M.N.H. P 22400. × 12.

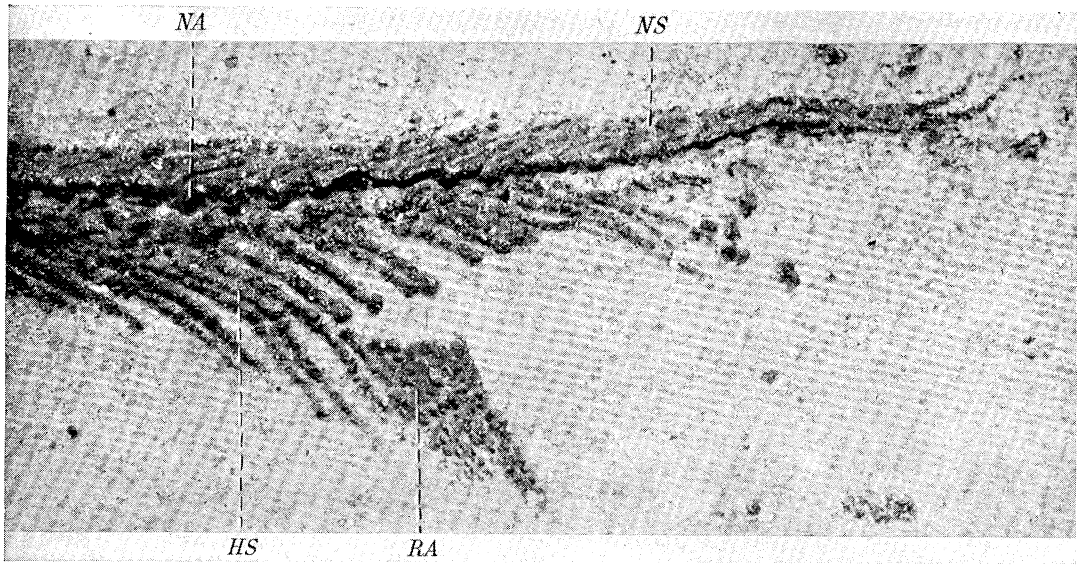


Figure 19. *Palaeospondylus gunni* Tr. The tail of B.M.N.H. P 22401. × 16.

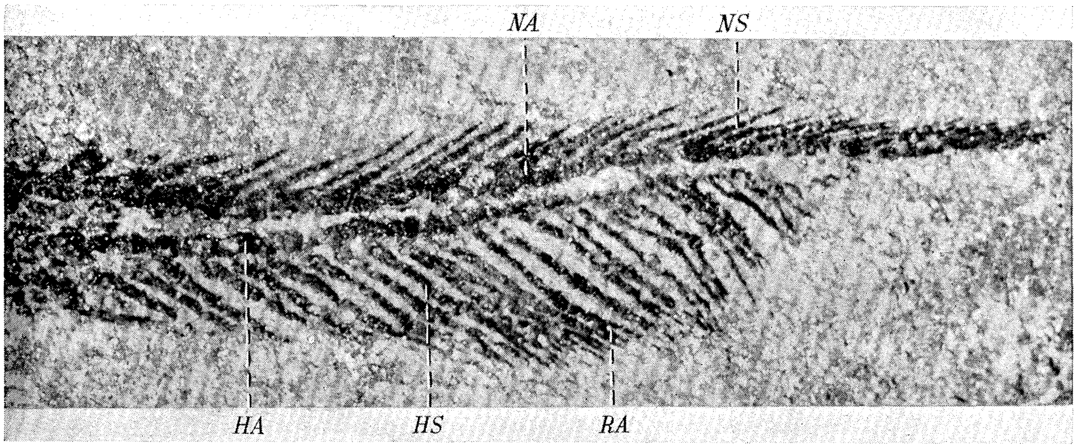
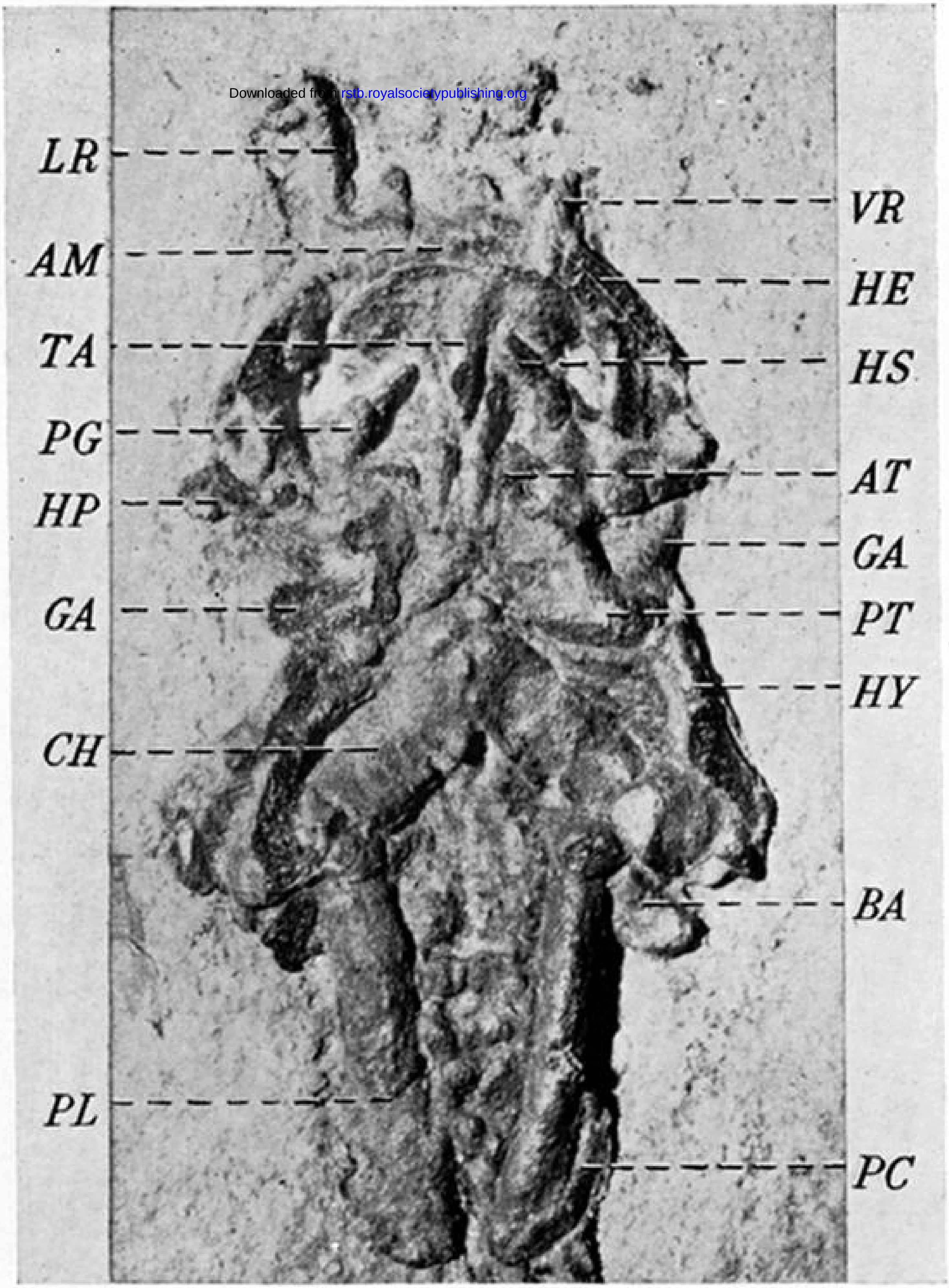
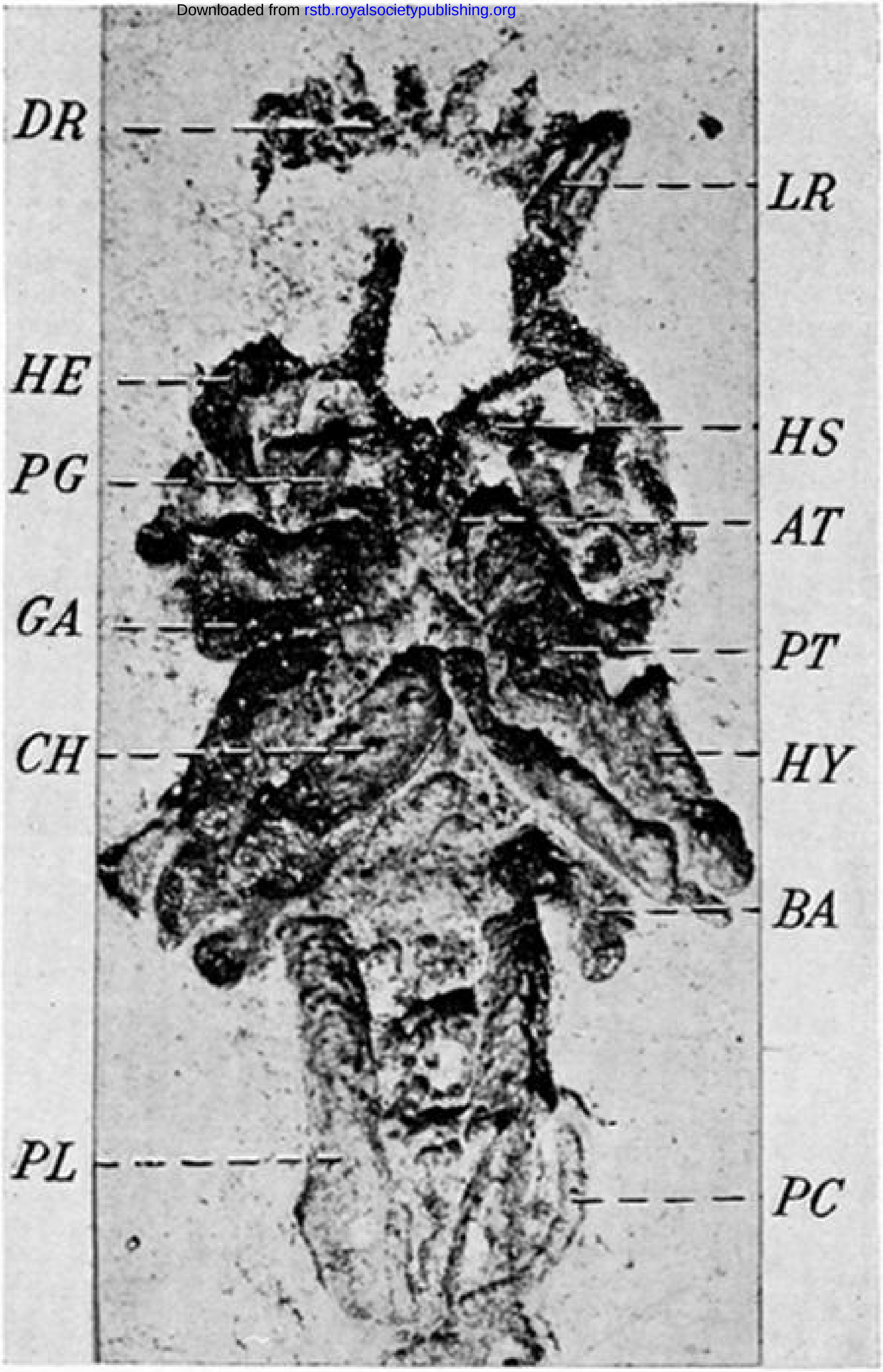


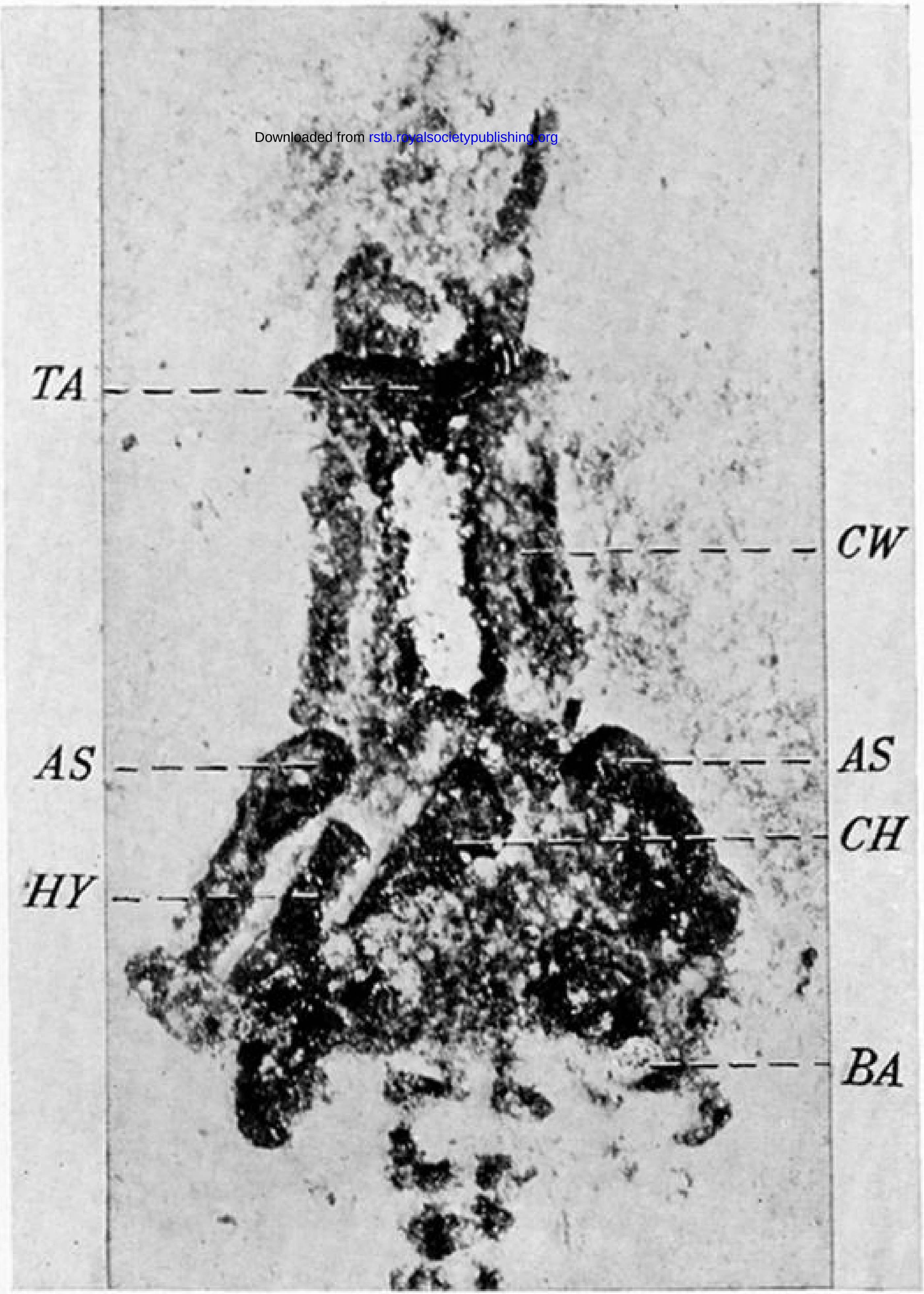
Figure 20. *Palaeospondylus gunni* Tr. The tail of R.S.M. 1893–145–6. × 13.



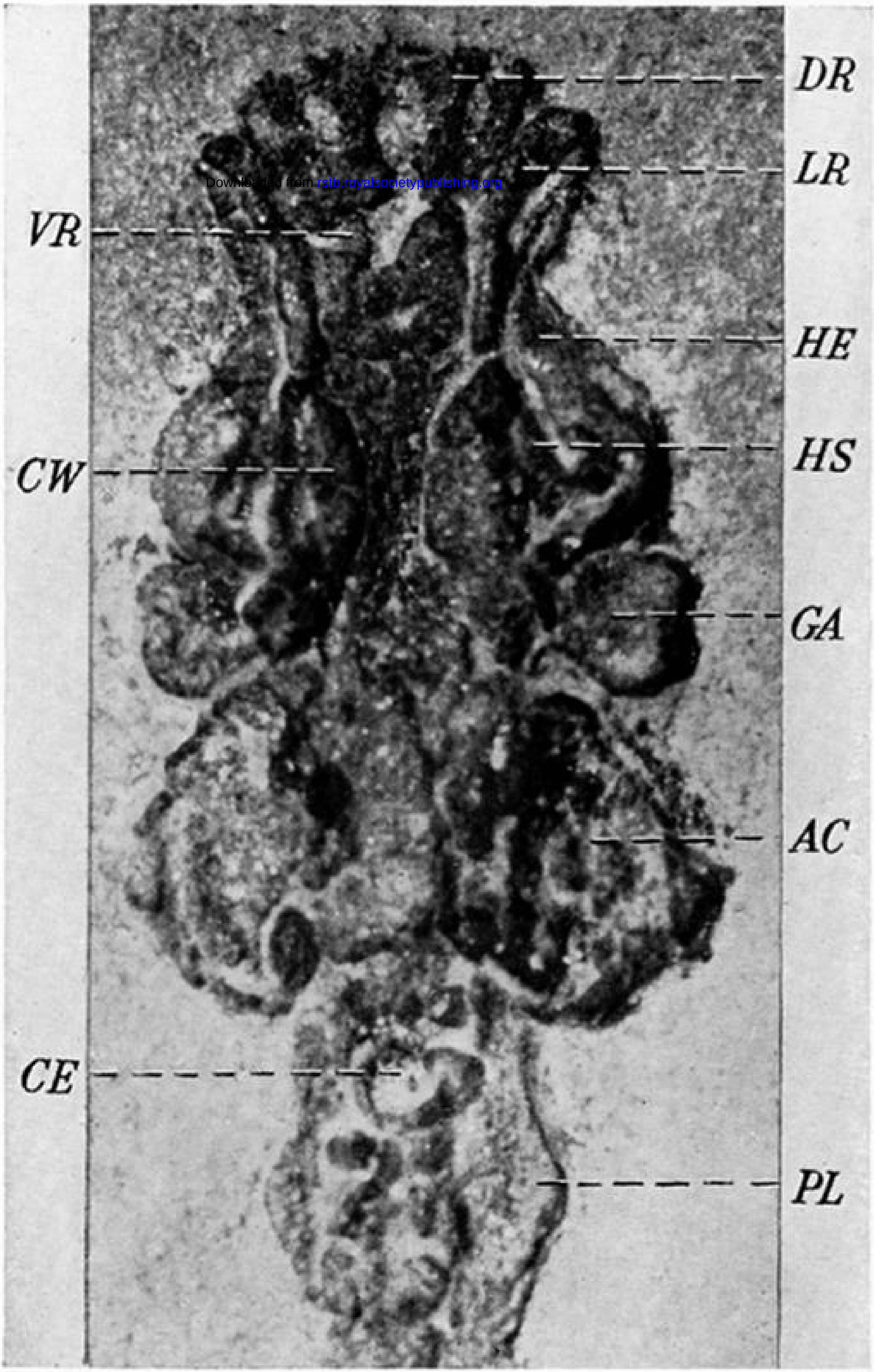
IGURE 8. *Palaeospondylus gunni* Tr. Ventral view of the skull of B.M.N.H. P 22396. ×12.



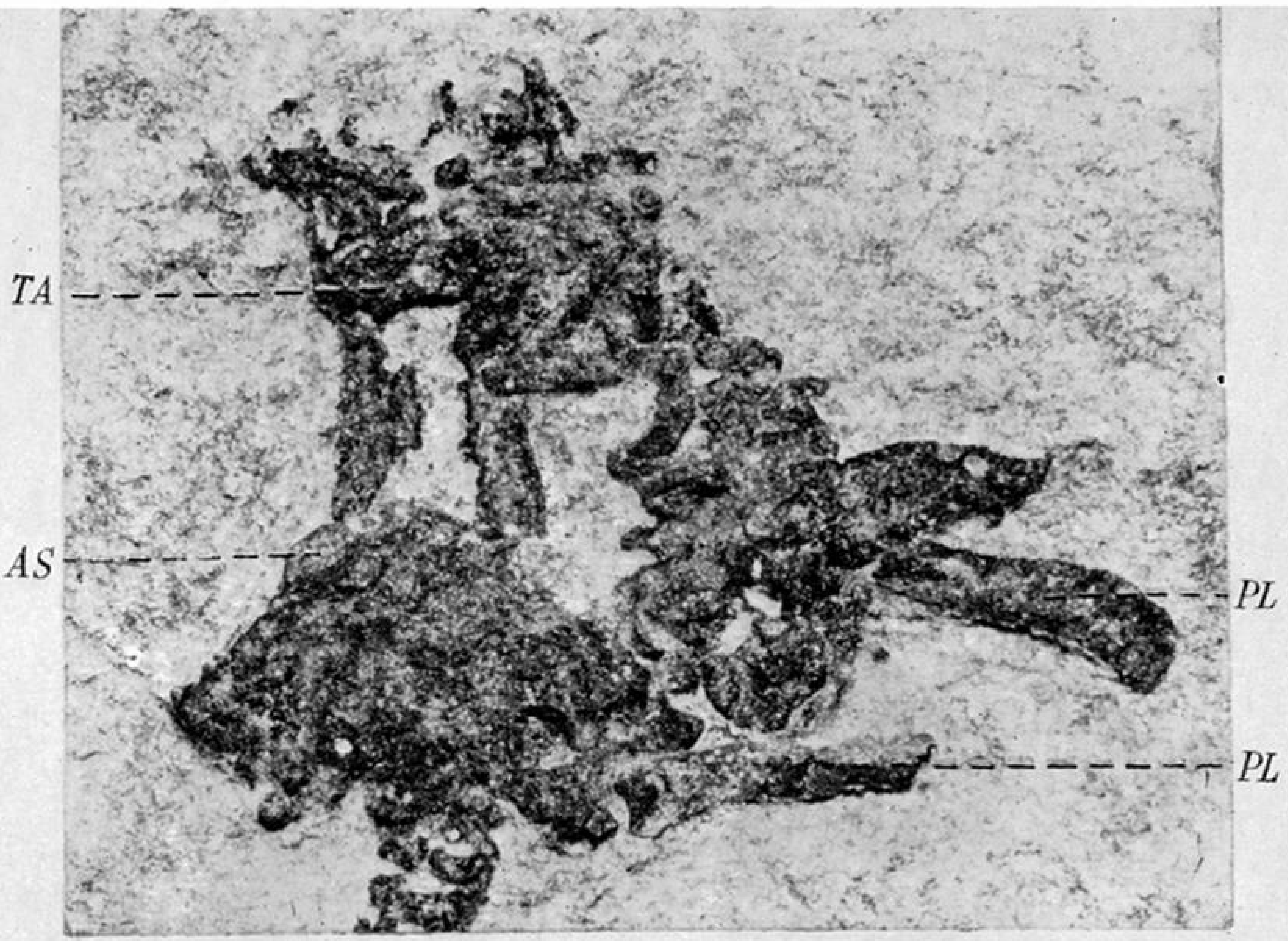
IGURE 9. *Palaeospondylus gunni* Tr. Ventral view of the skull of B.M.N.H. P 22401. ×10.



IGURE 10. *Palaeospondylus gunni* Tr. Ventral view of the disarticulated skull of R.S.M. 1893–68–3. ×14.



IGURE 11. *Palaeospondylus gunni* Tr. Dorsal view of the skull of B.M.N.H. P 22394. ×14.



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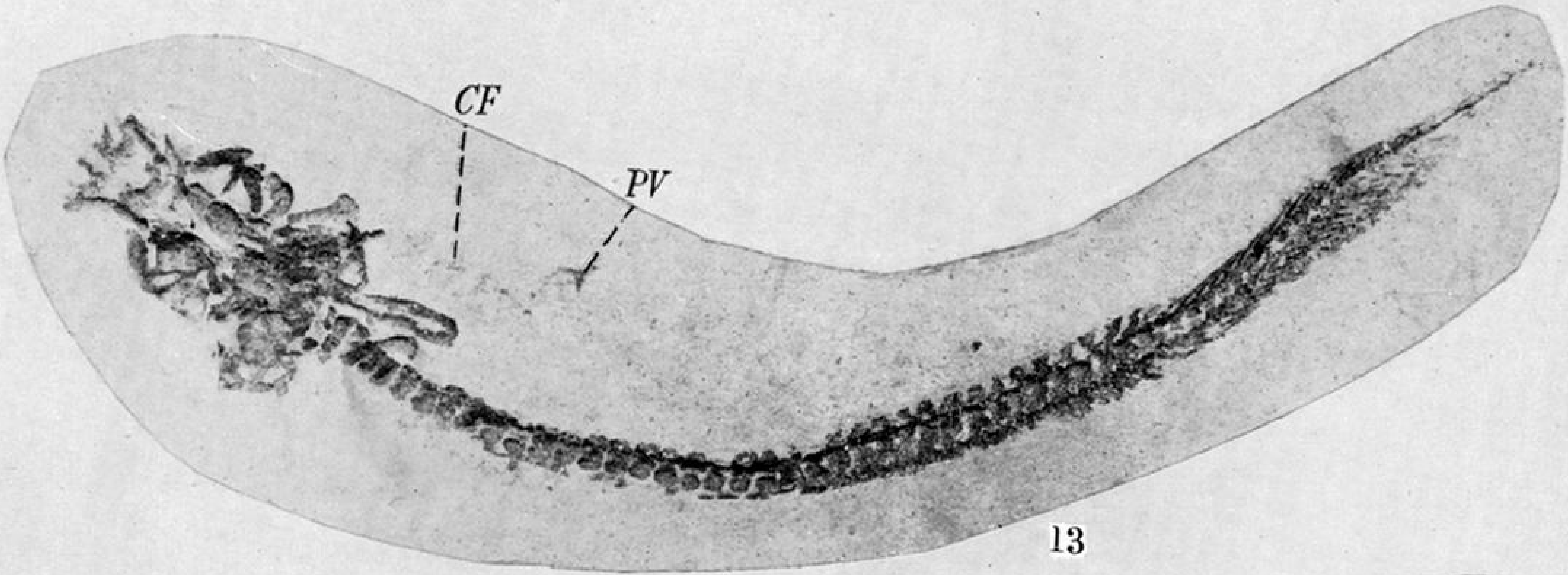

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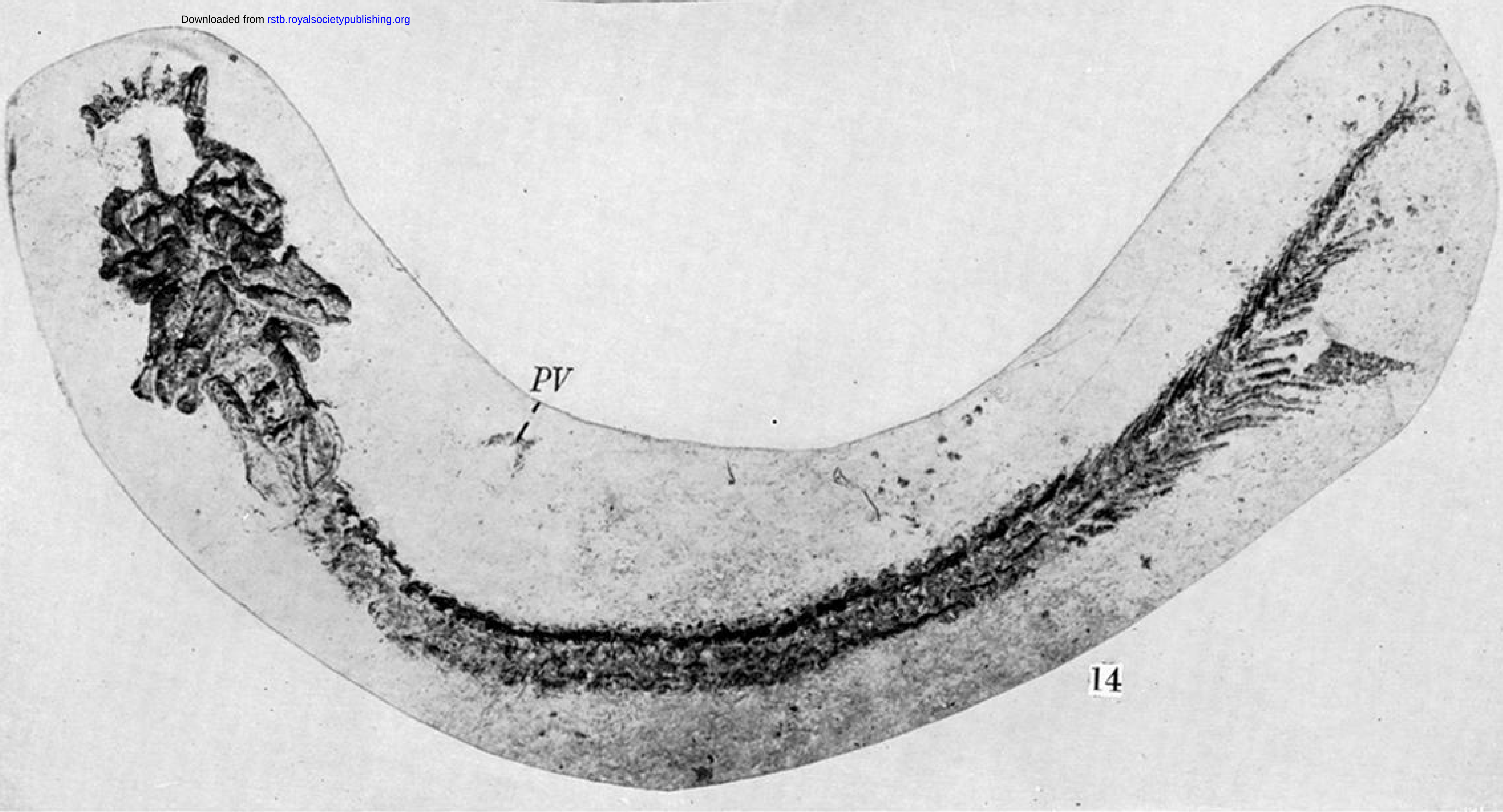

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FIGURE 12. *Palaeospondylus gunni* Tr. Ventral view of the disarticulated skull of R.S.M. (unnumbered). A. ×15.

FIGURE 13. *Palaeospondylus gunni* Tr. B.M.N.H. P 22400. ×4$\frac{3}{4}$.

FIGURE 14. *Palaeospondylus gunni* Tr. B.M.N.H. P 22401. ×5.

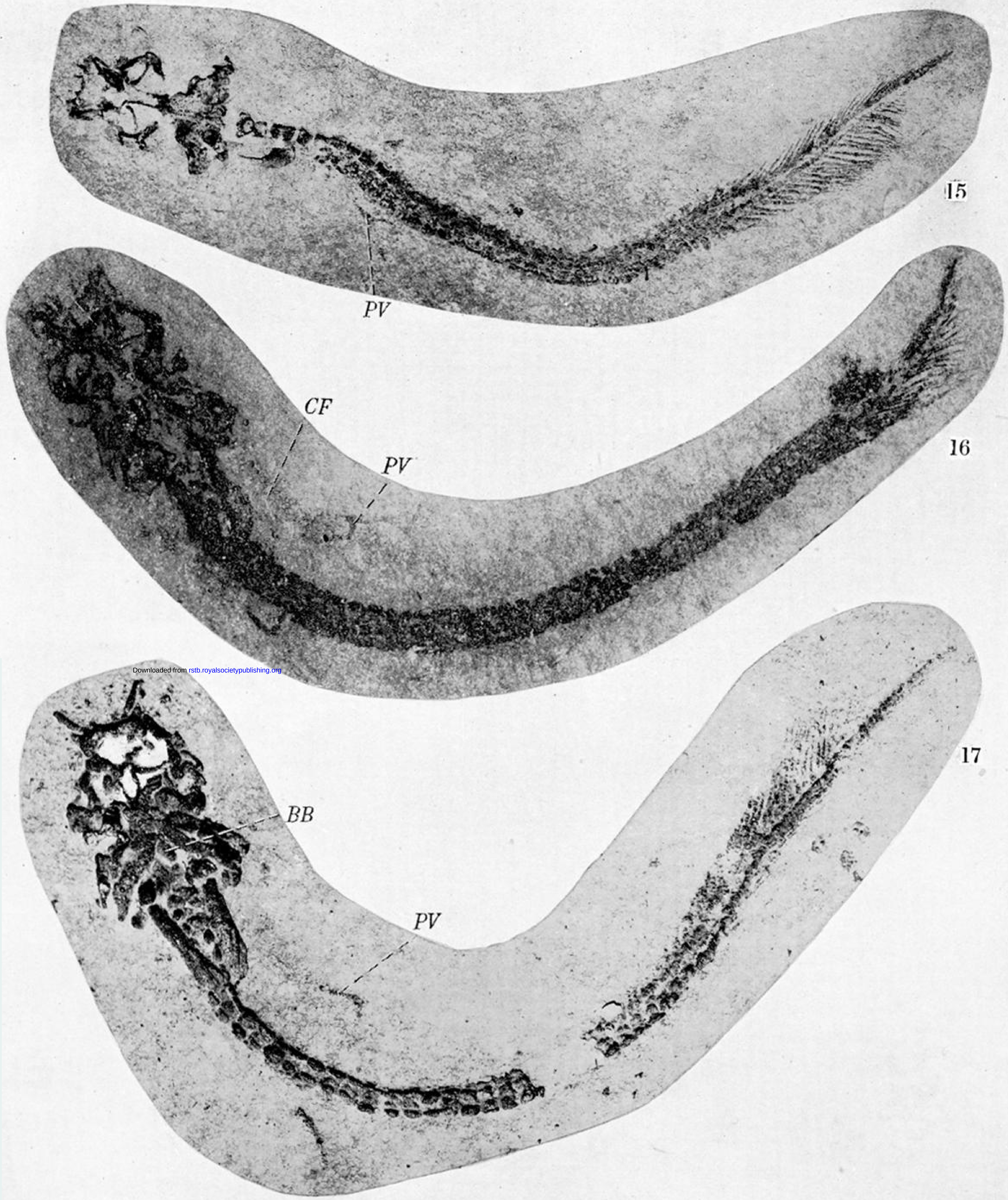
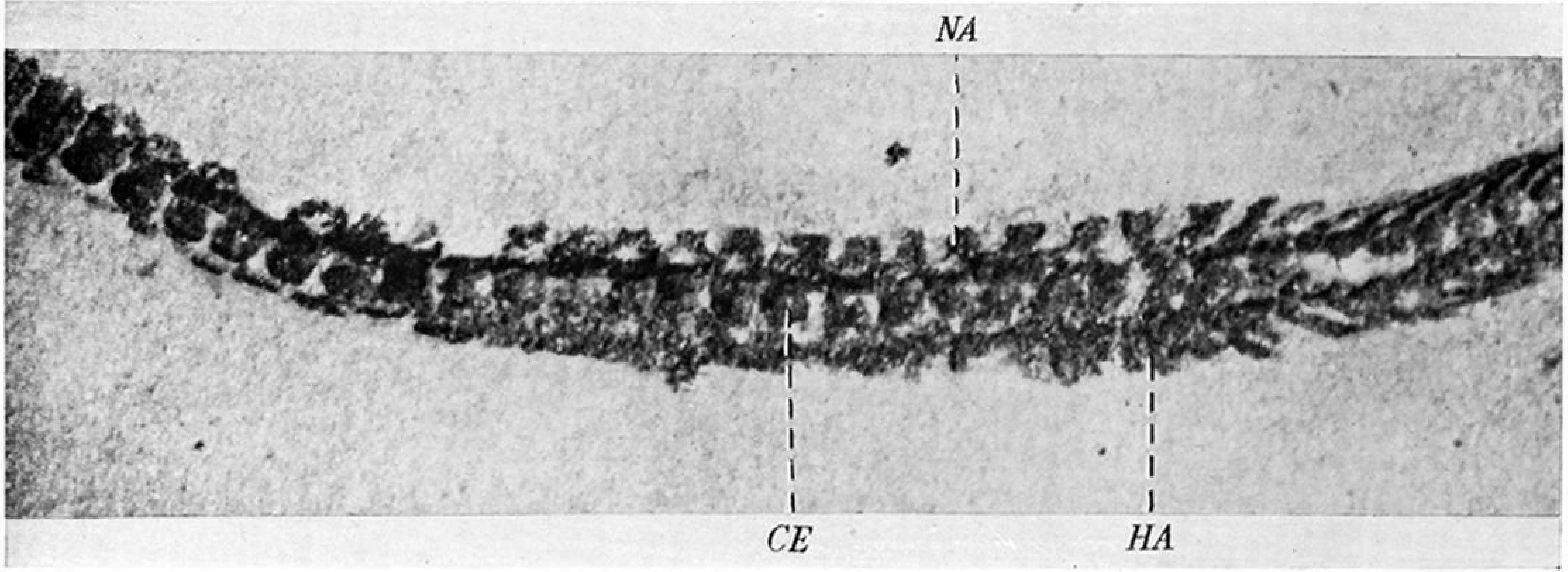


FIGURE 15. *Palaeospondylus gunni* Tr. R.S.M. 1893–145–6. ×4.
FIGURE 16. *Palaeospondylus gunni* Tr. B.M.N.H. P 22404. ×5½.
FIGURE 17. *Palaeospondylus gunni* Tr. B.M.N.H. P 22392 A. ×8½.



IGURE 18. *Palaeospondylus gunni* Tr. Part of the vertebral column of B.M.N.H. P 22400. × 12.

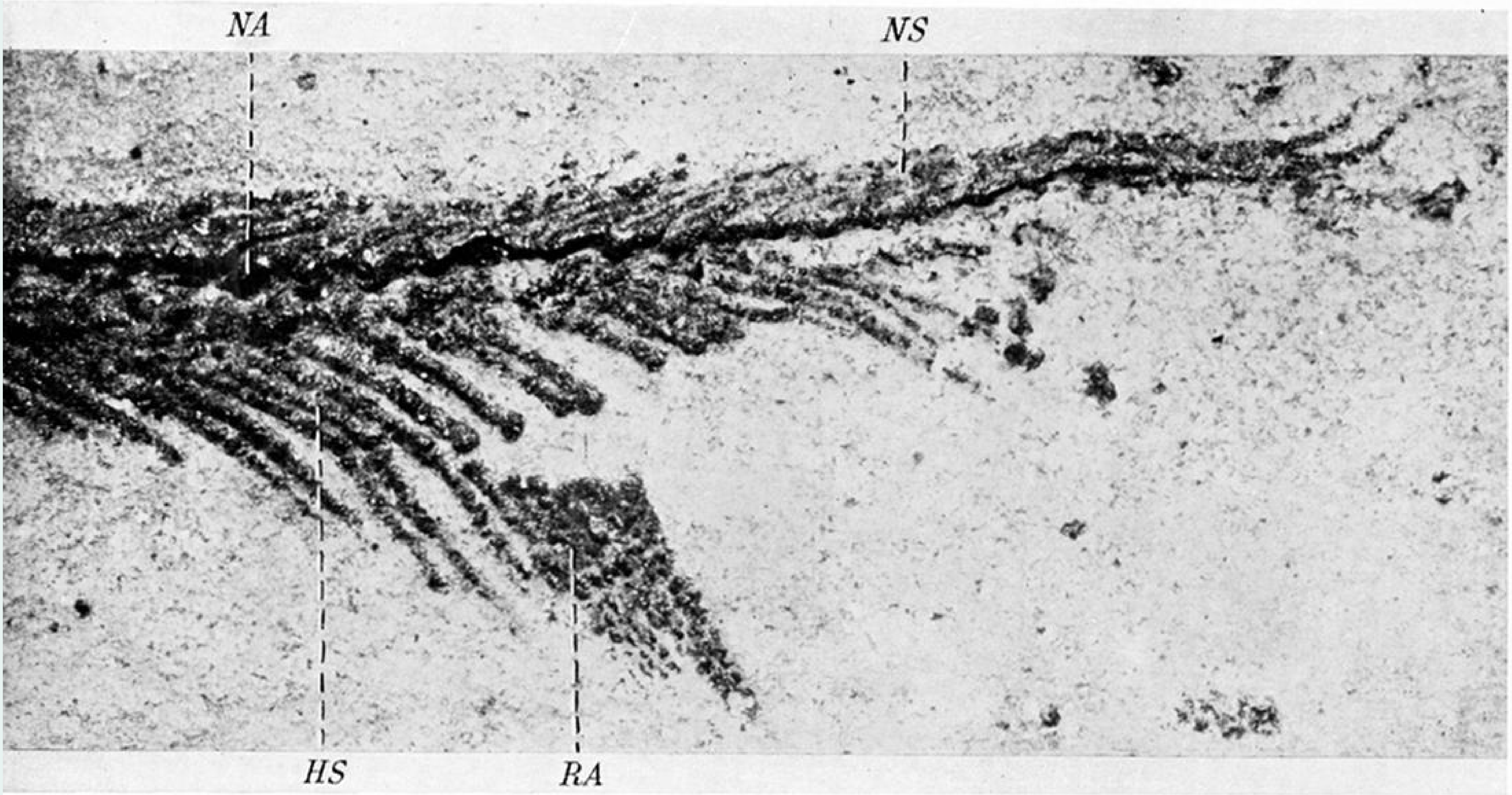


Figure 19. *Palaeospondylus gunni* Tr. The tail of B.M.N.H. P 22401. × 16.

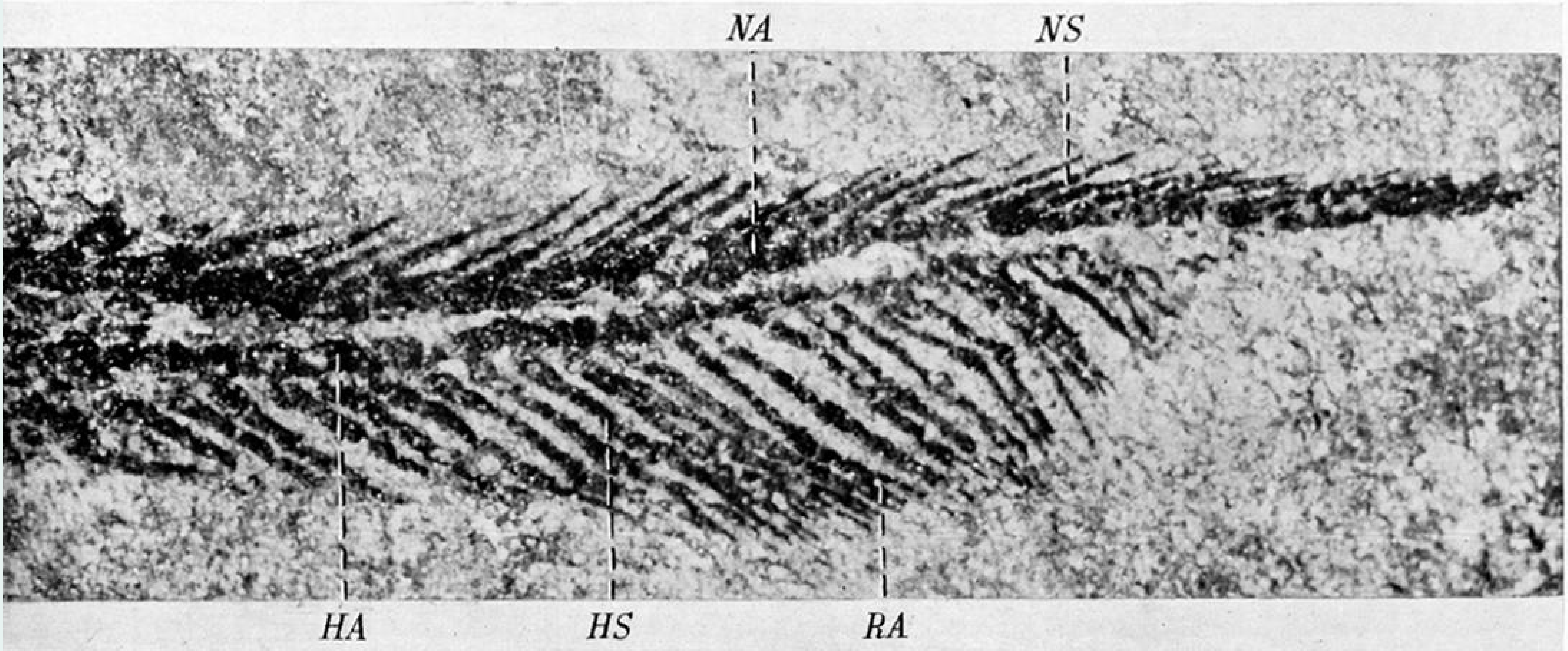


FIGURE 20. *Palaeospondylus gunni* Tr. The tail of R.S.M. 1893–145–6. × 13.