# THE AXIAL SKELETON OF THE CARBONIFEROUS AMPHIBIAN PTEROPLAX CORNUTUS

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ABSTRACT. The vertebrae and ribs of the Carboniferous amphibian *Pteroplax cornutus* Hancock and Atthey, 1868 are described. The vertebrae are embolomerous and in most respects similar to those of the much-larger embolomere *Eogyrinus attheyi* Watson, 1926. *Pteroplax* vertebrae differ from those of *Eogyrinus* in possessing intercentra which are as thick dorsally as ventrally and in the presence of a supraneural canal in at least the anterior trunk vertebrae. The supraneural canal may have housed a longitudinal ligament serving to strengthen an elongate presacral vertebral column. The trunk centra of sub-adult individuals exhibit large notochordal foramina, and the intercentra lack a ventro-lateral covering of periosteal bone. The precocious development of the lateral boss in such juvenile intercentra suggests that this structure, rather than the depression ventral to it in the fully formed centrum, formed the site of the capitular articulation.

*PTEROPLAX CORNUTUS* Hancock and Atthey, 1868 is a medium-sized anthracosaur amphibian of the infra-order Embolomeri from the Coal Measures of Great Britain. The type material of the species, stored in the Hancock Museum, Newcastle upon Tyne, is from the black shale immediately overlying the Low Main Seam at Newsham in Northumberland. This horizon lies within the Upper *Modiolaris* zone of the Middle Coal Measures (Land 1974) and is Westphalian B in age in European terminology. The lectotype specimen, so designated by Romer (1963), consists of a well-preserved skull table in association with two trunk ribs. The lectotype skull table was first described by Hancock and Atthey (1868) and was redescribed and figured in great detail by Atthey (1877). The taxonomy and relationships of *Pteroplax* have recently been discussed by Panchen (1970, 1972).

Despite being one of the first Carboniferous amphibians to be described, *Pteroplax cornutus* has, by reason of the paucity of described material, remained poorly known. Although numerous isolated skull and postcranial elements were referred to this species by Hancock and Atthey (1868) and Atthey (1877), almost all have since proved to belong to other species of amphibian and crossopterygian fish (e.g. Watson 1926; Andrews 1972; Boyd 1978). Of the specimens originally attributed to *Pteroplax* by Hancock and Atthey, only the vertebrae and ribs noted by Atthey (1877, p. 374) appear to belong to this form. Amongst the amphibian specimens from Newsham in the collections of the Hancock Museum, however, are a number of further specimens of embolomerous vertebrae and ribs, listed below, which are in this present study attributed to *Pteroplax*.

Although no vertebrae are preserved in association with the lectotype skull table of *Pteroplax*, there is little doubt that the attributed axial skeletal elements do pertain to this form. The large numbers of embolomerous vertebrae from Newsham fall into two distinct size ranges. Many of those in the larger category, having centra mostly ranging between 38 and 48 mm in diameter, have been described as belonging to the large eogyrinid *Eogyrinus attheyi* Watson (Watson 1926; Panchen 1966), the only embolomere other than *Pteroplax* which is known to occur at Newsham. A series of vertebrae of this size are, indeed, preserved with the lectotype skull of *E. attheyi* (Panchen 1972). The embolomerous vertebrae which comprise the smaller size group possess centra of between 21 and 26 mm in diameter. Reference of these vertebrae to *Pteroplax* is clearly justifiable on the principle of parsimony of hypotheses, and the dimensions of the lectotype *Pteroplax* skull table, which is markedly narrower than that of *Eogyrinus* (Atthey 1877; Panchen 1972), are in accordance with such

an attribution. Somewhat more positive evidence is afforded by the close similarity in size and morphology between the two ribs associated with the *Pteroplax* lectotype and those preserved with the vertebrae attributed to this form. It is of interest, also, to note Atthey's (1877) statement that the vertebrae which comprise Hancock Museum specimen G83.68 were collected from 'the same part of the mine' as the lectotype skull table of *Pteroplax*.

Although an account of the axial skeleton of the large embolomere *E. attheyi*, contemporary and sympatric with *Pteroplax*, has been given by Panchen (1966), no detailed description has hitherto been published of the vertebrae and ribs of a member of the smaller of the two embolomere size groups noted by Romer (1963). *P. cornutus* falls within the smaller of Romer's embolomere size groups and this, together with the fact that its vertebrae differ from those of *Eogyrinus* in several points of structure, would appear sufficient to justify detailed description of the axial skeleton, so far as known, of this species.

## MATERIALS AND METHODS

All the specimens employed in the present study are from the black shale overlying the Low Main Seam at Newsham, Northumberland, and are stored in the Hancock Museum in Newcastle upon Tyne. A complete list of specimens used, with their Hancock Museum registration numbers, is as follows. G4.83, caudal intercentrum with haemal arch; G15.73, seven articulated trunk vertebrae in association with four ribs (cited and referred to *Megalocephalus pachycephalus* (as '*Loxomma*') by Hancock and Atthey 1870); G15.76, (?*Pteroplax*), presacral rib from mid-trunk region; G15.77, (?*Pteroplax*), posterior trunk rib; G15.78, (?*Pteroplax*), presacral rib from mid-trunk region; G15.80, (?*Pteroplax*), posterior trunk rib; G83.68, trunk pleurocentrum, intercentrum, and one indeterminable central element in association with two neural arches and three ribs (referred to *Pteroplax* by Atthey (1877) but not figured by this author); G83.69, two trunk pleurocentra, two intercentra, and fragments of five ribs; G83.72, (?*Pteroplax*), rib from posterior region of trunk; G83.73, (?*Pteroplax*), rib from (?)pectoral region of trunk; G83.74, (?*Pteroplax*), posterior trunk rib; G86.61, caudal intercentrum with haemal arch.

Preparation of specimens has been accomplished by the use of an S. S. White Industrial Airbrasive Unit (Stucker 1961), employing sodium bicarbonate as the abrasive powder. When necessary this procedure was supplemented by the use of mounted needles. A dilute solution of 'Perspex' in chloroform was applied to reinforce areas of friable or damaged bone surface and a more concentrated solution was used in the mending of broken fragments.

## TRUNK VERTEBRAE

Three specimens, each including a number of trunk vertebrae, are available for study.

Specimen G15.73 (text-fig. 1A) consists of the complete articulated centra of seven successive dorsal vertebrae. This series commences anteriorly with the incompletely preserved pleurocentrum of the vertebra preceding the seven represented by both central elements. Dorsal and posterior to this pleurocentrum is a single, incomplete, neural arch, consisting of the neural spine, postzygapophyses, and right pedicel only. The articular heads, and most of the shafts, of two trunk ribs are also preserved, and lie on the morphologically left side of the vertebral series; that this is their true position is confirmed by the relationships between their tubercular and capitular heads. Almost all of the centra have undergone some degree of distortion due to compression during preservation; all except the two most anterior intercentra of the series therefore yield little useful information on the finer points of their structure.

Specimen G83.68 (text-fig. 1C) is a slab of shale bearing one pleurocentrum, one intercentrum, a third indeterminable central element, two incomplete neural arches, and the proximal parts of two trunk ribs. G83.68 was very briefly described by Atthey (1877, p. 374), who attributed it to *Pteroplax*.

Specimen G83.69 (text-fig. 1B) consists of a slab of shale on which are preserved two pleurocentra,

two intercentra, and five incomplete ribs. Both intercentra and one pleurocentrum exhibit very large notochordal foramina; this, and other details of their structure, noted below, suggest that they are the centra of a juvenile individual.

*Centrum.* As is characteristic of the embolomerous condition in amphibian vertebrae, both pleurocentrum and intercentrum of *Pteroplax* form completely ossified discs of bone. Although the pleurocentra and intercentra of specimen G83.69 exhibit large notochordal foramina, these centra would appear from other features of their structure to be those of a juvenile individual, and it is probable that the dimensions of the foramina are related to this fact. In several of the articulated centra which compose specimen G15.73, the notochordal foramen would appear to have been occluded by growth of bone. Centra in which the foramen is so occluded have also been described in the eogyrinid embolomere *Eobaphetes kansensis* (Panchen 1977*a*), and large embolomerous centra with occluded notochordal foramina have been attributed to *Anthracosaurus russelli* (Huxley 1863; Panchen 1977*a*).

The pleurocentrum, which lies posterior to the intercentrum in the complete vertebra (text-fig. 3), is approximately circular in transverse section although somewhat flattened dorsally where it forms the floor of the neural canal. The pleurocentrum of *Pteroplax* has in all known specimens a much greater antero-posterior length than has the intercentrum, several of the pleurocentra of G15.73 being twice as thick as their respective intercentra. A similar disparity in thickness of pleurocentrum and intercentrum has been described in the vertebrae of the eogyrinid *Eogyrinus attheyi* (Panchen 1966), the Lower Permian archeriid *Archeria* (Case 1911), and the tiny *Calligenethlon watsoni* (Carroll 1967).
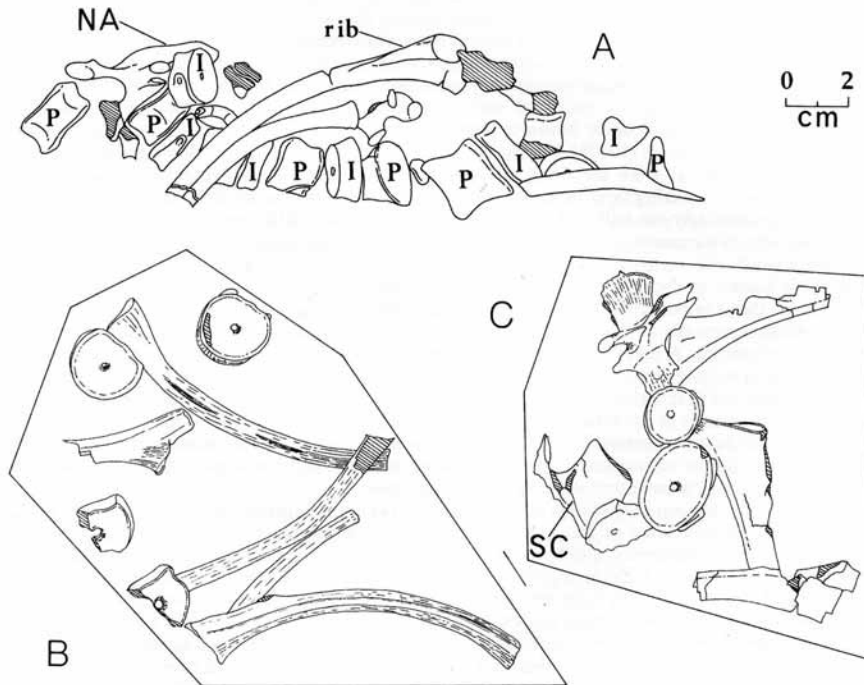


TEXT-FIG. 1. Presacral vertebrae and ribs of *Pteroplax cornutus* as preserved, × 0·5. A, diagrammatic representation of articulated vertebral series of specimen no. G15.73 in left lateral view; B, vertebrae and ribs of specimen no. G83.69; C, vertebrae and ribs of specimen no. G83.68. I, intercentrum; NA, neural arch; P, pleurocentrum; SC, supra-neural canal.

The pleurocentrum is deeply amphicoelous, both anterior and posterior articular faces being markedly concave. The anterior and posterior articular faces of the pleurocentrum have a surface of spongy bone, no covering of periosteal bone being present. The pleurocentrum shows no tendency to taper dorsally and has approximately the same antero-posterior length both dorsally and ventrally. Ventrally and laterally the circumference of the pleurocentrum has a coat of smooth periosteal bone which, in the case of the pleurocentra of specimen G83.69, is pierced by a number of nutrient or nerve foramina. The circumference of the pleurocentrum where it possesses a periosteal bone covering is strongly concave, with the result that the pleurocentrum is much constricted ventrally and laterally between its anterior and posterior faces. The median area of the dorsal surface of the pleurocentrum representing the floor of the neural canal lacks a surface of periosteal bone and is shallowly concave, forming a depression extending from the posterior to the anterior margin of the centrum.

In the anterior half of the dorsal surface of the pleurocentrum, and lying on either side of the depression marking the floor of the neural canal, there is a pair of facets for articulation with the pedicels of the neural arch. The articular faces of these facets are roughly elliptical in shape and are orientated in an antero-dorsal direction at an angle of approximately forty-five degrees. The two articular faces also have a very slight lateral inclination. The facets each project anteriorly a little way beyond the anterior rim of the pleurocentrum. Because of the antero-dorsal inclination of the articular faces of the two dorsal facets of the pleurocentrum, the posterior margin of each is considerably raised above the level of the floor of the neural canal and is supported on a stout buttress, the lateral surface of which has a covering of smooth periosteal bone. Details of the structure of the pleurocentrum will be apparent from text-fig. 2A–D.

The intercentrum (text-fig. 2E–H) is, like the pleurocentrum, a completely ossified disc of bone pierced longitudinally, at least in the case of juvenile individuals, by a notochordal foramen. It is, however, in all known cases considerably thinner than the pleurocentrum, having usually only about one-half of the antero-posterior length of the latter element. The intercentrum is, in an adult animal, almost circular in transverse section, although exhibiting dorsally a flattened antero-posterior strip of bone which represents the floor of the neural canal. The intercentrum of *Pteroplax* is less deeply amphicoelous than the pleurocentrum, the articular faces being markedly excavated only in the region immediately surrounding the notochordal foramen. The intercentrum would thus probably have had a 'ball and socket' type of articulation with the deeply amphicoelous pleurocentrum. Such an articulation between pleurocentrum and intercentrum has been noted in other embolomere genera by Panchen (1977b). The anterior and posterior articular faces of the intercentrum have a surface of spongy bone, as does the floor of the neural canal. The ventral and lateral portions of the circumference possess a covering layer of smooth periosteal bone which extends, in all the intercentra available for study, for approximately one-half of the height of the lateral surface of the centrum. It is probable, however, that this dorsal limit of the extent of the periosteal bone surface of the circumference of the intercentrum was not constant throughout the vertebral column. In *Eogyrinus* the height of the lateral periosteal bone of the intercentrum is known to decrease from front to back of the vertebral series, so far as the latter is known (Panchen 1966), and it is probable that this was also the case in *Pteroplax*.

There is a shallow, roughly circular, concavity a little way ventral to the dorsal limit of the lateral periosteal bone of the intercentrum. A raised boss lies immediately dorsal and a little anterior to this depression. It is probable that one or both of these two structures was involved in the articulation of the capitular head of the rib. As no ribs are preserved in actual articulation with any known intercentrum of *Pteroplax*, it is not possible to be certain of the precise nature of this articulation. Panchen (1966) has noted that in the intercentrum of *Eogyrinus*, where a precisely similar arrangement of concavity and boss is present, the former appears to be situated too far ventrally to be the articular surface and that it may have served as the point of origin of a ligamentous structure holding the capitulum in articulation with, or behind, the boss.

The two intercentra present in specimen G83.69 (text-fig. 1B) are of especial interest because they appear to belong to a sub-adult individual of *Pteroplax*. This is strongly suggested by the relatively large size of the notochordal foramina of the centra, and by a number of other features of their structure. The circumference of each of the juvenile intercentra is flat or slightly convex, rather than concave, between the anterior and posterior articular faces of the element, and lacks any covering of smooth periosteal bone. In transverse section the intercentra do not approach the circular so closely as those characteristic of the adult animal, but terminate dorsally in an approximately horizontal surface which has a width very nearly as great as the diameter of the centrum itself. The over-all impression is that of a circle with a segment removed from its most dorsal part. A restoration of one of the juvenile intercentra of G83.69 is figured for comparison with the intercentrum of the adult animal (text-fig. 2I–K). The more fully preserved of the two juvenile intercentra bears, at the lateral extremity of the flattened dorsal surface, a massive laterally projecting boss. The capitular and tubercular heads of the ribs preserved in specimen G83.69 are well ossified and resemble those of the adult animal, and it would thus seem likely that the dorso-lateral boss of the intercentrum represents the site of articulation of the capitular

head. If this is the case, as seems very probable, then this precocious development of the boss in the absence of a concavity ventral to it might be taken as indicating that the former structure formed the sole site of articulation of the capitulum of the rib in the adult intercentrum as well as in the juvenile.

In all specimens available for study, the intercentra of *Pteroplax* show no tendency to taper dorsally (when seen in lateral view), but have approximately the same antero-posterior length dorsally as ventrally.

There is no evidence in any of the intercentra of *Pteroplax* available for study of the presence of any facets which may have served for an articulation of this element with the neural arch. As has been noted by Parrington (1967), to join the neural arch of an embolomerous vertebra securely to the intercentrum, as well as to the pleurocentrum, would be to reduce the flexibility of the vertebral column, thus abandoning the main advantage originally gained by diplospondyly.

*Neural arch.* Only fragmentary and relatively poorly preserved material representative of this structure is preserved in association with the vertebral centra attributed to *Pteroplax*. Three neural arches are thus preserved, one being associated with the most anterior pleurocentrum of the articulated length of vertebral column G15.73, and two further specimens being associated with the isolated centra of specimen G83.68. All
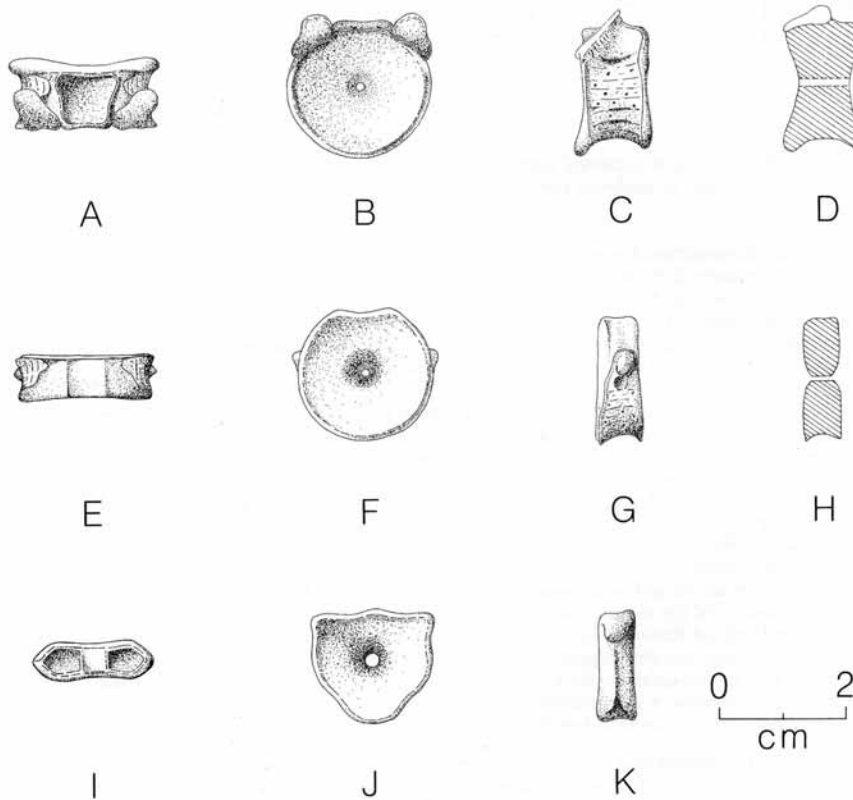


TEXT-FIG. 2. Presacral centra of *Pteroplax cornutus*, × 1. A–D, anterior trunk pleurocentrum in A, dorsal view; B, anterior view; C, left lateral view and D, longitudinal section; E–H, anterior trunk intercentrum in E, dorsal view; F, anterior view; G, left lateral view and H, longitudinal section; I–K, anterior trunk intercentrum of juvenile individual in I, dorsal; J, anterior and K, left lateral views.
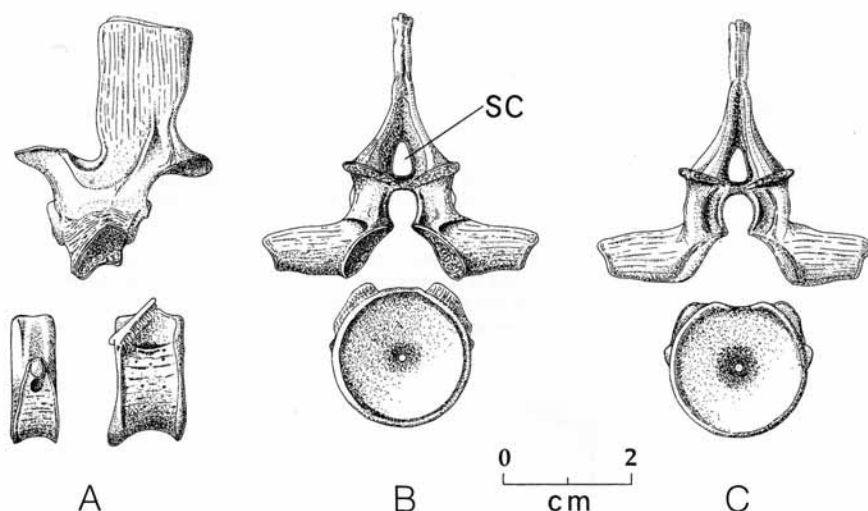
TEXT-FIG. 3. Restoration of 'exploded' anterior trunk vertebra of *Pteroplax cornutus*, × 1. A, left lateral view; B, posterior view; C, anterior view. SC, supra-neural canal.

three neural arches have sustained some crushing during preservation and are somewhat distorted. No one of the three specimens is preserved in its entirety but, as the parts absent or unrecognizable in each neural arch are present in at least one of the other two specimens, and as all three appear to be those of presacral vertebrae, a composite reconstruction of the salient features of the neural arch of a trunk vertebra may be attempted with some confidence. Where details of structure are in doubt, as in the case of the form of the neural canal, these have been restored as in *Eogyrinus*. The morphology of the presacral neural arch of *Pteroplax* will be apparent from text-fig. 3.

The most interesting feature of the neural arch is the presence of a supra-neural canal in the ventral part of the neural spine. Owing to the absence of the dorsal part of the neural spine in the more completely preserved of the two neural arches of specimen G83.68, the supra-neural canal is open dorsally and forms a channel extending from between the prezygapophyses to the posterior part of the neural spine between the postzygapophyses. In the second of the two neural arch specimens of G83.68, which consists of the neural spine and right prezygapophysis only, the former has been split vertically and the right lateral wall of the supra-neural canal is exposed to view (text-fig. 1c). It is clear from this specimen that the walls of the supra-neural canal have a lining of smooth periosteal bone.

The structure of the neural arch of a presacral vertebra of *Pteroplax*, as revealed by the available material, is, except for the presence of the supra-neural canal, very similar to that of *Eogyrinus* as described by Panchen (1966). The neural arch of *Pteroplax* is, as might be expected from the dimensions of the centra, considerably smaller than that of *Eogyrinus*, being approximately one-half the size of those of the latter genus. It would appear that the neural arch of *Pteroplax* is also a rather more gracile structure than that of *Eogyrinus*.

The mode of articulation of the intercentrum, pleurocentrum, and neural arch will be evident from the restoration of these three elements in text-fig. 3.

*Regional variation.* The paucity and the poor state of preservation of the known vertebral material of *Pteroplax* are such that the identification of regional variation within the dorsal vertebral column is not possible with any degree of certainty. The only articulated series of vertebrae available for study, specimen G15.73, consists of the complete centra of only seven successive dorsal vertebrae and it is not likely that any regional variation originally present within the vertebral column of *Pteroplax* will be readily apparent in so short a series. Panchen (1966) has described a number of trends present in the vertebral column of *Eogyrinus* and it seems probable that similar regional variations in form of the vertebrae were present also in *Pteroplax*.

## CAUDAL VERTEBRAE

Two isolated caudal intercentra, from the Low Main Seam at Newsham, are attributed, on grounds of size, to *Pteroplax* and yield useful information as to the structure of the tail in this form.

Specimen G4.83 (text-fig. 4A–C) consists of the intercentrum of a proximal caudal vertebra, with a fused haemal arch bearing a short, blade-like haemal spine. It is preserved in posterior view, the anterior face of the intercentrum lying within the matrix which surrounds the specimen. The intercentrum and haemal arch have suffered some post-mortem compression and the arch has been twisted in such a way that the left lateral face of the haemal spine now faces posteriorly. The specimen bears a remarkable resemblance in both structure and mode of preservation to a much larger, isolated caudal intercentrum and haemal arch of *E. attheyi* described and figured by Watson (1926, fig. 23).
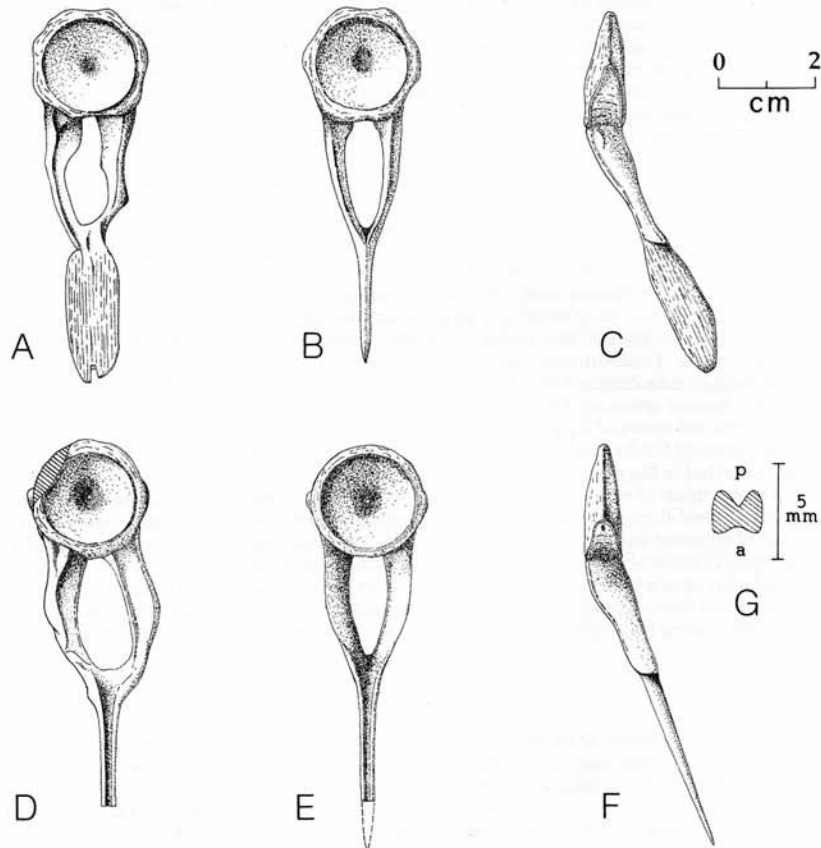


TEXT-FIG. 4. Caudal intercentra of *Pteroplax cornutus*. A–C, proximal caudal intercentrum of specimen no. G4.83 in A, posterior view as preserved; B, posterior view, restored and C, left lateral view, restored; D–F, distal caudal intercentrum of specimen no. G86.61 in D, posterior view as preserved; E, posterior view, restored and F, left lateral view, restored; G, transverse section of haemal spine of specimen no. G86.61. A–F, ×0·6; G, ×3. a, anterior; p, posterior.

The intercentrum possesses a posterior articular face which, like those of the trunk intercentra, is markedly concave only in the immediate vicinity of the small notochordal foramen. The centrum appears to become thinner dorsally, tapering when seen in lateral view. A covering of smooth periosteal bone would appear to have extended approximately half-way up the lateral surface of the intercentrum. This finished area is strongly concave and appears, like the centrum itself, to taper dorsally. It is uncertain whether or not a facet for the capitular articulation of a caudal rib is present in specimen G4.83.

Ventrally, the intercentrum bears a large haemal arch, the pedicels of which enclose a spacious haemal canal which has, in cross-section, the form of a vertically elongated oval. The haemal spine itself is a broad blade-like structure, compressed laterally and bearing a number of fine vertical striations.

In *E. attheyi* the haemal arches and spines of the proximal caudal vertebrae are directed posteriorly as well as ventrally (Panchen 1966) and a similar orientation of these structures has been restored in the reconstructions of the caudal intercentra of *Pteroplax* (text-fig. 4B-C, E-F).

Specimen G86.61 (text-fig. 4D-G) consists of the intercentrum and fused haemal arch of a caudal vertebra more distal than that of specimen G4.83. The intercentrum has a diameter of approximately 24·0 mm. The relatively large size of the intercentrum, despite its presumed distal position in the tail, makes attribution to *Pteroplax* uncertain. It is possible that the specimen in fact belongs to the larger *Eogyrinus*, its small diameter when compared with typical trunk centra of this form being due to its original situation in the distal part of the caudal vertebral series. It is, however, equally possible that it pertains to a large specimen of *Pteroplax* and it will be here described as belonging to this genus.

As is the case in specimen G4.83, the intercentrum appears to taper dorsally when seen in lateral view. The vertical extent of the lateral covering of smooth periosteal bone is uncertain, and this has been restored as extending only a very short distance above the base of the haemal arch pedicel. In specimen G86.61 the haemal spine is not laterally compressed but forms a truly spine-like structure, roughly quadrangular in transverse section. The haemal spine bears a distinct longitudinal groove on both anterior and posterior faces, the posterior groove being apparently the deeper and better defined of the two (text-fig. 4G). The haemal spine of G86.61 is unfortunately broken off short approximately 30·0 mm from its origin at the point of fusion of the arch pedicels, and it is thus not possible to estimate with certainty its original length.

Case (1911, fig. 51G) figured (as '*Cricotus*') a series of articulated distal caudal vertebrae of *Archeria*. The intercentra of the vertebrae appear to bear postero-ventrally directed elongate and tapering haemal spines below the haemal arches present. These structures, although all broken and lacking their distal parts, appear to closely resemble that present in intercentrum G86.61 of *Pteroplax*. It is, however, not possible to ascertain from Case's figure whether the haemal spines of *Archeria* are also quadrangular in section.

The haemal arches and spines of the proximal caudal vertebrae of *Pteroplax*, such as are shown by specimen G4.83, presumably served for the support of the ventral part of a laterally compressed tail. Haemal arches of this type have been described in *Eogyrinus* (Watson 1926; Panchen 1966), where they are matched dorsally by neural arches bearing neural spines of normal laterally compressed type. The elongate haemal spines of the distal caudal vertebrae of *Archeria* and *Pteroplax* may have served to support the distal part of a laterally compressed tail and the ventral part of a distinct caudal fin. The neural arches of the caudal vertebrae of *Archeria* figured by Case (1911) bear posteriorly inclined elongate neural spines and Romer (1956) has described the presence in this form of a dorsal caudal fin supported by either the neural spines of the distal caudal vertebrae or by supra-neural spines articulating with them. A caudal fin, both epaxial and hypaxial in extent, has been restored in *Eogyrinus* by Panchen (1972) and it seems highly probable that a similar fin was present in at least the distal region of the tail in *Pteroplax*.


## RIBS

In the collections of the Hancock Museum are a large number of isolated ribs belonging to 'labyrinthodont' amphibians, from the Low Main Seam at Newsham. The majority of these ribs may be placed in one or other of two distinct size ranges. Panchen (1966), noting this fact, has suggested that those ribs in the larger category most probably belong to *Eogyrinus* and the contemporary loxommatid *M. pachycephalus* (Barkas), and those in the smaller size range to *Pteroplax*. On the basis of this hypothesis, a series of large trunk and caudal ribs, many of which were also definitely associated with *Eogyrinus* specimens, were described (Panchen 1966) as belonging to that genus.

It would seem more likely, however, considering the relatively small size of the skull of *M. pachycephalus* (Beaumont 1977), for which unfortunately no certainly attributable postcranial remains are known, that if any ribs of this species are represented amongst the Hancock Museum collections from Newsham, these would fall into the smaller size range, with those of *Pteroplax*. There can be little doubt that the ribs of *Pteroplax* are of the

smaller type. Two ribs of this size are preserved with the lectotype skull table of *Pteroplax*, and a number of rib specimens are associated with various of the vertebrae attributed to this form, including the articulated length of vertebral column G15.73.

In the absence of any description of the morphology of the ribs of *Megalocephalus*, it is not possible to determine with certainty which, if any, of the smaller isolated ribs from Newsham belong to this genus rather than to *Pteroplax*. Although the trunk ribs of some Permian temnospondyls such as *Eryops* bear well-developed uncinate processes, there is no real reason to suppose that the ribs of *Megalocephalus*, which was probably largely aquatic in habit, might be expected to exhibit these structures and thus be distinguishable from those of anthracosaurs such as *Pteroplax*. Neither may the apparent absence of any *Megalocephalus* vertebrae from the Hancock Museum's Newsham collections be cited as reason to suppose that the ribs of this form might also be rarely, if at all, represented. If, as has been postulated by Romer (1947) and at least partly vindicated by Baird (1957), the loxommatids possessed vertebrae of rhachitomous type, the rarity of *Megalocephalus* vertebrae from Newsham might be explained as due to the dissociation of the relatively small, and easily overlooked, central elements subsequent to the death of the animal.

Because it would thus appear impossible to distinguish between isolated ribs of *Pteroplax* and *Megalocephalus*, the ribs described below as belonging to the former genus have, whenever possible, been selected from those associated with the embolomerous vertebrae attributed to this form. Several of the isolated ribs described as those of *Pteroplax* do, however, closely resemble those described for *Eogyrinus* by Panchen (1966).

The ribs of *Pteroplax* are dichocephalous in typical early tetrapod manner, exhibiting in the articular head a tubercular facet, usually slightly concave, for the reception of the diapophysis of the neural arch and, ventral and usually slightly anterior to this, a capitulum continuing the curvature of the rib shaft and articulating with the intercentrum of the vertebra. In the more anterior members of the presacral series of ribs the capitulum is situated mesial to the tuberculum of the rib head but, correlated with the presumed posterior decrease in the transverse span of the diapophyses of the vertebrae, the two articulations of the rib approach closer to the same vertical plane in the more posterior members of the series. The radius of curvature of the rib shaft varies according to the position occupied by the rib in the presacral vertebral column. In specimen G15.76 (text-fig. 5B), a rib from the anterior trunk or 'thoracic' region of the body, the shaft clearly extends as far as the lateral margins of the ventral body surface. It is likely that, as in many modern Crocodilia and the more unspecialized members of the Lepidosauria, the more anterior trunk ribs continued distal to their ossified extremities in cartilage and articulated ultimately with a cartilaginous sternum extending posteriorly from the interclavicle.

The shaft of an anterior trunk rib is expanded in the region of the articular head, a dorsal extension of the shaft extending posteriorly and dorsally, and linking the shaft proper and the tuberculum of the rib. The structure of this region is clearly evident from the more anterior of the two ribs preserved in association with specimen G15.73 (text-fig. 1A). As in *Eogyrinus* (Panchen 1966), the postero-dorsal surface of the rib in this region is deeply concave, the concavity extending for a distance of several centimetres lateral and ventral to the tubercular facet. In the majority of the anterior trunk ribs available for study, the postero-dorsal concavity of the articular head region is continued as a shallow longitudinal groove extending for the greater part of the length of the shaft. The shaft in all specimens lacks any evidence of the presence of an ossified uncinate process, and in this respect corresponds to the pattern apparently common to all Batrachosauria.

Seven of the isolated ribs from Newsham attributed to *Pteroplax* are figured (text-fig. 5A–G) in an attempt at restoration of a series of presacral ribs, showing the modifications in structure characteristic of different regions of the trunk. The resemblance of certain of the ribs in this series, and in particular of the more posterior members, to the much larger rib specimens figured by Panchen (1966) for *Eogyrinus* is noteworthy and might be taken as some confirmation of the correctness of the attribution of these ribs to *Pteroplax*.

The first and most anterior rib of the figured series (text-fig. 5A), specimen G83.73, is placed in this position, with some reserve, largely because of its apparent resemblance to a rib specimen of *E. attheyi* figured by Panchen (1966) as possibly representing an anterior member of the rib series underlying the pectoral girdle in that species. Like the latter specimen, the rib attributed to *Pteroplax* is characterized by the presence of a blade-like postero-dorsal extension of the proximal shaft, which may have served to support part of the endochondral shoulder girdle.

The apparently widely separated tubercular and capitular facets of G83.73 would appear to debar this specimen from representing a posterior trunk rib, but it is interesting to note that in the seymouriamorph *Kotlassia* the proximal caudal ribs exhibit similarly widely separated articular facets (Bystrow 1944), as, indeed, do those of *Eogyrinus* (Panchen 1966). It is possible, therefore, that G83.73 actually represents an incompletely preserved caudal rib.
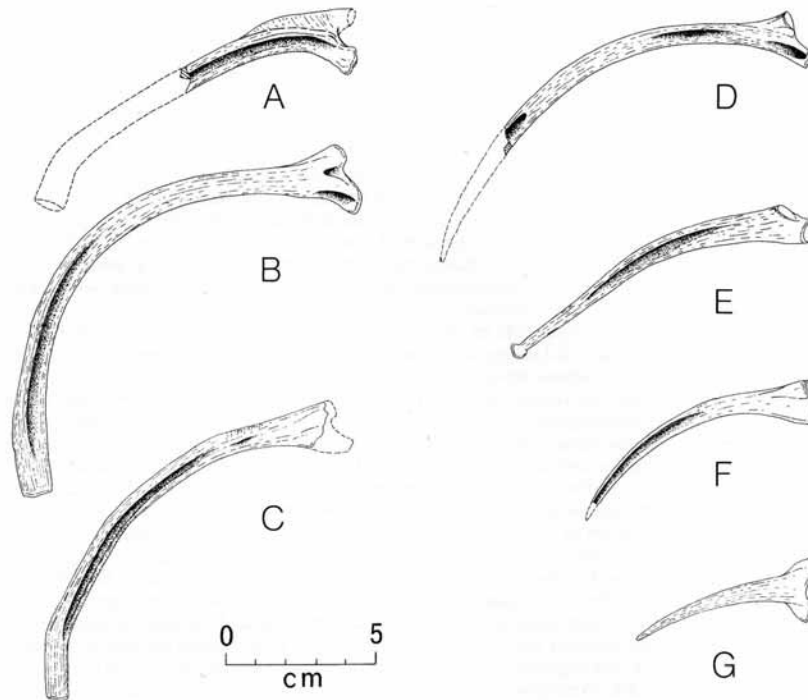
TEXT-FIG. 5. Series of trunk ribs of *Pteroplax cornutus* in reconstructed anterior-posterior sequence, ×0·5. A–C in anterior view, D–F in posterior view. A, pectoral rib specimen no. G83.73; B, 'thoracic' rib specimen no. G15.76; C, 'thoracic' rib specimen no. G15.78; D, 'thoracic' rib specimen no. G15.80; E, 'lumbar' rib specimen no. G83.72; F, 'lumbar' rib specimen no. G83.74; G, immediately presacral rib specimen no. G15.77.

## DISCUSSION

In most respects the vertebrae of *Pteroplax* conform to the pattern described by Panchen (1966) in *Eogyrinus*. In two points of structure, however, the vertebrae of *Pteroplax* differ from those of the latter genus.

In at least the trunk region, the intercentra of *Pteroplax* are as thick in their dorsal part as ventrally. In this feature the intercentra resemble those of *Archeria*, which, as indicated by the figures of Case (1911, fig. 51), also retain the same thickness throughout their height. The condition of the intercentrum in *Pteroplax* and *Archeria* is, however, in contrast to that present in *E. attheyi*. In this last species the intercentrum is usually wedge-shaped in lateral view, the anterior and posterior faces meeting dorsally (Panchen 1966). Whether the apparent similarities in the intercentra of *Pteroplax* and *Archeria* are of any phylogenetic significance is uncertain. The less completely ossified nature of the intercentra of *Eogyrinus* may be related merely to the much larger size of this form, the centra of which typically have a diameter approximately twice that of those of *Pteroplax*. It is, however, of interest to note at this point that the intercentra of the vertebrae of the North American Pennsylvanian embolomere *Cricotus* (Cope 1875), which are of approximately the same diameter as

those of *Archeria* and *Pteroplax*, differ from those of the last two genera in being, as noted by Romer (1947), 'pinched dorsally', presumably in a manner similar to the intercentra of *Eogyrinus*.

It is, however, also possible that the degree of ossification of the intercentra may be related to their position within the vertebral column or to the age of the individual animal, and it would thus be unwise to attempt to draw any definite conclusions from the apparent resemblance of the intercentra of *Pteroplax* to those of *Archeria* and the differences between these genera and *Eogyrinus* and *Cricotus*. It may nevertheless be noted that the presumed juvenile intercentra of *Pteroplax*, described above, show no tendency to taper dorsally.

Aside from the differences in absolute size and proportion, the only apparent point of significance in which the dorsal neural arch of *Pteroplax* differs from that of *Eogyrinus* lies in the presence in the former genus of a longitudinal supraneural canal piercing the neural spine of the arch dorsal to the neural canal proper. The supraneural canal is separated from the neural canal by a thin floor of bone.

Case (1915) figured (as '*Cricotus*') a neural arch of the Lower Permian embolomere *Archeria* in which, although the dorsal part of the neural spine is absent, a supraneural canal similar to that present in the vertebrae of *Pteroplax* is clearly present (Case 1915, pl. 22, fig. 1). Case noted the presence of such a supraneural canal in several further *Archeria* dorsal vertebrae, noting also that the canal appeared to have a greater cross-sectional area in those vertebrae possessing wide diapophyses than in those in which the diapophyses were relatively short. In *Eogyrinus* the anterior trunk vertebrae are characterized by the possession of diapophyses of greater lateral extent than those present in the more posterior trunk region (Panchen 1966) and it seems probable that a similar condition existed in *Archeria*. This being the case, it would appear from the information given by Case (1915) that the supraneural canal in *Archeria* is developed to a much greater degree in the anterior trunk vertebrae than in the posterior members of the vertebral series. Case also noted that the supraneural canal is not present as such in the case of a number of the more posterior trunk vertebrae of *Archeria* available to him, being represented only by a deep pitting of the anterior and posterior surfaces of the neural spine, and that this is also the case in the sacral vertebra.

In *E. attheyi* the neural spine is excavated anteriorly and posteriorly by a dorsally tapering groove, corresponding in position to the supraneural canal of *Pteroplax*, but the two depressions, anterior and posterior, are not known to join to form a continuous canal in the vertebrae of this species.

The function of the supraneural canal of *Pteroplax* and *Archeria* is not certainly known. Embryologically, the neural arches of vertebrates typically arise as paired structures which grow upward and mesially to fuse above the spinal cord, and it is thus possible that the supraneural canal in the vertebrae of the two above genera represents the partial retention of an ontogenetic stage prior to complete fusion of the two neural arch elements. However, it does not appear likely that the presence of this canal in *Pteroplax* and *Archeria* may be explained as due to the vertebrae which exhibit it being those of juvenile individuals. The dorsal vertebra of *Archeria* figured by Case (1915) as exhibiting a supraneural canal has the neural arch firmly attached to the pleurocentrum, and this, and the small size of the notochordal foramen of the centrum, do not suggest that the vertebra is that of a juvenile animal. The centra associated with the known neural arches of *Pteroplax* also possess small, or possibly occluded, notochordal foramina and would therefore appear to be those of well-grown individuals. Furthermore, the surface of periosteal bone which is present on the walls of the supraneural canal in *Pteroplax* suggests that this space does not simply represent an unossified area of the neural spine, occupied in life by cartilage, but that it served some more definite function.

Case (1915) suggested that the supraneural canal of *Archeria* was occupied in life by a longitudinal ligament or ligaments, extending as a continuous structure through the neural arches of the majority of the series of presacral vertebrae. In the case of the (usually posterior) vertebrae in which the canal was represented only by deep anterior and posterior pitting of the neural spine, the course of the ligament was assumed to be interrupted, extending only between successive vertebrae. This interpretation of the function of the supraneural canal of *Archeria* appears to be the most likely. *Archeria* is known to possess an elongated presacral vertebral column of approximately forty vertebrae (Romer 1947) and the presence of the continuous longitudinal ligament postulated by Case may be correlated with this fact, the ligament serving to compensate for the weaknesses inherent in such

a long vertebral series, even in an aquatic animal like *Archeria*. If this is indeed the case, then the presence of a supraneural canal in *Pteroplax* is a feature of some interest.

As noted above, no supraneural canal has been described in the vertebrae of *E. attheyi*. This species has been restored by Panchen (1966, 1972) as possessing a presacral vertebral column of approximately forty vertebrae and, if the supraneural canal of *Archeria* and *Pteroplax* does indeed serve for the passage of a longitudinal ligament acting as a tension member to strengthen an elongate presacral vertebral series, the absence of this structure in *Eogyrinus* is somewhat surprising. It is, however, interesting to note that the presacral vertebral column of *Eogyrinus* is known from no specimen comprising more than twenty-four individual vertebrae (Panchen 1966).

Neither a supraneural canal in the dorsal vertebrae, nor a degree of elongation of the presacral column even approaching that of *Archeria* (which has forty vertebrae) has been described in any member of the larger of the two embolomere lineages postulated by Romer (1963). It is tempting to speculate, in the absence of any positive evidence to the contrary, that these specializations may have been restricted to the smaller of Romer's suggested lineages. The number of presacral vertebrae present in *Pteroplax* is, however, unknown and, although the presence of a supraneural canal in this form suggests, if the interpretation of its function which is suggested above is correct, some elongation of the dorsal vertebral column, this may not have been so great as in the Lower Permian *Archeria*, the length of whose dorsal region may perhaps represent the culmination of trends originating in the Carboniferous forms ancestral to it. Certainly it is difficult to conceive of the earliest embolomeres exhibiting a 'jump' from the approximately twenty-four presacral vertebrae apparently primitive for 'labyrinthodont' amphibians (Romer 1947) to the forty known to be present in *Archeria* without any intermediate stages. It is unfortunate that the nature of the known specimens of Carboniferous embolomeres so far described makes it impossible to be certain of the degree, if any, of elongation of the dorsal vertebral column present in these forms.

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