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A NEW CAMARASAURID SAUROPOD *OPISTHOCOELICAUDIA SKARZYNSKII* GEN. N., SP. N. FROM THE UPPER CRETACEOUS OF MONGOLIA

(plates 1—14)

Abstract. — An almost complete postcranial skeleton lacking cervicals of *Opisthocoelicaudia skarzynskii* gen.n., sp.n. (Sauropoda, Camarasauridae) from the Upper Cretaceous Nemegt Formation, Gobi Desert, is described and figured. The reconstruction of the muscle system and sternum as well as the restoration of the whole animal is made. It is shown that *Opisthocoelicaudia* was a straight backed sauropod with the tail carried in a horizontal position. The neck is supposed to have been of medium length (about 5 m) and was carried low. The possibility of habitual assuming a tirpodal position is suggested by the opisthocoelous structure of the anterior caudals. The importance of some osteologic features of sauropods for the understanding of their attitudes as well as for the systematics is discussed. It is argued that the length of neural spines depends on both the curvature of the back-bone and the length of the neck and tail in sauropods. Forked neural spines are indicative of the habitual lowering of the neck, or even of the low carrying of the neck, if the anterior dorsals lack traces of the nuchal ligament insertion. Some titanosaurid characters of *Opisthocoelicaudia* are regarded as progressive ones in sauropods, whereas its camarasaurid features seem to indicate a true relationship in spite of their highly behavioural character.

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INTRODUCTION

The postcranial skeleton of *Opisthocoelicaudia skarzynskii* gen. n. sp. n. described in the present paper comes from the Nemegt Formation, (?Late Campanian or Early Maastrichtian), locality Altan Ula IV, Nemegt Basin, Mongolian People's Republic (see Gradziński *et al.*, 1969, text-figs 4.4, 5.4 and Gradziński, 1970). It was discovered and excavated in 1965 during the Polish-Mongolian Palaeontological Expedition to the Gobi Desert (Kielan-Jaworowska & Dovchin, 1969).

The relatively high degree of completness of the specimen indicates that the skeleton was probably buried before the complete decay of the soft parts. A part of it (axial skeleton) was found articulated and the remaining bones lay in the anatomical position. However the neck and head must have been separated before burial. Probably the dead animal had been subjected to the action of carrion feeders, as shown by traces of gnawing visible on its bones, especially on the pelvis and the right femur. The skeleton displayed a passive position (as already mentioned by Gradziński, 1970), characterized by a ventral attitude and spread limbs. The right side limbs and ribs were lying at the left side of the excavated specimen and conversely (see text-fig. 1)

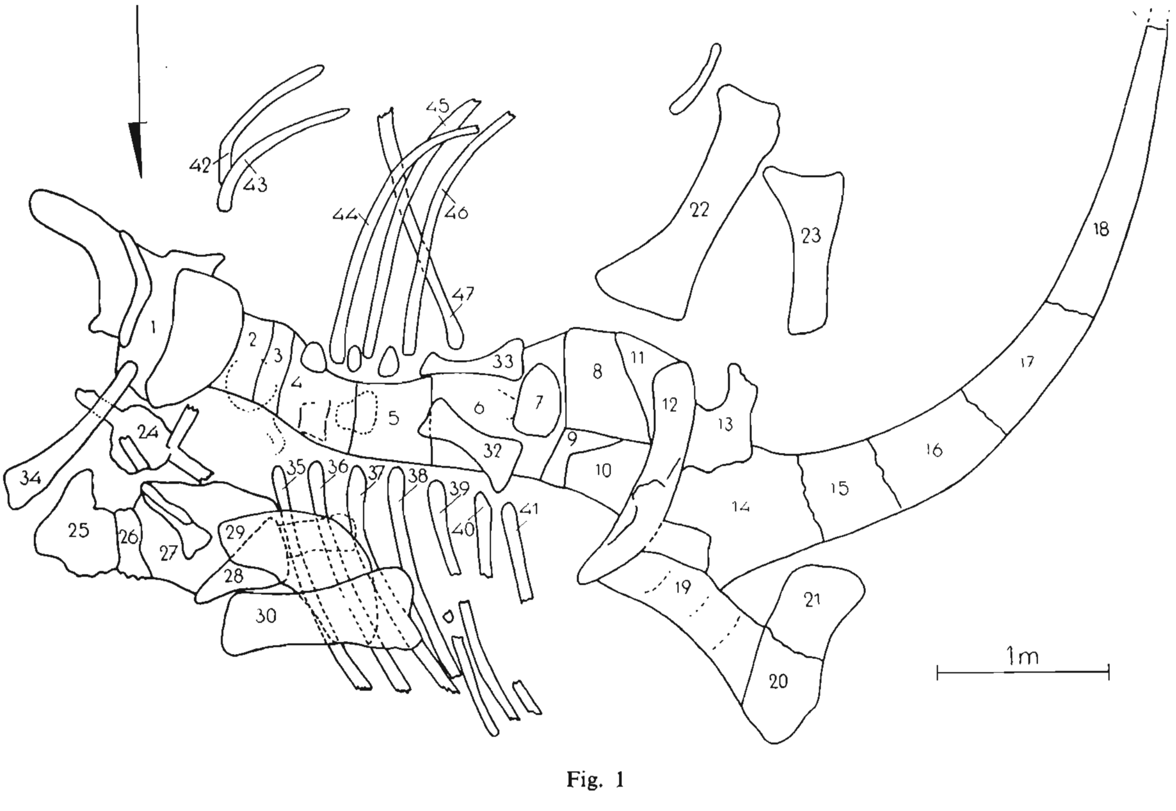

Fig. 1

Arrangement of bones of *Opisthocoelicaudia skarzynskii* gen.n., sp.n. ZPAL MgD-I/48 in the outcrop Altan Ula IV, Nemegt Basin. *1* — left scapulocoracoid and left sternal plate, *2—6*-dorsals from 4 to 9, *7*-right metacarpus, *8*-last dorsals and a part of sacrum, *9—10* — a part of pelvis and sacrum, *11*, *13* — left half of pelvis, *12* — right half of pelvis, *14—18*, caudal series, *19* — right femur, *20* — dorsal 1, *21* — dorsal 2, *22* — left femur, *23* — left tibia, *24* — dorsal 3 and fragmentary rib, *25*, *26* — left radius, ulna and metacarpus, *27*, *28* — right scapulocoracoid *29* — right sternal plate, *30* — right humerus, *32* — right radius, *33* — right ulna, *34* — left humerus (partly exposed), *35—41* — right ribs from 3, to 9, *42—47* — left ribs from 3 to 8. Drawing by R. Gradziński the hind limb and ribs of the left side were situated at the right side. The transportation of the body by floating must have been still very short. Otherwise the degree of disarticulation would have been higher.

Sauropod remains are not very abundant in Central Asia and are very often rather fragmentary. Most of them have been reported from China (WIMAN, 1929, YOUNG 1935, 1942, 1948, 1954 and 1958, YOUNG & JAN, 1972, HOU LIAN-HAI *et al.*, 1975). The most important sauropod specimen known hitherto from the Mongolian territory is the skull of *Nemegtosaurus mongoliensis* collected by the Polish-Mongolian Palaeontological Expedition in 1965 from the same formation as *Opisthocoelicaudia skarzynskii.* It was described by NOWIŃSKI (1971) as a typical representative of Atlantosauridae MARSH, 1877. The remaining sauropod materials from Mongolian localities are isolated bones and teeth (GILMORE, 1953, OSBORN, 1924, BOHLIN, 1953). All these materials are too fragmentary and uncertain as regards the stratigraphic age to give any complete picture of the sauropod faunas in Mesosoic of Central Asia. But, incomplete as they are, these materials prove undoubtedly the presence of both the main lines of sauropods, Atlantosauridae and Camarasauridae in Central Asia. It must be, however, noticed that no typical camarasaurid skull is known from this territory, the skull of *Euhelopus zdanskyi* (WIMAN, 1929) being of somewhat intermediate character, but the spatulate teeth typical of the Camarasauridae are rather common there (*Asiatosaurus mongolicus* OSBORN, 1924, *Asiatosaurus kwangshiensis* HOU LIAN-HAI *et al.*, 1975, *Chiayusaurus lacustris* BOHLIN, 1953 and *Euhelepus zdanskyi* WIMAN 1929 itself). From nine sauropod genera present in Central Asia only two, *Euhelopus* and *Mamenchisaurus* (YOUNG, 1958, YOUNG & JAN, 1972) have been comprehensively known hitherto as regards the postcranial skeleton. *Opisthocoelicaudia* is the third one. The satisfactory preservation of the here described specimen ZPAL MgD-I/48 permitted the accurate reconstruction of the skeleton of *Opisthocoelicaudia skarzynskii.* This reconstruction differs from these of most other sauropods in the horizontal position of its tail, which is unequivocally indicated by the osteologic features of this part of the body. This was probably one of the two main types of the tail attitude which are supposed to have been present in sauropods; they were probably correlated to some extent with the overall attitude of the vertebral column as well as with the structure of the chevrons. However the problem needs further investigations. Such an uncommon feature of *Opisthocoelicaudia* as opisthocoelic caudals seems to indicate a buttressing function of its tail and hence suggests the possibility of assuming a tripodal attitude probably in connection with the feeding habits.

Unfortunately the present investigation on *Opisthocoelicaudia skarzynskii* does not add any arguments of importance to the COOMBS (1975) discussion of the terrestrial versus aquatic habits of Sauropods.

As *Opisthocoelicaudia* is a monotypic genus I often use only the generic name for the sake of brevity.

The material of *Opisthocoelicaudia skarzynskii* described here is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw (ZPAL).

The other abbreviation used in this paper is YPM — Yale Peabody Museum of Natural History, New Haven.

I wish to express my thanks to Dr J. S. MCINTOSH (Wesleyan University, Conn. USA) for bringing me into the problems of sauropod palaeontology and for critical reading of the manuscript and to Dr. H. OSMÓLSKA (Institute of Paleobiology in Warsaw) for significant comments on my text and valuable discussions throughout this study. Thanks are also due to Dr. K. FISCHER (Humboldt University, East Berlin) for making the Berlin sauropod collection available for comparative studies. I am indebted to Mr. W. SKARŻYŃSKI for the skilfull preparation and mounting the skeleton; to Mrs. K. BUDZYŃSKA for drawings and to Mr. W. SICIŃSKI for arranging plates and figures (all from the Institute of Paleobiology in Warsaw) as well as to Mrs. BENTKOWSKA for valuable remarks on the English of the manuscript.

DESCRIPTION

Infraorder **Sauropoda** MARSH 1878
Family **Camarasauridae** COPE 1877
Subfamily **Euhelopodinae** ROMER 1956
Genus *Opisthocoelicaudia* nov.

Type species: Opisthocoelicaudia skarzynskii nov.
Derivation of the name: because of the opisthocoelian structure of the anterior caudals.

Diagnosis. — The genus is monotypic; see the diagnosis of the species.

Stratigraphic and geographic range. — Known only from the Upper Cretaceous, Nemegt Formation (?Upper Campanian or Lower Maastrichtian) Gobi Desert, Mongolia.

Opisthocoelicaudia skarzynskii sp.n.

(pls 1—14; text-figs 1—19)

Type specimen: Postcranial skeleton without cervicals (ZPAL MgD-I/48); pls 1—14, text-figs 1—19.
Type horizon: Nemegt Formation, ?Upper Campanian or Lower Maastrichtian.
Type locality: Altan Ula IV, Nemegt Basin, Gobi Desert, Mongolian People's Republic.
Derivation of the name: named in honour of Mr. WOJCIECH SKARŻYŃSKI who prepared the specimen.

Diagnosis. — Species of medium size and of straight-backed type. Dorsal centra not deeply cavernous. Dorsal spines divided into two low metapophyses overhanging the postzygapophyses. Sacral spines low. Six sacral vertebrae. The second caudo-sacral fused with the ischium. Caudals without pleurocoels. Their number is about 35. Simple transverse processes. Unforked chevrons. No chevrons exist beyond caudal 19. Centra opisthocoelous in the anterior half of the tail. Scapula little expanded distally. Coracoid subquadrangular. Ilium with strong anterior flare. Ischium forming a larger part of acetabular boundary, otherwise being relatively short element making only about 2/3 of pubis length. Prominence for ambiens origin present. Fore limbs about three quarters the length of hind limbs. Humerus about 72% of the femoral length. No carpals. Phalanges probably reduced in the anterior limbs. Calcaneum lacking. Astragalus reduced in dimensions Phalangeal formula of the pes: 2, 2, 2, 1, (0?).

Material. —Type specimen ZPAL MgD-I/48 is a postcranial skeleton lacking cervicals. It belonged to an old individual. The dorsals are strongly crushed but fairly complete. Eight of them represent the articulated series connected with 6 sacrals and 34 caudals. The three anterior dorsals were found disarticulated and are the worst preserved. The sacrum is strongly damaged in its right half by weathering, but much better preserved on the left side. The sacral spine posteriorly to the first primary sacral and the whole arch of the last caudo-sacral are strongly damaged too. The caudals together with their chevrons are almost perfectly preserved. Only three metacarpals (I, II and III) are preserved on the right side. Otherwise both the anterior limbs together with their pectoral girdles and the sternal plates are complete, although some of the bones are slightly deformed. The pelvis lacks the distal end of the left pubis and part of the proximal portion of the right one. The anterior part of the left ilium, the posterior part of the right one and the dorsal borders of the both ilia are strongly damaged (obviously due to the activity of the predators) in the right one. The left tibia and fibula are distorted and only three metatarsals (I, II and IV) and some phalanges are preserved in that pes. The left astragalus seems to be coalesced with the tibia, which is not the case on the right side.

ZPAL MgD-I/25c. — A scapula and coracoid of a young individual. The coraco-scapular suture is unfused. The distal end of the scapula as well as a proximal part of its posterior border are damaged.

VERTEBRAL COLUMN
(pls 1—6, 12, fig. 2, 4, text-figs 2, 3)

Fifty vertebrae are preserved: 11 presacrals, 5 sacrals and 34 caudals. All but three of them represent an atriculated series, beginning with eight dorsal vertebrae, ending with much reduced caudal centra (see table 1). The three vertebrae, which were found disarticulated are strongly damaged. They belong probably to the very anterior part of the thoracic region or to the cervical region and therefore reveal the transitional type of structure. They were assigned provisionally the three first numbers, the articulated series of the dorsals being numbered from 4 to 11.

Table 1

Measurements (in cm) of dorsal vertebrae of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

Vertebra number	Length of centrum total	Length of centrum without ball	Height of vertebra total	Width of centrum	Height of centrum	Maximum spread of diapophyses	Height of neural spine *	Length neural arch at the base	Angle between surfaces of prezygopophyses
D_1	28	18	—	21	16.5	—	—	12	—
D_2	24	15	47.5	22.5	15	66	23	11	110
D_3	27	17.5	47	26.5	16	67	25	11	116
D_4	30	22	44	—	—	61	about 22	15	—
D_5	30	22	44	25	14.5	58	19	16.5	—
D_6	30	22.5	42	23.5	15	44	20	17	90
D_7	31	23	48	25	15	42	19	17	—
D_8	30	22	45	27	16.5	51	18.5	16	—
D_9	30	23	45	31	14.5	50	18	16.5	90
D_{10}	30	19.5	49	31	16	50	22	16.5	97
D_{11}	22	17	50	30.5	16	41	19.5	15	102
DS	—	14	50	—	about 17.5	—	21.5	—	—

* Above the level of the medial borders of the postzygapophyses.

Dorsal vertebrae (pls 1—3, pl. 12, figs 2, 4, text-figs 2, 3).

Centra. All centra are distinctly opistocoelous. The convexity of the balls changes to a small extent within the dorsal series, especially between the fourth and ninth vertebrae, the curvature being more pronounced in the three transitional vertebrae, from the anterior part of the dorsal region. The increase of the convexity in the dorsal 10 together with the somewhat pointed shape of its ball is probably due to the post mortem flattening of the vertebra 9 and the joint between vertebra 9 and 10. The articular surfaces of the centra are usually perpendicular to their axes, except in vertebra 3, where the anterior articular surface points slightly upwards and in vertebra 1, where it is probably turned downwards. The centra are characterized by dorsoventral flattening which increases in the posterior part of the dorsal series due to the broadening of the centra in that region, whereas their height does not show any regularity in variation. The centra from 8 to 11 as well as in the sacrum were, however, subject to deformation, the stress coming from the left. The length of the centra is rather stable in the central thoracic region from dorsal 4 up to 10 fluctuating near the mean value of 30 cm. Outside this series it decreases, the centra of the immediately postcervical region (1—3) and the very posterior dorsal vertebrae (10—11) getting shortened along the sagittal axis. A pronounced contraction of the centra with the maximum situated immediately behind the head, gives them a spool-like shape. The ventral concavity of the centra, which is delimited by two ventrolateral crests and divided by a strengthening sagittal lamina, becomes increasingly deeper when passing towards the sacrum. The pleurocoels are present throughout the whole dorsal series getting larger and more rounded posteriorly, towards the vertebrae 9, 10 and probably 11, which have the most extensive and most rounded cavities. An additional pleurocoel cavity appears above the posterior part of the main pleurocoel in vertebrae 6, 7 and 9. It is, however, well formed only at one side of the vertebrae. The main pleurocoel cavities are undivided except in dorsal 9 (right side), 7 (right side) and 1 (left side), where a slight subdivision by means of a bone bar can be observed anteriorly (see text-fig. $2A_1B_2$). The bad state of preservation does not permit a more detailed observation of the pleurocoels, especially at the beginning of the dorsal series. Here the pleurocoels are probably single, with a trace of the internal subdivision in one vertebra only (dorsal 1). Owing to the low position of the parapophyses, the pleurocoels of the last named vertebra are strongly deformed in their anterior halves (pl. 3, fig. 7).

Neural arches. The neural arches are characterized by their considerable length, changing to small extent only, according to the changes of the centra. The walls of the neural arch are massive as compared with the size of the neural canal, the breadth of which makes up about one fifth of the anterior vertebral breadth measured at the base of the neural arch. This ratio remains about the same in the whole dorsal series, the breadth of the neural increasing simultaneously with the thickening of the walls of the neural arch. The anterior border of the neural arch called the infraprezygapophyseal lamina is formed as a flattened or slightly concave wall facing forwards. It makes a main support for the prezygapophysis and is therefore strengthened by two pilaster-like convexities; but it supports the middle part of the prezygapophysis, its narrow medial part being buttressed by a framework of bone bars situated above the neural canal. The outer part of the prezygapophysis constitutes about 2/5 of its breadth in the last dorsals and increases anteriorly up to more than a half of its breadth. It is buttressed by the so called centroparapophyseal lamina (hintere Centroparapophysialleiste of JANENSCH, 1950) in the anterior part of the dorsal series and by the infraparapophyseal lamina (vordere Centroparapophysialleiste) in the posterior one. Both laminae contribute to the support of the parapophysis too. Extending between the wall of the neural arch, prezygapophysis and the parapophysis of the posterior dorsals, the infraparapophyseal lamina is a thin bone plate. It is often poorly preserved because of its fragility. The centroparapophyseal lamina is a pilaster-like element running from the base of the neural arch forwards and upwards to the base of the parapophysis or to the prezygapophysis crossing the infraparapophyseal lamina on its way (see e.g. dorsal 7, text-fig. $2A_1$, pl. 3, fig. 4). The latter tends to disappear in the anterior dorsals in connection with the downward shifting of the parapophysis. The prezygapophyses are connected with the diapophyses by means of the horizontal laminae strengthening both of them. No supraprezygapophyseal lamina is developped in the majority of the vertebrae, or it is hardly recognizable owing to the bad state of preservation. The infrapostzygapophyseal laminae, which represent the posterior borders of the neural arch, are formed as simple rounded columns in all the dorsals posterior to the forth one. They contribute mainly to the buttressing of the massive upper part of the neural arch, the metapophyses included, giving a support for postzygapophyses only to a small extent. The bulk of the bifid spine overhangs the postzygapophyses carrying them suspended by means of the so called suprapostzygapophyseal laminae strongly comparable morphologically to the infraprezygapophyseal laminae. They are formed by about three rounded columns separated from one another by concavities, and runnig from below the metapophyses down to the postzygapophyses (see text-fig. $2A_2C_2$).

Prezygapophyses. The prezygapophyses are oval in shape, their longer diameters being directed transversally; the shorter ones are parallel to the sagittal body axis. Their surfaces are more rounded in the transition vertebrae (1—3), especially in the first one. They get more elongated transversally towards the dorsal 6 and become increasingly rounded again from the seventh up to the tenth one. In the posterior dorsals the prezygapophyses are inclined downward toward each other at an approximately constant angle of about 90°. In the anterior dorsal region beginning from the vertebra 6 they tend to approach horizontality, but attain only an angle of about 110°. The distance between the prezygapophyses changes within the dorsal series as well. The prezygapophyses of the first three vertebrae are situated far apart. In the posterior dorsals beginning with 6 they are very close to each other, the dorsals 4 and 5 represent a transition from one condition to the other.

Postzygapophyses. The postzygapophyses resemble their anterior mates as regards their dimensions, shape, distance from each other and the obliquity of their axes.

Hyposphene-hypantrum articulation. No unquestionable traces of the hypophene-hypantrum articulation can be observed in the dorsal series and it certainly did not exist in the anterior dorsal region in front of the dorsal 6. The same cannot be stated with any certainty for the rest of the dorsal series because of the state of preservation of the vertebrae, which are slightly compressed laterally. The trace of what could have been the hypantrum can be seen at the vertebra 8. Some rudiments of bone lying between the postzygapophyses of the vertebrae 8 and 9 could represent the crushed hyposphene; but they are situated too deeply between the postzygapophyses to contribute to the strengthening of the articulation. Hence the presence of the hyposphene-hypantrum articulation in *Opisthocoelicaudia skarzynskii* is rather problematic.

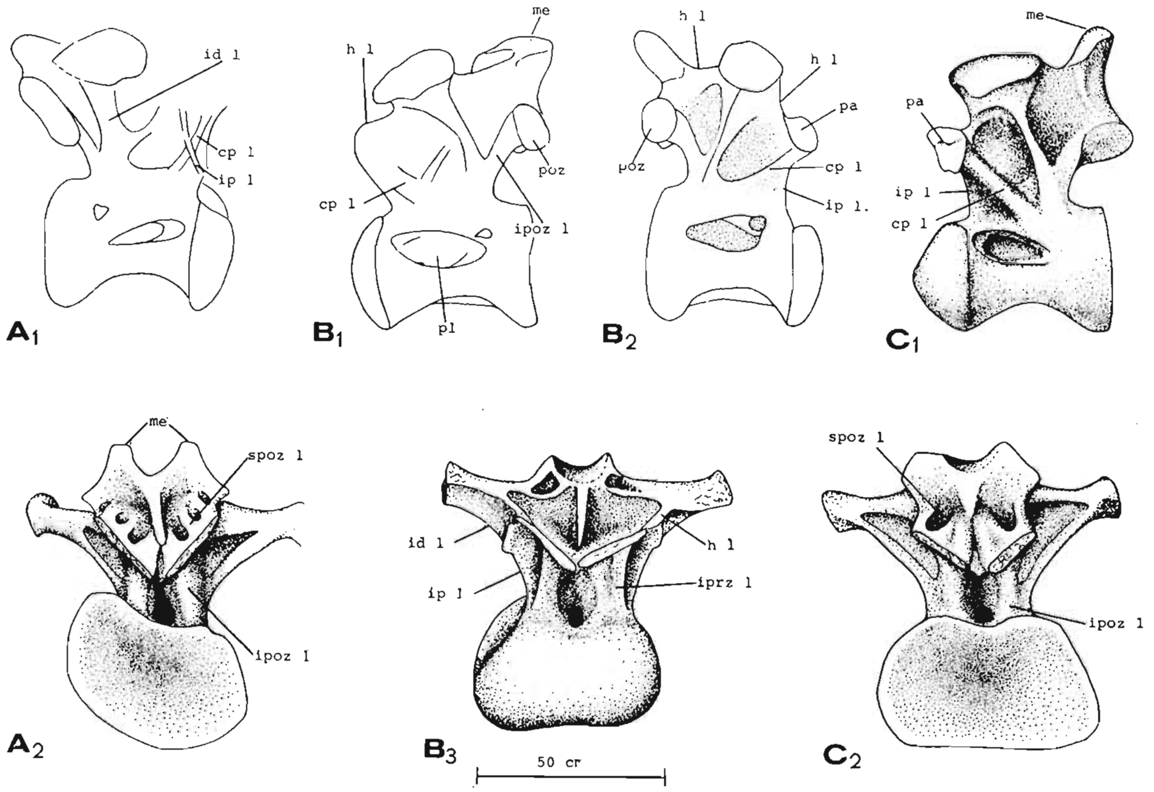

Fig. 2

Opisthocoelicaudia skarzynskii gen.n., sp.n. *A* — dorsal 7, A_1 — right side view, A_2 — posterior view, *B* — dorsal 9, B_1 — left side view, B_2 — right side view, B_3 — anterior view, *C* — dorsal 10, C_1 — left side view, C_2 — posterior view (explanations see text-fig. 3).

Parapophyses. The parapophyses are small processes buttressed by infraparapophyseal and centroparapophyseal laminae, when situated on the arch, or sitting much lower without any buttress. In the posterior dorsals they are situated immediately below the prezygapophyses. Only in the dorsal 4 they shift downwards to the base of the neural arch. In the first vertebra of the present series the parapophyses occur on the sides of the centrum, causing thus the deformation of the pleurocoels.

Diapophyses. The diapophyses are subquadrangular processes bearing the elliptical surfaces for the costal heads. Each diapophysis is connected with the neural arch by two so called horizontal laminae, the anterior running to the parapophysis, the posterior one to the metapophysis. These two laminae constitute in fact two margins of the oblique lamina extending in the same plane as the prezygapophysis to the base of the spine, then curving decidedly upwards to the top of the metapophysis. This lamina is strengthened by folds, difficult to describe because of the poor state of preservation. This character was probably subject to individual variation. The only strenghtening element which is always present here is the so called supradiapophyseal lamina, running from the base of the metapophysis to the posterior part of the base of the diapophysis. The main buttressing element is the infradiapophyseal lamina, which extends from about the middle of the lower ridge of the diapophysis obliquely down to the base of the infrapostzygapophyseal lamina. It causes the triangular shape of the transverse section of the distal part of the diapophysis. Two concavities are present on both sides of the infradiapophyseal lamina. The anterior one is limited from the front part by the centroparapophyseal lamina. The second one, lying posteriorly and more dorsally is bordered from behind by the infrapostzygapophyseal lamina. Both concavities become deeper downwards, the laminae forming their bottoms being strengthened by the framework of bone bars. The position of the diapophysis changes gradually from very high in the posterior dorsals to much lower in the anterior ones. The spread of the diapophyses increases in the opposite direction, the most anterior dorsals having the most extended diapophyses.

Neural spines. The spine does not exist as a single element all along the dorsal region of the vertebral column. It is represented by two stout metapophyses situated above the postzygapophyses in the way described above. They are joined by an arcuate concave surface the length of which equals to about 12 cm, decreasing abruptly in the anterior transitional vertebrae simultaneously with the shortening of the neural arch. The conspicuous prespinal lamina formed from the fused elongations of both metapophyses, lies deep in the interior of the laminar bracing of each vertebra, below the metapophyses. The prespinal laminae are very strong and protruding in three last dorsals (9—11) and could be also very strong in two subsequent ones, where they are damaged. The lower parts of the prespinal laminae could have been slightly bifid in the posterior dorsals from 7 to 11 but all of them are poorly preserved in this region. In the vertebra 6 the prespinal lamina becomes flat and shows two ridges running its total length in continuity with the metapophyses. They merge into the posterior borders of the prezygapophyses standing for the supraprezygapophyses otherwise not represented. The last trace of the prespinal lamina occurs in vertebra 5, then disapears. The postspinal lamina occurs in all dorsals from 6 to 11 being more thick in the posterior vertebrae, in the way similar to that of the prespinal lamina.

The first three vertebrae of the series representing a transition to the cervical vertebrae differ very much from the remaining dorsals (as mentioned above several times). They have very short neural arches, high, deeply notched and arcuated spines (pl. 1, figs 1, 2, 4 pl. 2, figs 1, 2 text-fig. $3A_1A_2$) lying in almost the same vertical plane as the posterior borders of the prezygapophyses, which is due to the shortening of the vertebrae. The prezygapophyses and postzygapophyses situated well apart are connected in pairs by interprezygapophyseal laminae and interpostzygapophyseal laminae accordingly, not present in the posterior part of the dorsal series except in vertebra 4 and 5 where they are very short. The first three vertebrae are also characterized by widely spread, rather low diapophyses and the parapophyses tending to be gradually shifted towards the centrum.

Ligamentous and muscular traces in dorsal series. The position and shape of the ligamentum nuchae can be easily reconstructed from the structure of the neural spines in the dorsal series, basing on the reconstructions done by Janensch (1929, 1950) for *Dicreosaurus* and *Brachiosaurus* respectively. This was a stout rounded rope pasing through the series of notched spines from the cervical region to the dorso-sacral spine where it was inserted. Its diameter decreased from front to back attaining about 2—3 cm at the insertion, while getting wider and higher anteriorly. However the great depth of the spinal notches at the anterior vertebrae can be also caused by the slight upwards inclination of the vertebral column in this region (see p. 56). The surfaces of the spinal notches are quite smooth, no traces of the attachments of the ligamentum nuchae to the separate vertebrae being left. The summits of the metapophyses, when preserved, are slightly rounded probably for the attachments of the paired interspinales muscles rather than the doubled supraspinal ligament. The diapophyses and tubercular parts of the ribs bear marked rugosities on their dorsal surfaces which could have served as the attachement places of the strong joint capsules and partly also for the insertion of the fascicles of the longissimus dorsi; the intertransversarii could have been attached at the anterior and posterior margins of the diapophyses. These rugosities are less pronounced in the anterior dorsals at least in the fourth one where the diapophyses are preserved and are very strong in the last dorsals. They are strongly pronounced in the sacrum, probably only in connection with the sacro-pelvic ligaments or fasciae. The prespinal and postspinal laminae which are very distinct beginning with the back surface of the dorsal 6, increase in height and strength posteriorly. They decrease anteriorly to disappear in the dorsal 4. They represent no doubt the attachment places of the interspinal ligaments checking the movements of the vertebral column in the sagittal plane. No traces of the puboischiofemoralis internus can be identified on the sides of the dorso-sacral and last dorsals.

Sacrum (pl. 12, figs 1*a*, 3, text-fig. 11). The sacrum consists of six vertebrae. These include three primary sacrals, one dorsosacral and two caudo-sacrals.

Centra. The centra of the six sacrals are completely coossified. Their length does not usually exceed that of the dorsals. The first two sacrals are the shortest of the series, the caudosacrals attain the maximum length. All but the last two sacrals are very slender, which is caused mainly by the lack of the much broadened articular ends present in the dorsals, and partly by the narrowing of the centra. The sutures between the centra are marked by slight broadenings, so that the spool-like shape, typical of the dorsals, is retained here, althought much less pronounced. The transverse section of the sacral centra from 2 to 5 is somewhat compressed laterally, the ventral concavity being bordered by two ventro-lateral crests. The sacrals 1 and 6 are flattened dorso-ventrally. No pleurocoels can be observed. Both ends of the sacrum are provided with the normal articular surfaces: the slightly convex anterior ball in the dorso-sacral and the deeply concave articular fossa in the last caudo-sacral. Both articular surfaces are approximately perpendicular to the axis of the centrum, showing no distinct upward turn described by GILMORE (1936) for sauropods. The same position is true for the posterior articular surface of the last dorsal, the axis of the vertebral column being therefore quite straight in that region. The upward bend of the vertebral column in the vicinity of the sacrum occurs at the tail's base, owing to the shifting of the anterior articular surface of the first caudal (see below).

Table 2

Measurements (in cm) of sacrum of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

Length of sacral centrum as a whole	100 (estimated)
Length of centrum of: dorso-sacral	14.5
primary sacral 1	14.5
primary sacral 2	17
primary sacral 3	16
caudo-sacral 1	19
caudo-sacral 2	19
Anterior width of centrum of:	
dorso-sacral	32
primary sacral 2	11
caudo-sacral 2	24

Neural spines. The neural spines have been preserved only in first two sacrals, being strongly damaged in their right halves and in the posterior part of the second vertebra. The two preserved spines are entirely coossified. The same was probably also true for the two consecutive sacrals at least, as can be judged from the continuity of their bases as well as from the theoretic premise that the primary sacrals should not be less fused than the additional ones. The common sacral neural spine represents a not very high crest, less than a half of the total height of vertebra. About a half of the neural spine protrudes upwards above the base of the diapophysis and strongly broadens upwards. Its anterior part attains the width of about 12 cm at the top, as estimated from the preserved left side, narrowing a little posteriorly. The upper part was probably single and strongly rugose. The anterior margin of the spine has a strongly protruding triangle-shaped prespinal lamina broadening upwards. The concave lateral wall of the spine is strengthened by the posterior part of the horizontal lamina. The supradiapophyseal lamina and other strengthening folds are rudimentary. The remaining parts of the sacrum can be described in a better way when considered consecutively in segments.

Dorso-sacral vertebra. The dorso-sacral can be regarded as a typical sacral vertebra, because of its complete fusion with the next sacral by means of centrum, arch and neural spine; its postzygapophyses are lost. Its rib is rudimentary and curves backwards fusing with the sacricostal yoke and laterally with the inner part of the ilium. But this vertebra still retains some features of the dorsals. The ball-shaped articular surface is very broad as compared with the rest of the centrum. The prezygapophyses, here covered by the postzygapophyses of the last dorsal, seem to be similar in shape and position to those of the foregoing vertebra. They are probably somewhat smaller and seem to pass into the hypantrum, the joint being strengthened by the hyposphene-hypantrum articulation. The diapophysis is characterized by its long base standing more vertically than those of the foregoing dorsals, which is caused by the shortening of the vertebra. Owing to this, the parapophysis is shifted backwards and situated in almost the same transversal plane as the diapophysis. These processes are joined by the infradiapophyseal lamina, the base of which is situated here exactly above the parapophysis. Both processes together with coossified rib produce a sort of transverse wing similar to the transverse wings of the primary sacrals. It differs from the latter by its much smaller extent downwards and by its slightly convex anterior surface. The triangular parapophysis is larger than that of the last dorsal, its lower margin attaining therefore a comparatively lower position; but it remains still within the neural arch. Neither the infraparapophyseal lamina nor the centroparapophyseal lamina is present. The joined diapophysis, parapophysis and rib border an oval shaped opening, which shows a tendency to be closed by a lamina of bone produced mainly by the infradiapophyseal lamina.

Primary sacrals and first caudo-sacral. The wing-like transverse processes of the sacrals from 2 to 5 are rather stout almost perpendicular bone blades. They retain their individual character in the upper parts, while fusing with each other to form a sacricostal yoke in their lower and distal parts. In the first two primary sacrals their upper and distal parts are separated from the sacricostal yoke by rounded notches. In the third primary sacral the upper part of the wing fuses with the sacricostal yoke just before fusing with the ilium (text-fig. 11 *C*), leaving a rounded opening of about 12 cm in diameter medially. This opening vanishes completely in the caudo-sacrals. The sacral wing is fastened to the upper part of the neural arch by means of three folds lying in the same subhorizontal plane. They represent from front to back: the anterior horizontal lamina, the supradiapophyseal lamina and the posterior part of the horizontal lamina (text-fig. 11 *D*, *h.l.*, *sd l. hl.*). The anterior part of the horizontal lamina of the first primary sacral is fused with the rudiment of the suprapostzygapophyseal lamina of the forgoing vertebra, owing to the loss of the postzygapophysis. It fuses directly with the posterior part of the horizontal lamina in the more posterior sacrals. The ventral part of the sacral wing is formed as a stout process (inferior bar of rib of OSBORN & MOOK, 1921) delimited from the centrum by a suture line. Its proximal end extends upon the whole length of the centrum, its middle part being narrower and rounded in transverse section, whereas the distal one extends again to produce the sacricostal yoke. Situated in the proximal part of the wing-like transverse process of the sacrum between the diapophysis and the „inferior bar of rib", is another stout strengthening fold (text-fig. 11 *B*, *C*, *pa*).

The homology of different parts of the transverse processes of the sacrum is not quite clear, particularly so in their ventral parts. The main problem is whether the middle broadening of the proximal part of the sacral wing or the lower one represents the parapophysis. The first of this supposition seems to be more probable, because there is a strong similarity between the middle and the upper part of the wing and the rib rudiment of the dorsosacral (see text-fig. 11 *A*, *B*). The middle strengthening fold of the sacral wing corresponds perfectly to the parapophysis by its position and form. The whole ventral part of the wing, the sacricostal yoke included, should be thus regarded as a new formed rib derivative.

The transverse process of the first caudo-sacral seems to be quite a solide bone blade as judged from the poorly preserved posterior part of the sacrum. It is lower and narrower at the same time. The fourth and fifth sacral ribs are extremely broadened in the region of the sacricostal yoke, contributing to the formation of the acetabulum not only in its superior part but also in the posterior one. Hence they broaden both in the sagittal and ventral direction.

Second caudo-sacral. The transverse processes of the last sacral, are strongly damaged, the contact between the sacrum, ilium and caudo-sacral vertebra being broken. It is however quite evident that this vertebra contributed to the formation of the sacricostal yoke. It fuses with the ischium by its lower and outer part and with the ilium by its outer part, the suture lines being quite distinct (see text-fig. 14).

Caudal vertebrae (pls. 4—6, text-figs. 19). *Centra.* The most outstanding character of the caudal centra is their being opistocoelous in the anterior half of the tail. This is strongly pronounced in five anterior caudals, which exceed the dorsals 1—3 in this respect, being more pointed in addition. The convexity of the anterior ball is much smaller but distinct in caudals 6—15, the depth of cups being always more pronounced than the convexity of the corresponding balls. The caudals from 16 to 27 are amphiplatyan, those from 28 to 34 become biconvex. The caudal centra from 20 to 27 were probably coossified, this part of the tail being stiffened. The same could be true for the caudals 17—18. The caudal 3 has the greatest total length of the centrum, while two first caudals are somewhat shorter. From the caudal 3 to about 16 the total length keeps decreasing. It fluctuates around the mean value of about 165 cm between caudals 16 and 28, decreasing again at the end. The decrease of the total length of the caudal centra is obviously connected with the gradual reduction of the anterior convexity in the anterior part of the tail; the length of the centrum, measured without the ball, is rather stable in that region (see table 3). A similar relation is true for the shape of the centra viewed in lateral aspect. It is more pronouncedly spool-like in the anterior half of the tail and becomes indistinct, where the articular surfaces of the centra are weak. But the walls of the centra are more or less concave throughout the series. The ventral concavity is bordered by ventro-lateral ridges throughout most of the series begining from caudal 3. This is not visible at the first two caudals, probably due to the deformation. None of the centra have pleurocoel cavities. The transverse processes are represented only by rudimentary inferior bars of ribs, except in the first caudal, where there is a very small rudiment of what was the sacral wing, in addition. At the beginning of the caudal series the transverse processes are heavy, blunt knobs projecting outwards and backwards, then only outwards, from the upper part of the centra and delimitted from them by distinct sutures. They decrease in size from front to back, being replaced by raised longitudinal ridges from caudal 11 to about 16, then disappearing entirely.

Neural arches. The neural arches are rather short and shifted forwards, which is more striking only in the posterior caudals, beginning from about 14, where they make half a length of centra. The infraprezygapophyseal lamina as well as infrapostzygapophyseal lamina are simple rounded columns, except in the first caudal where the first of them is a broadened bone plate with a concave anterior surface. They are linked by a connecting lamina formed by the supraprezygapophyseal lamina in the first two caudals or by the infrapostzygapophyseal lamina itself in the more posterior ones. The supraprezygapophyseal lamina of the first two caudals shows a certain bifidity in its posterior part, the stronger superior part going up to the lateral part of the spine, the feeble lower part running to the postzygapophysis (see text-fig. 19). Both parts are shifted somewhat upwards and medially in the more posterior caudals losing their contact with the postzygapophysis. At the same time the very base of the infrapostzygapophyseal lamina shifts forwards to fuse with the posterior margin of the infraprezygapophyseal lamina, thus making a new connecting ridge. Both laminae make an angle of about 90° in the first two caudals; posteriorly they tend to get a horizontal position forming a common straight, horizontal ridge provided with the zygapophysis at both ends, beginning from the caudal 11. From this place on there is in fact nothing more at the archs' walls than fingerlike prezygapo-

Table 3

Measurements (in cm) of caudal vertebrae of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

No	Length of centrum total	Length of centrum without ball	Height of vertebra total	Width of centrum	Height of centrum	Neural Spine		
						Height	Breadth	Length
C_1	23	12	49	28	24	18	14	10
C_2	25	12	49.5	—	21	16	12	9.5
C_3	27.5	14	44.5	28	20	17·5	—	—
C_4	—	13.5	44	—	21	16	11	8
C_5	—	13.5	42.5	—	22	14	—	8
C_6	22	14	37	24.5	20	10	9	7.5
C_7	16.5	12.5	34	—	19	9	9	7.5
C_8	—	13.5	30	—	18	—	7	7
C_9	18	14	31.5	19	18	9	5	7.5
C_{10}	—	14	30.1	—	16	8	2	6.5
C_{11}	16.5	14	—	18	17	—	—	—
C_{12}	—	13.5	30	—	—	7	2	7.5
C_{13}	—	14	28	—	—	7	2	8.5
C_{14}	—	14	—	—	—	—	—	—
C_{15}	—	14	24	16	—	5	1.5	10.5
C_{16}	15.5	14	20.5	17.5	15	3·5	1.4	11
C_{17}	16.5	15	18.5	16.5	—	3	1.4	12
C_{18}	16	15.5	17.5	16.5	—	—	—	—
C_{19}	16.5	15	17	16.5	14	2	1.9	12
C_{20}	16	15	16	—	12	2·5	2.5	13.5
C_{21}	16.5	15	13.5	16	—	—	1.1	12
C_{22}	16.5	15	13	15	—	8	1.3	12
C_{23}	16	15	12.5	14	—	6	1.1	12
C_{24}	16	15	12	14	10	—	—	—
C_{25}	16	14.5	11	13	—	—	—	—
C_{26}	15	14	10	12	—	—	—	—
C_{27}	15	14	10	11	8.5	—	—	—
C_{28}	16	13·5	—	10.5	7	—	—	—
C_{29}	12	—	—	7	6	—	—	—
C_{30}	11	—	—	6	4.5	—	—	—
C_{31}	11	—	—	4.5	4.5	—	—	—
C_{32}	10.5	—	—	4	3.5	—	—	—
C_{33}	9.5	—	—	—	—	—	—	—
C_{34}	7	—	—	—	—	—	—	—

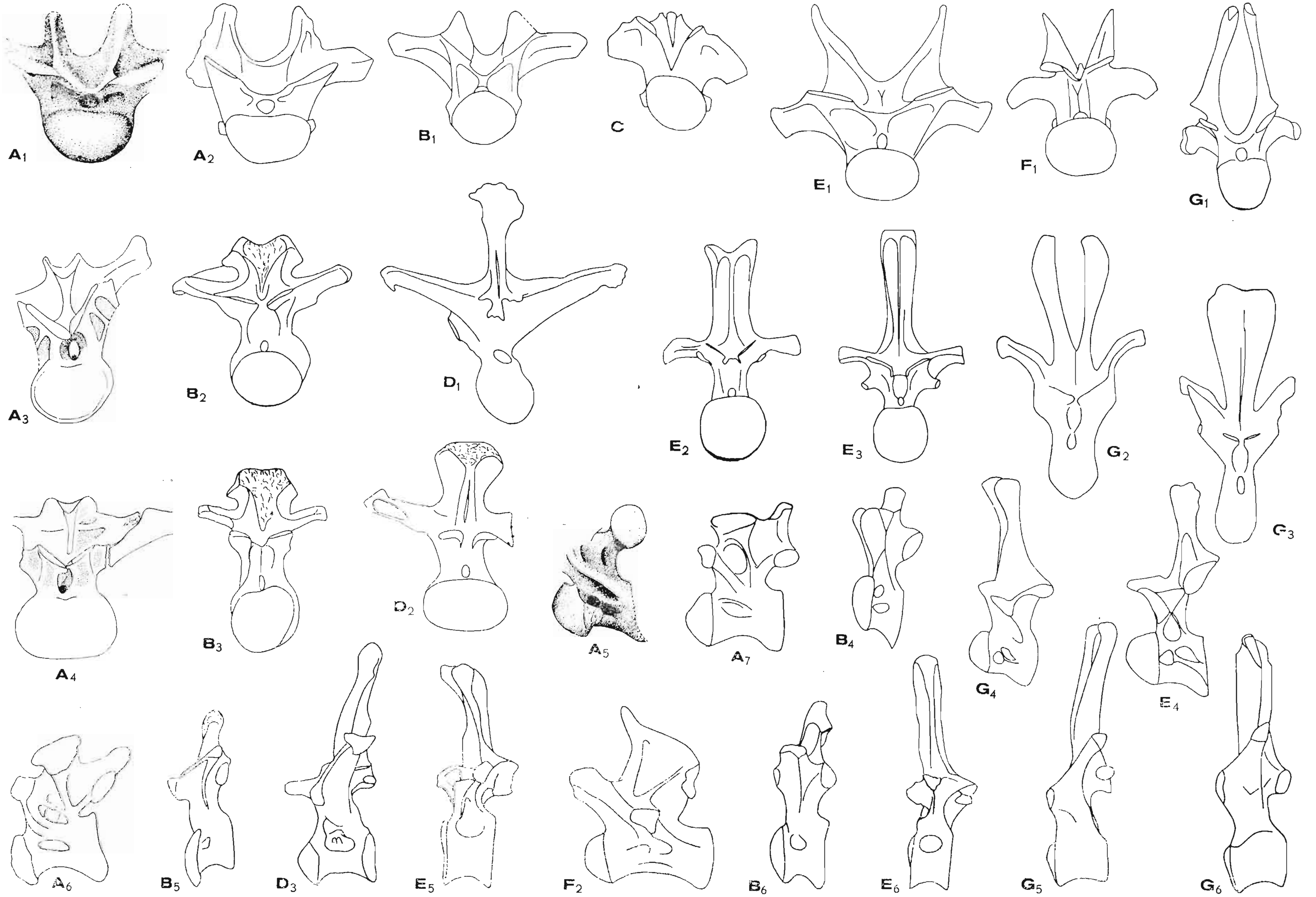

Fig. 3

Dorsal vertebrae in selected sauropods; *A — Opisthocoelicaudia skarzynskii* ZPAL MgD-I/48, *B — Camarasaurus supremus* after OSBORN & MOOK 1921, *C — Euhelopus zdanskyi* after WIMAN 1929, *D — Brachiosaurus brancai* after JANENSCH 1950, *E — Apatosaurus luisae* after GILMORE 1936, *F — Diplodocus carnegii* after HATCHER 1901, *G — Dicraeosaurus hansemanii* after JANENSCH 1929, A_1, B_1, C, E_1, F_1, G_1 — dorsal 1, anterior view, A_2 — dorsal 2 anterior view, A_3, B_2, E_2, G_2 — dorsal 6 anterior view, D_1 —dorsal 6 posterior view, A_4, B_3, D_2, E_3, G_3 — dorsal 10 anterior view, A_5, B_4, G_1, E_4, F_2 — dorsal 1, left side view A_6, B_5, D_3, E_5, G_5 — dorsal 6 left side view, A_7, B_6, E_6, G_6 — dorsal 10 left side view. *cp l* — centroparapophyseal lamina, *h l* — horizontal lamina, *id l* — infradiapophyseal lamina, *ip l* — infraparapophyseal lamina, *ipoz l* — infrapostzygapophyseal lamina, *iprz l* — infraprezygapophyseal lamina, *me* — metapophysis, *pa* — parapophysis, *pl* — pleurocoel, *poz* — postzygapophysis. Not to scale.

physyses protruding forwards from the arch beyond the anterior margin of the centrum and small postzygapophyses sitting at the spine base, on both sides of it. The zygapophyseal articulations are functional as far back as caudal 20, then zygapophyses become rudimentary. Articular facets of the prezygapophyses are rather small oval surfaces looking inward and slightly upward in the first caudals, then turning gradually into a vertical position, their longer diameters standing always in transverse plane. The postzygapophyses correspond in their shape, dimensions and position with the prezygapophyses; they look outwards.

Neural spines. The height of the arch with the spine included makes somewhat less than a half of the total height of the first caudal. The height of the spine, measured from the upper margin of the zygapophysis makes less than a quarter of it. In the first caudal the neural spine is very stout, its width exceeding its length. Its top is strongly roughened, especially laterally, the rugosities going down its lateral walls to about their middle, or even lower in caudals 3 to 9. The enormous triangular prespinal lamina broadened upwards and corresponding postspinal lamina are developed. The first one has two supraprezygapophyseal laminae at its sides, the second one two weak suprapostzygapophyseal laminae and postzygapophyses themselves. The spine decreases in size posteriorly, becoming merely a quadrangular thin plate with roughened borders at about caudal 10. From this point on it increases quickly in length (see table 3), decreasing at the same time in height. It represents nothing but a ridge from caudal 20 backwards.

Ligamentous and muscular traces in tail. The very strong supraspinal ligament was present in the anterior part of the tail, from the caudal 1 to about 8, as evidenced by the important width of the spines' tops. The interspinal ligaments running between the prespinal and postspinal laminae were very strong as well, decreasing posteriorly, beginning with the caudal 9. Both supraspinal and interspinal ligaments checked the movements in the sagittal plane, increasing the elasticity of the tail by the lateral movements at the same time. The stretch resistance of these ligaments could be also of importance (JANENSCH, 1929), in view of the considerable weight of caudals. These ligaments acted thus as ligamentum nuchae in the neck. The tuberosities situated at the lateral walls of the spines from 1 to 9, as well as tubers sitting upon the prezygapophyses must have served for the attachments of some epaxial muscles acting as lateral flexors of the tail. In the case of the lateral spinal tuberosities it could have been the longissimus dorsi, as JANENSCH (1929) stated for the crocodiles, or some parts of the transversospinalis system; the same muscles can be taken into account in the case of the tubers present at the prezygapophyses. The lateral and ventral surface of the sacro-caudals and caudals is completely smooth giving no evidence as to the insertions of the caudifemorales brevis and longus and the ilioischiocaudalis. The weakness of the transverse processes seem to

Table 4

Measurements (in cm) of chevrons of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

Vertebra number	Length	Vertebra number	Length
2	21	11	22
3	25	12	18
4	30	13	18
5	32	14	16
6	32	15	—
7	34	16	13
8	31	17	—
9	27	18	10
10	—	19	—

indicate the weak development of the caudifemoralis longus. But this is in disagreement with the strong development of the fourth trochanter on the femur's surface. The enormous width of the posterior part of the ilium indicates the strong development of the ilioischiocaudalis or its part.

Chevrons. Commencing with the last sacro-caudal the chevron bones are present as far back as the caudal 19. Back to the caudal 19 they were probably absent or quite rudimentary and left no traces in the present material. The general type of the chevrons in *Opisthocoelicaudia skarzynskii* is that of Camarasaurinae and Titanosaurinae. No one of them is bridged across with bone on the articular end, and no one has a double-branched distal end characteristic of *Diplodocus.* The heamal openings are deep, constituting about the third of the total length of the chevron in first caudals, increasing to half a total length in more posterior ones. Its volume changes evidently with the progress of the coossification of haemal arches, which increases from back to front and possibly also with the individual age to some extent. The distal ends of the haemal arches from 4 to about 16 are bilaterally flattened and fuse firmly with each other to form a laterally compressed spine. This spine is elongated in fore and aft direction, its posterior part being pointed, the anterior one rounded in caudals 4 to 8 or rounded both anteriorly and posteriorly in the more posterior caudals. Lying just proximally from the distal spine the fused margins of the haemal arches from 4 to about 16 are concave both anteriorly and posteriorly. In the first four caudals the distal ends of the chevrons are flattened dorso-ventrally and situated side by side between the proximal ends of the next ones, close to the centrum. They are weakly or not at all fused with each other. The last chevrons of the series, beginning with the 16th, are also weakly fused. The chevrons from 6 to about 15 are strongly coossified with the posterior borders of the centra, which produce a sort of processes for that purpose. Hence the position of the chevrons is very well known in the described species. It is almost parallel to the surfaces of the centra from 1 to 5, then more oblique from 6 to 11, the obliquity decreasing again from 12 to 16, the last chevrons lying subparallelly to the centra.

THORACIC RIBS
(pl. 10)

Eleven pairs of the thoracic ribs are supposed to exist in *Opisthocoelicaudia skarzynskii* corresponding to the number of the thoracic vertebra. Dorsals 3 through 8 have both left and right ribs. Apart from them only two right ribs belonging to the dorsal 9 and 2 (?) are satisfactorily well preserved. The ribs of the dorsal 11 were probably rudimentary and coalesced with the vertebra. Only the right capitulum with its peduncle is preserved from the tenth pair of ribs. It is coossified with the parapophyses suggesting that this pair of ribs also lost its independence. But the diapophysis of the left side presents a well formed articular surface for the rib tubercle indicating the opposite. The length of the ribs does nor vary very much within the rib series from 4 to 9, but it decreases forwards and backwards from it. Rib 3 is slightly shorter than the more posterior ones. The abrupt shortening could have occured when passing to rib 2, which is, however, not complete in the present specimen. The ribs present a striking differentiation as regards the transverse section of the shaft especially in their distal parts. Ribs 3 and 4 are decidedly flattened bilaterally. Their distal ends are expended antero-posteriorly and fit the rib surfaces of the sternal plates. They were probably connected with these bones by means of the fairly long cartilaginous ribs which have left the distinct traces on their distal surfaces as well as on the sternal plates. Rib 5 and the distal part of 6 are flattened likewise but no distinct distal articular surfaces are to be seen on them. Their distal ends seem to be much weaker and therefore rather badly preserved, but it is possible that they also were articularly connected with the cartilaginous parts of the sternum. Ribs from 6 to 9 are suboval or even rounded in transverse section. Whether they were connected with the sternum is unknown, but they are reconstructed as such on text-fig. 4. This reconstruction is based on the structure of the sternum in crocodiles (GUIBÉ, 1970a, fig. 44 and 55). If the ribs 6 and 9 were joined to the sternum, it should have been much thicker posteriorly than anteriorly. The ossified sternal ribs known in *Apatosaurus excelsus* YPM 1980 (MARSH 1896, figs 12, 13) correspond probably to those numbered 4, 5 and 6 of *Opisthocoelicaudia*. As shown by the volume of the thorax (text-fig. 5) length of the cartilaginous sternal ribs 4, 5, 6 should have been relatively larger than it was in *Apatosaurus excelsus*. There is no evidence of the coossification of the sternal ends of these ribs in *Opisthocoelicaudia*, as shown by the clearly determined articular surfaces present on the sternal plates (see p. 21). Neither is there any evidence of the ossification of the sternal ribs, in spite of a rather old age of the specimen ZPAL MgD/I-48. The articular surfaces of the capitulum and tuberculum are fairly large in the anterior ribs decreasing posteriorly. The peduncle of the capitulum is shorter and less protrudent in the anterior ribs (2 and 3) and the proximal parts of those ribs are lager as a whole. Posteriorly the capitular peduncle gets longer and the whole proximal part becomes more slender. Apart from this there is a tendency for the rib capitulum to be situated in the plane perpendicular to the long axis of the tubercule surface. This tendency appearing about the dorsal 4 increases posteriorly.

Table 5

Measurements (in cm) of right ribs of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

Rib number	Length from tubercule over curve	Length of peduncle of tubercule	Diameters about middle of shaft
2	105 (preserved part)	—	4.8/5.3
3	133	10	3/9
4	153	10	3.5/10.5
5	172	10	4.5/8.5
6	about 170	—	5/7
8	150	—	4/5.5
9	140	—	4/6.5

STERNUM
(pl. 11, fig. 1, text-fig. 4)

The sternum is represented by paired, elongated, sternal bones, which are among the largest sternals known is Sauropoda, taking into account the absolute size of the animal. The

Table 6

Measurements (in cm) of sternal plates of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

	left	right
length	(damage) 68	76
maximum breadth (in projection)	48	50

relation of the length of the sternal plates to that of the humerus is approximately the same as in *Alamosaurus sanjuanensis.* The better preserved right sternal plate is semilunar in shape, its external border being distinctly concave, all the remaining borders making a strongly convex common curve. The external border is rather thin (15 mm across), sharp and even, the opposite one is covered with rugosities almost all over its length. The antero-external end of the sternal plate forms the most massive part of it, having a greatest thickeness of about 93 mm. This end of the sternal plate was probably joined with the coracoid by means of cartilage, which may

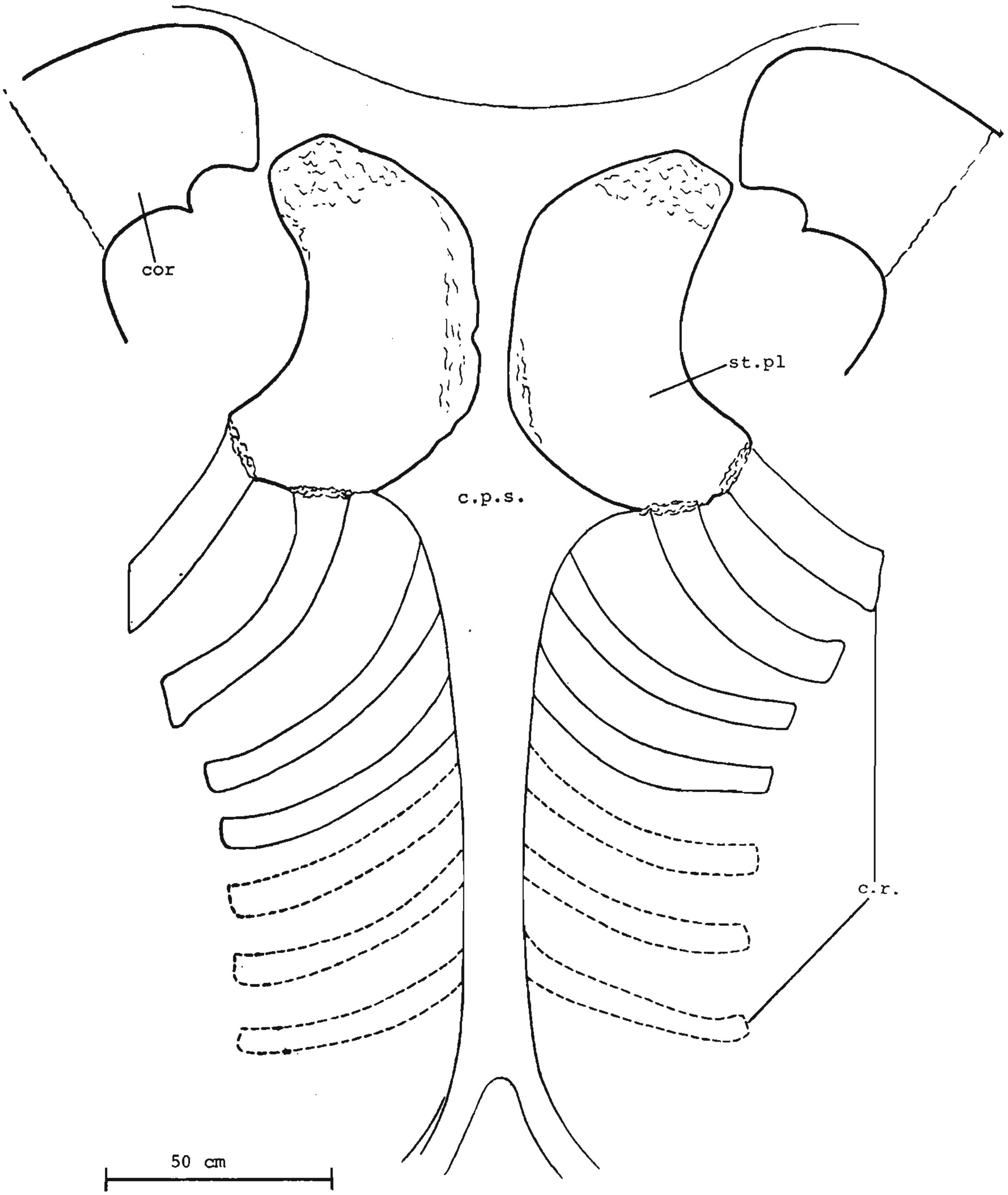

Fig. 4
Reconstruction of the sternum in *Opisthocoelicaudia skarzynskii* gen. n., sp. n.; *st.pl.* — sternal plate, *c.p.s.* — cartilagineous part of the sternum *c.r.* — cartilagineous ribs, *cor* — coracoid.

be judged only from the supposed life position of the sternal plates, because it does not fit to the coracoid. From this end on, the border of the sternal plate becomes gradually thinner towards the sagittal body axis, attaining the values: 51 mm in the middle of the anterior border and 35 mm in the anteromedial region. The extreme medial border is still thinner being 30 mm across about the middle of its length and 16 mm in the postero-medial region. On the posterior part of the border two oval, strongly roughened surfaces occur, which are designed for the attachment of the cartilaginous sternal ribs. They are about 40 mm high and extend over the length of 156 mm (the medial one) and 140 mm (the external one). The morphology of the inner borders of the sternal plates indicates their medial fusion by means of cartilage. Although the medial borders of the sternal plates show a certain asymmetry, the overlapping of them is rather improbable and the differences are rather caused by the post mortem deformation. Both surfaces are almost flat the visceral surface being somewhat concave, the external one slightly convex. In the anterior part of the visceral surface, in about one sixth of its length, strong ridges and rugosities are developed which served probably for a thick cartilage placed dorsally. Extending along the external surface from the thick truncated corner of the sternal plate obliquely a distinct blunt ridge disappears at the postero-medial border. The huge pectoral muscles which should have been inserted on the outer surface of the sternalia have not left any distinct traces.

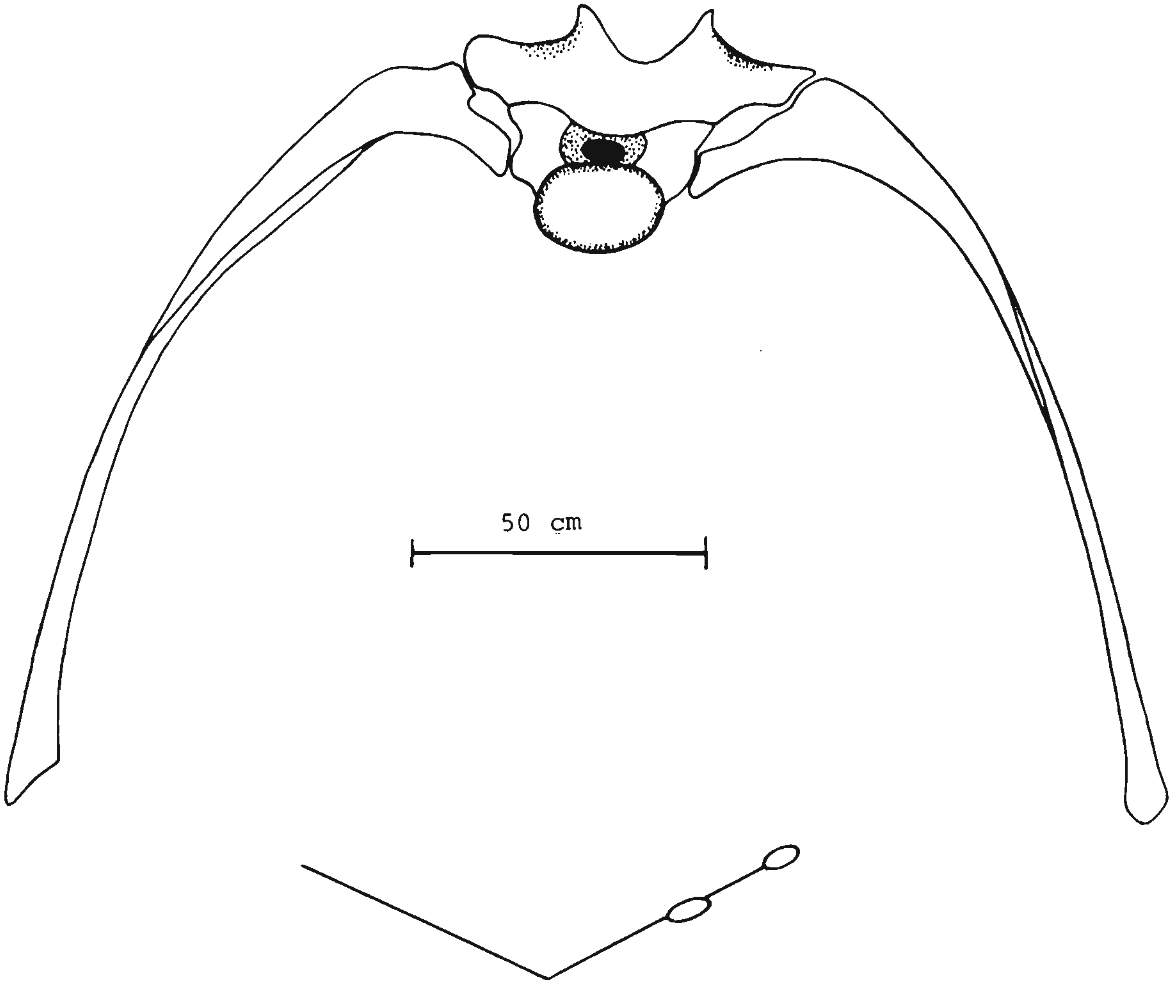

Fig. 5

Opisthocoelicaudia skarzynskii gen.n., sp.n. Cross section through the anterior thoracic area, at the level of the dorsal 4. The position of the sternal plates marked by straight lines.

PECTORAL GIRDLE

(pl. 7, fig. 1, text-fig. 6)

The pectoral girdle is represented by the paired scapulae and coracoids. No traces of the claviculae or interclavicula have been stated. The scapula and coracoid are firmly coossified so that their line of coalescence is difficult to recognize, except in the neighbourhood of the glenoid where it is discernible. Both surfaces of the sutural region of the girdle are distinctly convex. This is more strongly pronounced at the inner side of the girdle, the sutural convexity of the outer side being limited to the glenoid's vicinity only. The scapulocoracoid is considerably curved medially with two regions displaying a more pronounced medial bent: the first one situated at the base of the scapular blade, the second one at the coracoid, just below the level of the glenoid cavity. Two muscles arose probably from the outer surfaces of those two regions of bent, the deltoideus from the scapula, the biceps brachii from the coracoid (see text-fig. 6*C*). The scapular blade is rather long and slender. It forms about 60% of the whole girdle's length, its minimum breadth, measured about the middle of its length, making up 30% of the maximum breadth of the girdle. The distal end is weakly expanded; the proximal part of the scapula represents the most expanded region of the girdle (see table 7). The axis of the last named region (the axis of greatest breadth of OSBORN & MOOK, 1921), emphasised by the convexity, running from the posterior border of the glenoid cavity to the acromion, (Querrücke of JANENSCH, 1961) makes an angle of about 57° with the long axis of the scapular blade[1].

Table 7

Measurements (in cm) of pectoral girdle of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

	ZPAL MgD-I/48		ZPAL MgD-I/25c
	left	right	right
Combined scapula and coracoid:			
greatest lehgth over curve	170	168	170
greatest length in projection	137	151 (flattening)	—
thickness on the suture line near glenoid	20	22	20
Scapula:			
length (glenoid fossa — distal end)	114	118	about 112
greatest breadth	(damage) 54	70	59
least breadth	22	25	23
distal breadth	30	33	29
Coracoid:			
greatest length	48	51	42
greatest breadth (distally)	—	51	50
Glenoid:			
greatest expanse	33	41	—

The distal end of the scapula is rounded, which may be partly caused by a damage. Its upper border is 5 cm thick and roughened for the attachment of the suprascapular cartilage. It is very flat near the upper margin but gets thicker and crescent-shaped in transverse section (externally convex) proximally. The total thickness of the scapula at the level of the deltoideus origin equals to 15 cm; the thickness of the bone about the middle of its breadth at the same level is about 8 cm. Both margins of the scapular blade are narrow. The posterior one is even sharp but it broadens towards the glenoid forming a triangular surface turned backwards and

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[1] This angle is commonly regarded as a feature of a certain taxonomic value in Sauropoda. But it is probably not the best one for showing the real differences in the position of the scapular blade in relation to the proximal part of the girdle between the different genera of sauropods. The angle between the long axis of the glenoid cavity and that of the scapular blade would probably be better for that purpose (see p. 46).

medially above it. In the external part of this surface there is a prominent supraglenoid buttress used by the scapular head of the triceps brachii as the attachment point. The middle third of the posterior margin bears tuberosites serving possibly for the origin of the serratus superficialis. Whether this muscle could extend further up this margin is uncertain because of the bad state of preservation of these parts of the margins of both scapulae. The similar tuberosities occur at the anterior border of the scapula as well, extending from the middle of its length up to its top. These scars could be connected with the attachments of the levator scapulae (the part of the collothoraciscapularis of lizards) or with the trapezius or with both. The proximal part of the scapulocoracoid is rather irregular in outline. Its anterior convex margin, formed mainly by the scapula, produces a prominent acromion, the opposite border forms the glenoid cavity. This part of the girdle is very well separated from the scapular blade by means of the transverse convexity mentioned above, as well as from the distal part of the coracoid, the line of bend of the coracoid together with the biceps convexity forming the boundary. The outer surface of this part of the scapulocoracoid forms two muscular fields. The first one concave, lying within the scapula served probably as a place of origin of the scapulohumeralis anterior, the second one

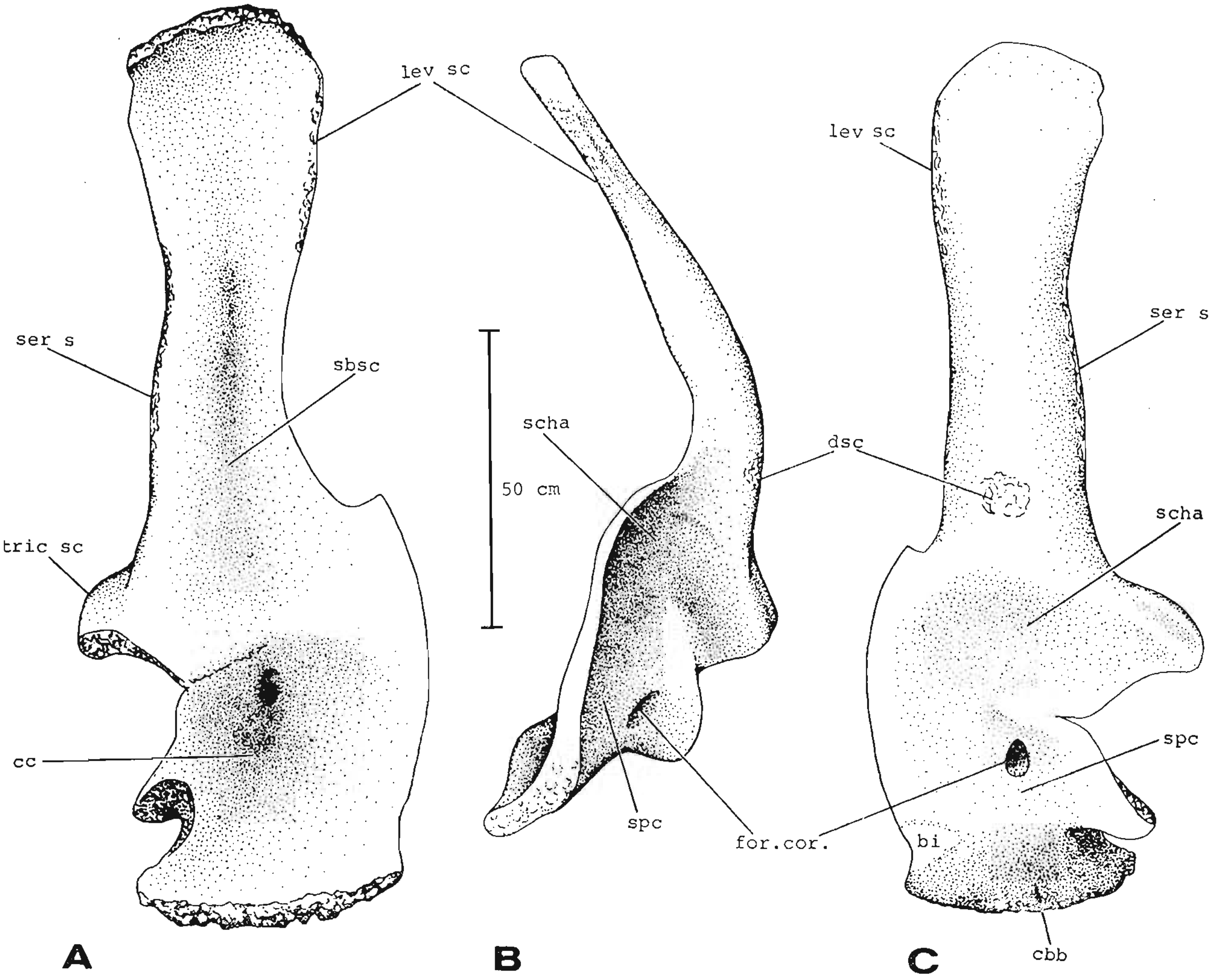

Fig. 6
Opisthocoelicaudia skarzynskii gen.n., sp.n. Left scapula and coracoid. *A* — medial view, *B* — antero-dorsal view, *C* — lateral view, *bi* — biceps, *cbb* — coracobrachialis brevis, *cc* — costocoracoideus, *dsc* — scapular deltoid, *for. cor.* — foramen coracoideum, *lev sc* — levator scapulae, *sbsc* — subcoracoscapularis, *scha* — scapulohumeralis anterior *ser s* — serratus superficialis *spc* — supracoracoideus, *tric sc* — scapular head of triceps.

almost flat, situated on the opposite side of the suture could be covered by the origin of the supracoracoideus, running to the lateral tubercule of the humerus (see text-fig. 6*C*). This part of the coracoid is perforated by a large elliptical foramen that passes diagonally backward through the bone, emerging on the inner side close to the coraco-scapular suture. The distal, medially bent part of the coracoid makes probably a place of origin for the coracobrachialis on its outer surface, as judged from the comparison with the lizard (ROMER 1956). This part of the coracoid displays a subquadrangular outline with rounded corners protruding forwards and backwards so as to produce two concave borders proximally to them (see text-fig. 6). The most distal border of the coracoid is slightly convex in the longitudinal direction and rounded in the transversal section. It is 5 cm thick and rugosely roughened, probably for the union with the cartilaginous part of the girdle. No traces of the direct union between the coracoids and sternal plates have been detected. The coracoid and scapula contribute about equally to the formation of the glenoid fossa with a certain preponderance of the scapula in the outer part of the glenoid. Two parts, joined by a straight suture are almost flat and form an angle of about 90° with each other. The surface is slightly rugose and was probably covered with cartilage. The thickness of the bone increases quickly while passing from the anterior (acromial) border of the scapulocoracoid (4 cm thick) towards the glenoid (19 cm thick). On the internal side the scapula is deeply excavated in its proximal two thirds by a muscle fossa of great extent, triangular in outline used without any doubt by the subcoracoscapularis as a place of origin. The inner surface of the coracoid is also concave. Maybe the costocoracoideus was present in sauropods as it is in crocodiles (GUIBÉ, 1970). It would have had its origin at this surface of the coracoid then.

FORE LIMB

Humerus. (pl. 8, fig. 3, pl. 9, fig. 3*a-d*, text-fig. 7) The humerus is typical of Sauropoda in having a long shaft flattened in antero-posterior direction with strongly expanded ends. It must be emphasized however, that the proximal end is broadened mainly internally, so that the outer side of the bone is rather straight. As in other sauropods there is only a small degree of torsion and rather feeble development of the epicondyles. The articular surfaces of the humerus are fairly well formed although the distal one bears some traces left by cartilage, especially in the left bone. The rounded head of the humerus measuring about 20 cm in diameter is distinctly convex antero-posteriorly and inclined posteriorly at an angle of about 55° to the long axis of the shaft, while the distal articular surface for the radius rises anteriorly making an angle of about 50° with the same. This does not bear very much on the distal end of the shaft which is only weakly concave anteriorly and respectively weakly convex posteriorly. Both angles determine the position of the humerus in relation to the adjoining bones (see p. 45). The humeral head is not distinctly separated from the muscular parts of the proximal extremity which are situated at the same level as the head. The shifting of the processus medialis and processus lateralis humeri upwards in Archosauria is an obvious consequence of the backwards turn of the elbow joint together with the more erect position of the humerus. The ridged surface of the processus medialis is subdivided into two parts probably occupied by two different muscles. The upper, wider part, facing upwards made the insertion place for the subcoracoscapularis, the lower one, facing medially could have served for the scapulohumeralis posterior. The rounded lateral muscular process of the humerus separated from the head by a slight contraction made the insertion place for the supracoracoideus. The posterior surface of the proximal half of the humerus is subdivided 'by the convexity buttressing the head and running down to the external part of the distal extremity. Two concavities formed this way were, covered by the origins of two heads of the triceps, the medial and the lateral one, caput humerale mediale and caput humerale laterale musculi anconei (FÜRBRINGER, 1875). The medial head ran along the shaft down to the entepicondyle, then went on the elbow joint capsule after having been fused with the remaining heads. Running down the medial concavity of the posterior surface of the humerus (text-fig. 7 *D*) a slender ridge may represent a lateral limit of the medial head of the triceps. No other scars of the humeral heads of the triceps are to be seen on the surface of the bone, as can be expected from the muscles characterized by large origins. Therefore the course of these muscles is reconstructed basing mainly on the comparative data concerning lizards, crocodiles (ROMER 1956, FÜRBRINGER, 1875) and mammals; the last one because of the presence of several evidently mammal-like characters in sauropod limbs. The lateral head of the triceps covered the postero-lateral part of the described surface, the insertion of the latissimus dorsi included. Proximally its origin should have attained the basis of the processus lateralis humeri, and externally touched the ridge bracing the lateral muscular tuberosity. The space between two heads of the triceps was filled superficially by its scapular head and, more deeply, by the posterior head of the same muscle (caput humerale posticum m. anconei, of crocodiles; FÜRBRINGER 1875) if it existed. The distinct muscular scars for the scapular deltoid and scapulohumeralis anterior (see text-fig. 7 *C*, *D*) are situated on the postero-lateral side of the humerus, within the rough surface of about 15 cm × 18 cm. The most distal part of this surface was probably occupied by the scapulohumeralis anterior. This muscle is supposed to have been shifted laterally in Sauropoda as compared with Lacertilia, owing to the backward turn of the elbow. Its insertion is similar in this respect to the insertion of the teres minor in mammals, which is in whole agreement with the homology of those two muscles supposed by ROMER (1962). The oval (approximately 7 cm × 5 cm) rough convexity situated distally and somewhat medially from the scar of the supposed scapulohumeralis anterior represents probably the insertion

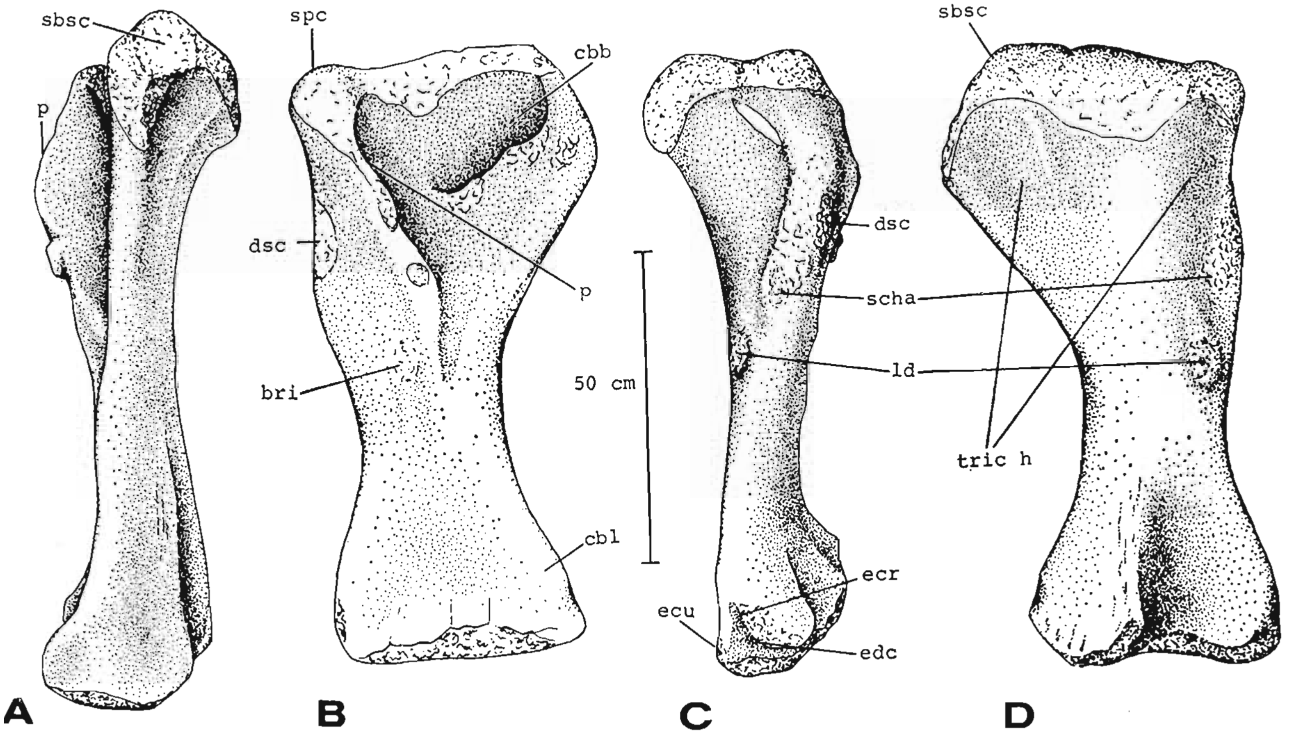

Fig. 7
Opisthocoelicaudia skarzynskii gen. n., sp. n. Right humerus, *A* medial view, *B* anterior view, *C* lateral view, *D* posterior view, *bri* — brachialis inferior, *cbb* — coracobrachialis brevis, *cbl* — coracobrachialis longus, *dsc* — scapular deltoid *ecr* — extensor carpi radialis, *ecu* — extensor carpi ulnaris, *edc* — extensor digitalis communis, *ld* — latissimus dorsi, *p* — pectoralis, *sbsc* — subcoracoscapularis, *scha* — scapulohumeralis anterior, *spc* — supracoracoideus, *trich* — humeric heads of triceps.

place of the latissimus dorsi (text-fig. 7*C*, *D*). The strongly roughened deltoid surface passing from the lateral to the anterior side of the bone is not connected by any ridge with the deltopectoral crest. This forms in fact the insertion place for the pectoralis only and therefore will be called here pectoral crest. This crest runs from the processus lateralis obliquely down the proximal one third of the shaft, strongly overhanging its anterior surface. The margin of the pectoral crest is roughened for the muscle attachment, the scar dividing into two distinct parts (see text-fig. 7*A*, *B*). The signification of this subdivision is obscure, the upper part constituting certainly the insertion place of the pectoralis. Medially to the pectoral crest there is an oblique but almost horizontal irregular ridge (text-fig. 7*B*) crossing the concavity of the proximal end of the bone. The joint capsule should have inserted on it together with the short head of the coracobrachialis, which used also the rugosities adjoining the ridge from below. It is highly possible that the long head of the coracobrachialis existed in Sauropoda, although it is absent in crocodiles (FÜRBRINGER 1875), where the fascicles of the brachialis inferior touch the medial head of the triceps. Such a contiguity is improbable in sauropods owing to the widening of the shaft, the brachialis inferior running from below and laterally of the pectoral crest obliquely to the radius, in a distance from the medial border of the humerus. In addition it would have been disadvantageous for the triceps to pass on the well delimited anterior surface of the humerus. The space formed thus between the two last named muscles was probably filled by a muscle, possibly the long head of the coracobrachialis, which could have inserted in the ridged antero-lateral corner of the distal extremity of the humerus, as well as on the surface of the elbow joint capsule. The lateral epicondyle bears two crests converging proximally, the posterior of them making a limit of the joint capsule, together with the whole border of the fairly well formed fossa olecranii. This crest passes distally into the rugosity for the m. extensor carpi ulnaris running to the metacarpale V. The anterior crest made certainly the place of the origin for the extensor carpi radialis, its distal part and the rugosities above it serving probably for the extensor digitorum communis. The surface of the medial epicondyle is completly deprived of muscle scars. The presumed arrangement of the flexors and ligaments attaching here is reconstructed (text-fig. 9*A*) basing on the comparison with the data of ROMER (1956, 1962) and FÜRBRINGER (1875) and on the author's own investigations on the sectioned legvan. It is indicated as well by the arrangment of their insertions on the antebrachial bones (see below). The shape of the distal articular surface of the humerus indicates without any doubt the position of the ulna behind the radius. No traces of the transverse division of this surface into the radial and ulnar condyle can be seen, the limit between the articular surfaces for the radius and ulna running rather parallel to the longer diameter of the distal extremity. The anterior part (adjoining the dorsal surface of the bone) constitute the negative of the proximal articular surface of the radius, the posterior one fitting to the articular surface of the ulna. The medial concavity of the articular surface of the radius fits into the medial convexity of the humerus; the lateral parts of joint surfaces are deflexed in the opposite way. The articular surface for the ulna lifted posteriorly makes an angle with the radial one. It is convex in its medial and posterior parts and almost flat in the lateral part. The whole distal articular surface of the humerus is somewhat narrower than the distal extremity of this bone, its extreme parts constituting probably the distal parts of the epicondyles. The difference between the width of the distal part of the

Table 8

Measurements (in cm) of humerus of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

	left	right
Greatest length	100	100
Greatest breadth of proximal end	52	56
Greatest breadth of distal end	35	43
Least breadth of shaft	20	24

humerus and that of the proximal parts of the antebrachial bones, when articulated with each other, is less pronounced than in many other Sauropoda.

Radius (pl. 7, fig. 4, 5, pl. 11, fig. 3, text-fig. 8). The radius is a pillar like bilaterally symmetrical bone, strongly flattened antero-posteriorly. Both ends are strongly expanded transversely, the proximal breadth making about 50% of the bone length, the distal one about 40% of the same, whereas it is only 20% in the most constricted region of the bone. The antero-posterior diameter is less variable. It constitutes 23% of the maximum length of the bone at its proximal end, about 28% of it at the distal end and about 20% about the middle of the shaft. The anterior surface is almost flat becoming somewhat concave at the extremities. The proximal extremity is subtriangular in transverse section, the base of the triangle facing anteriorly and its top posteriorly. The posterior surface of the proximal extremity is accordingly convex. The convexity which articulates with the concave anterior surface of the ulna goes down into a crest extending downwards and outwards. This consitutes a posterior border of the lateral surface in the distal 2/3 of the bone. The short interosseous muscle of a rather unclear holmology probably inserted on this crest, as may be judged from its situation just opposite to the longitudinal scar of the ulna (see text-fig. 8*A*, *C ios*). Extending from about the proximal one third of the postero-medial border of the bone distally and slightly laterally over the posterior surface of the bone there is another crest (text-fig. 8*C pt*). It is supposed to be the insertion place of the pronator teres. The latter is reconstructed here as a muscle fused proximally with the flexor carpi radialis, based on the situation in lizards figured by ROMER 1956. The rugosities serving probably as the insertion place of the last named muscle are to be seen on the medial side of the distal end of the bone (text-fig. 8*C fcr*). The joined tendons of the biceps brachii and brachialis inferior inserted probably only on the radius, the ulnar insertion being lost as the effect of the backwards turn of the elbow joint and of the consecutive changes of the relation between the pectoral girdle and antebrachial bones. Such an insertion is reminiscent of the situation known in mammals but not identical with it, because the scar is situated much more medially than it is in mammals and is much less pronounced. It is represented by several rough crests extending vertically on the medial side of the proximal end (text-fig. 8*B bi+bri*) and probably by the shallow concavity situated on the anterior surface of the bone nearby. The proximal articular surface fully corresponds to the distal surface of the humerus. Its posterior part is convex, the anterior one variable; it is convex in the lateral one fifth of its breadth, then concave and convex again in its medial two fifth. This surface is well formed, no traces of the cartilaginous parts being left. The distal articular surface is pear-shaped, its narrower part turning laterally. It is slightly convex as a whole but almost flat in its medial part. This part, making

Table 9

Measurements (in cm) of radius and ulna of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

	left	right
Radius		
greatest length	62.5	63.7
breadth of proximal end	26.0	29.2
breadth of distal end	25.0	24.5
fore and aft diameter at distal end	17.8	16.4
breadth of shaft about midlength	11.6	12.4
fore and aft diameter about middle of the shaft	9.8	8.3
fore and aft diameter at proximal end	17.8	15.0
Ulna		
greatest length	78.3	67.7
articular length	61.0	60.7
greatest breadth at proximal end	34.4	34.0
fore and aft diameter at proximal end	29.6	29.6
greatest breadth at distal end	23.7	24.5

about 2/3 of the distal breadth of the bone, fits more or less to the proximal surface of the metacarpal I. These two bones were separated by a cartilage, which has left distinct tracse over this part of the articular surface of the radius and hence was the integral part of it. The rest of this surface is deprived of such traces, but it was also separated from the metacarpals by the cartilaginous carpals, as evidenced by the mutual relations of the bones when articulated with each other. The measurements and some details of this description refer to the right radius which is perfectly preserved, whereas the left one is strongly deformed.

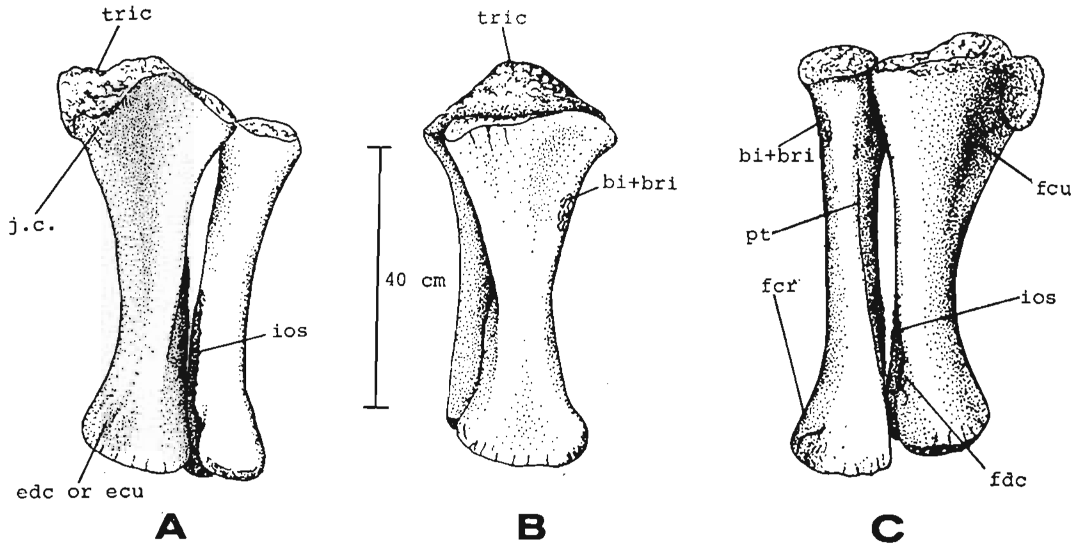

Fig. 8

Opisthocoelicaudia skarzynskii gen.n., sp.n. Right ulna and radius, *A* — lateral view, *B* — anterior view, *C* — medial, view. *bi* — biceps, *bri* — brachialis inferior, *ecu* — extensor carpi ulnaris, *edc* — extensor digitorum communis, *fcr* — flexor carpi radialis, *fcu* — flexor carpi ulnaris, *fdc* — flexor digitorum communis, *ios* — interosseus, *j.c.* — joint capsule, *pt* — pronator teres, *tric* — triceps.

Ulna (pl. 8, fig. 5, pl. 9, fig. 1, pl. 11, fig. 3, text-fig. 8). In its proximal part the ulna is much stouter than the radius. It gets more slender distally. Its proximal breadth (i.e. mediolateral dimension) makes about 56% of its articular length. The proximal antero-posterior dimension is about 49% of the same. At the distal end of the ulna its breadth and antero-posterior diameter constitute 43% and 34% of this length correspondingly. The transverse section of the bone is presistently triangular-shaped, but more rounded at the distal end. The proximal articular surface consists of the two parts separated from each other by the convex olecranon. The medial part is concave. It fits to the posterior part of the medial condyle of the humerus. The lateral one is convex and does not fit well to the lateral condyle. Both surfaces bear traces left by cartilage but the cartilaginous pad must have been thicker on the lateral side. The low but distinct olecranon was also supplemented by a cartilage. The common tendon of all the heads of the triceps brachii inserted mainly on the posterior wall of the olecranon. It extended also over its roughened lateral wall as well as over its medial wall fusing with the joint capsule of the elbow articulation. The cartilaginous part of the olecranon was situated within the joint capsule. The anterior surface of the ulna, adjoining the radius bears the traces of the following mucles. The short fascicles of the interosseus muscle connecting the antebrachial bones inserted on the longitudinal tuberosity extending over the whole length of the anterior surface of the ulna, the proximal end excluded (text-fig. 8*A*, *C*). It is situated opposite to the corresponding scar of the radius. The origin of the flexor palmaris profundus is situated in the distal 1/4 of the length of the bone. This is a strong tuberosity extending downwards and medially (text-fig. 8*C fdc*), representing probably the origin of the flexor digitorum communis or of a part of it, as suggested by ROMER'S (1956) figures of a sectioned lizard. The concavity situated on the medial wall of the proximal half of the bone was probably filled up by the additional origin of the flexor carpi ulnaris extending from the medial epicondyle of the humerus to the fifth metacarpal (see text-fig. 9*A*) as in lizards (ROMER, 1956). The distal articular surface of the ulna is similar to the distal surface of the radius in being pear-shaped and narrowing laterally (pl. 11, fig. 3). It is slightly convex as a whole, but its medial part is flat and bears traces left by cartilage, which probably covered the whole medial part of the proximal end of the antebrachium.

Manus. The carpal elements have not been preserved in any of the anterior limbs of the described specimen (ZPAL MgD-I/48). Their presence is suggested by the shape of the space present between the antebrachial bones and metacarpals, when the bones are properly articulated with each other, but their number and homology is difficult to determine. Such a disk-shaped space is to be seen between the external parts of the distal surfaces of the radius and ulna and metacarpals I, II, III. It was presumably filled up by a cartilaginous element, independent from the antebrachium and metacarpal bones, representing the unossified carpal (or carpals). The cartilages were also present between the medial parts of the radius and ulna and the medial parts of metacarpals I and V, but these were rather cartilaginous prolongations of the bones, and not independent elements.

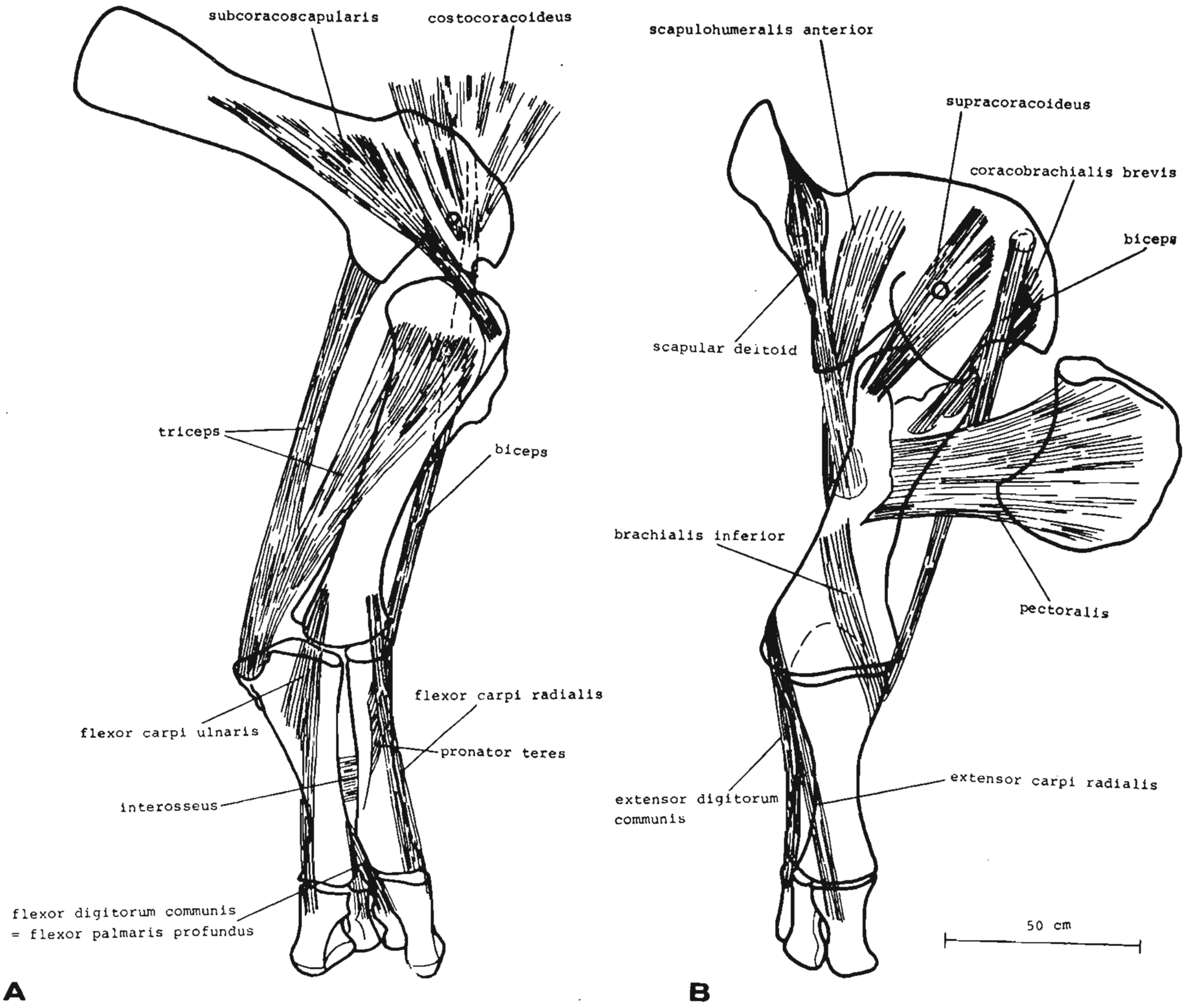

Fig. 9

Opisthocoelicaudia skarzynskii gen.n., sp.n. Reconstruction of the musculature of the pectoral girdle and limb. *A* — medial view, *B* — anterior view.

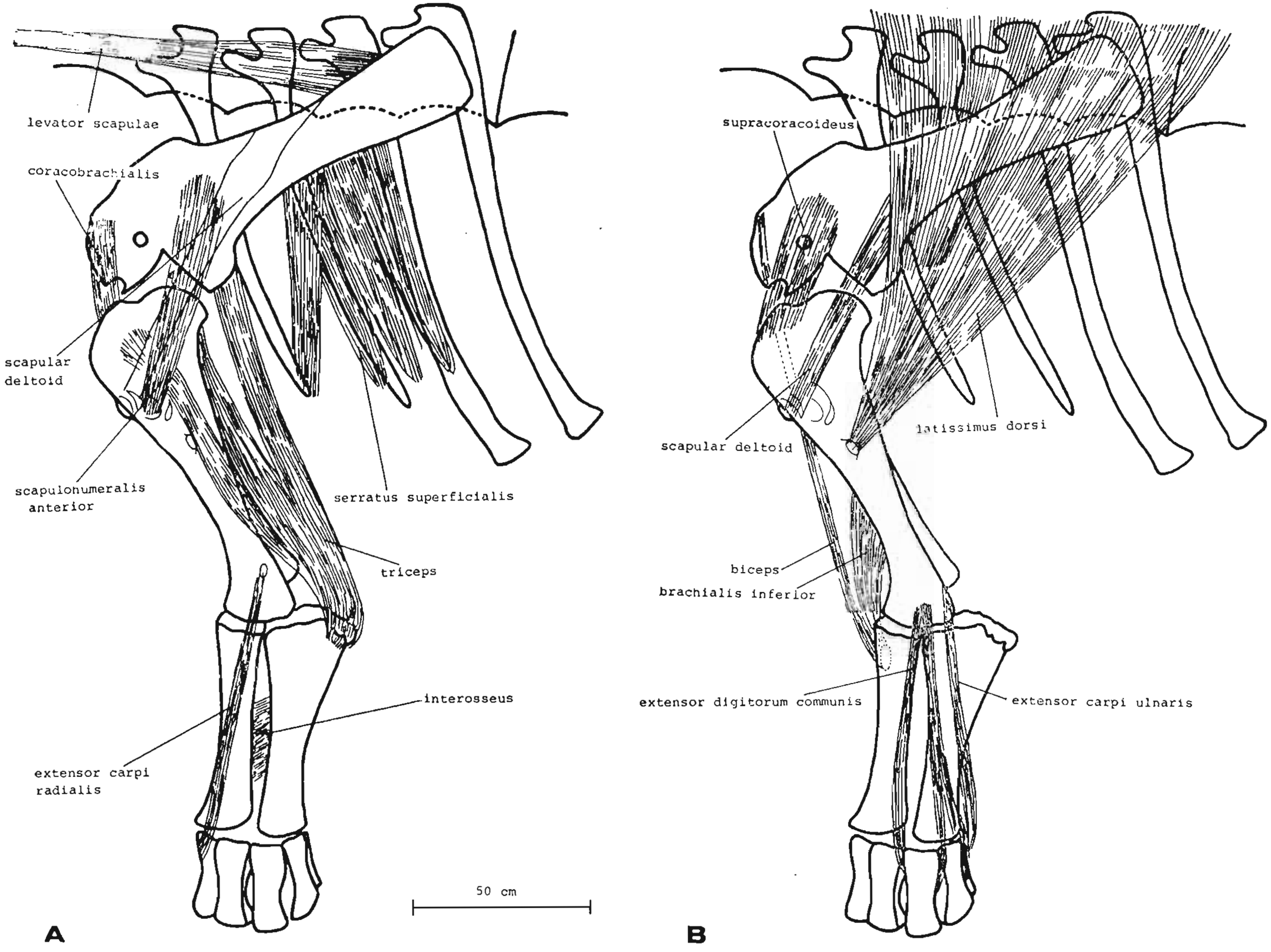

Fig. 10
Opisthocoelicaudia skarzynskii gen.n., sp.n. Reconstruction of the musculature of the pectoral girdle and limb. *A, B* — lateral view, different muscle sheets.

Metacarpals (pl. 7, fig. 3, pl. 11, fig. 2) fit closely to each other by the walls of their proximal ends. When articulated they are situated almost vertically. The metacarpals I—III are almost parallel to each other, whereas metacarpals IV and V diverge distally, being slightly opposed in relation to the medial ones. The metacarpal I (pl. 7, fig. 3, pl. 11, fig. 2*ab*) is the stoutest and the longest of the series. Its proximal articular surface is almost flat. It fits to the medial part of the articular surface of the radius and is slightly rugose for cartilage. The metacarpals II and III are almost of the same length as metacarpal I but slightly shorter. They are much more slender than the metacarpal I. Their proximal surfaces are correspondingly smaller than that of metacarpal I. The proximal articular surface of the metacarpal II makes a horizontal prolongation of that of the metacarpal I. The proximal surface of the metacarpal III is situated slightly lower than those of the more medial ones. This causes the increase of the space between the metacarpus and radius and ulna designed for the carpals. The metacarpals I and II buttress the radius; metacarpal III is situated opposite to the interosseous space of the antebrachial bones, contributing to the support of both the radius and ulna by means of a cartilaginous carpal. The metacarpal IV is the shortest and the narrowest of all. Its proximal articular surface is the smallest one. It is wedge-shaped and slightly sloping down medially. The metacarpal V is intermediate between the metacarpal III and IV as regards the length, but it is stouter than all but metacarpal I. Its proximal articular surface, which is only slightly smaller than that of the metacarpal I fits more or less to the enlarged medial part of the distal articular surface of the ulna. These bones were connected presumably with each other by means of a thin cartilage. All metacarpals are subtriangular or wedge-shaped in transverse section in their proximal parts. The basis of the triangles are directed towards the anterior side of the manus and their tops to the posterior one. This is caused by the presence of the prominences of the bone extending along the shaft on its posterior side and strongly protruding. They were probably connected with the flexor palmaris profundus and the plantar aponeurosis and probably also with the interossei of the posterior side of the manus or tendons substituting them. In the articulated metacarpus the posterior crests or tuberosities are turned to each other. This turn is very pronounced in metacarpal I, decreasing laterally. The crest is directed outwards in metacarpals I—III. In metacarpal IV it is directed to the long axis of the manus, whereas turned medially in metacarpal V. The transverse sections of the metacarpals become more quadrangular in their distal halves. The distal surfaces are quadrangular, slightly convex and roughened for cartilage. In the life position they are directed straight downwards.

Table 10

Measurements (in cm) of metacarpals of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

	Mtc I		Mtc II		Mtc III		Mtc IV	Mtc V
	right	left	right	left	right	left	left	left
greatest length	29.5	29	28	29	—	27.5	23.5	24.5
proximal breadth	19.5	19	11.5	11.5	13	12.5	8 ant.	13.5
distal breadth	13.5	12.5	13	13.5	12	12.5	12	13
least breadth	10	10	7	6	6	6.5	6	8
proximal fore and aft dimension	14	13.5	12	11.5	11 med.	11	13	11
distal fore and aft dimension	9.5	9	9	9	8.5	9.5	8.5	9
east fore and aft dimension	7	7	7	6.5	6	6	7	6.5

ant. — anteriorly
med. — medially

No traces of the phalanges have been left, except for a small rounded body fused with the distal surface of the metacarpal IV, which is probably a rudimentary phalanx. Some muscle scars can be discerned on the dorsal surface of the metacarpals. Extending from the outer part of the proximal end of the metacarpal I towards the middle end of its anterior surface there is a roughened longitudinal field designed probably for the extensor carpi radialis. The designation of the remaining scars is less clear. These are the tubercle situated in the middle of the proximal part of the anterior surface and the strong tuber overhanging the outer part of the distal surface. In the proximal medial angle of the metacarpal II there is a concave field, some centimeters in diameter, of the rather unclear significance (probably for a part of the extensor carpi radialis). The strong tuberosity, which is present on the outer border of the metacarpal III as well as the roughened external border of the metacarpal IV and the roughened medial border of the metacarpal V are probably connected with the insertion of the extensor digitorum communis.

PELVIC GIRDLE

(pl. 3, fig. 6, pl. 12, fig. 1, text-figs 11—14)

The pelvis is characterized by a considerable amount of lateral flare of the anterior parts of the iliac blades. The maximum spread of the dorsal parts of the iliac blades is estimated 169 cm. The pubis is much stouter and longer than the ischium. The ratio: length of the pubis to length of the ischium (both measured along the symphysis) is about 14 to 9. The contribution of these bones to the formation of the acetabulum is quite the inverse; the pubical border is to the ischiadic one as 7 to 12 (the lengths measured along the chord on the outer side). The fused symphysis pelvis extends from the distal ends of the pubis to about half a length of the ischium. It is strongly concave ventrally. The pelvic canal is rounded but contracted by the massive pubo-iliac sutures and by the sacrum. Its diameter is about 70 cm. In the posterior aspect it is flattened dorso-ventrally. It becomes more or less oval-shaped, the diameters equaling to 32 cm and 59 cm. The almost round acetabulum (see table 12) gets narrower medially, but the diameter of the interior fenestra does not differ very much from the external one. The anterior border of the acetabulum is situated opposite the first primary sacral and the posterior one about the middle of the third one. The greatest breadth of the acetabular wall is in the region formed by the pubic peduncle of the ilium and in the one formed by both ilium and sacricostal yoke. These parts are directed respectively anteriorly and upwards in the life position of the pelvis. Posteriorly and downwards the acetabular wall gets narrower, the most constricted region of this wall being situated within its ischiadic part.

Table 11

Measurements (in cm) of pelvic girdle of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

Right ilium		
maximum length	114	
maximum height above pubic peduncle	52	
height above acetabulum	44	
maximum anterior breadth of iliac blade (tangentially to the bone surface)	58	
length of pubic peduncle	31	
Right pubis		
maximum length	112	
maximum thickness of the distal end	15	
Maximum breadth of pubic part of pelvis (about the level of ambiens insertions)	90 (estimated)	
Ischium	left	right
maximum length	72	72
breadth of distal end	28	20
thickness of distal end	8	7.5

Ilium (pl. 12, fig. 1*ac*, text-figs 11, 12). The iliac blade is massive bone plate extending forwards and backwards from the acetabular region more or less uniformly with a probable preponderance of the anterior part. The region of the greatest iliac height is probably situated over the pubic peduncle as reconstructed from the preserved parts of the right iliac blade (see text-fig. 12). The rather strong outward curve of the iliac blade is connected with the concavity of the outer surface. This is supposed to have been occupied by the iliofemoralis. The anterior border of the iliac blade (strongly damaged by predators in the present specimen) is very massive but tapers posteriorly, getting thicker again in the posterior part of the ilium. The very massive postacetabular part of the ilium makes a large and very rough muscular surface for the epaxial musculature of the tail (the iliocaudalis) on its posterior wall and distinct insertion places for the iliofibularis, and the flexor tibialis on its lateral wall (text-fig. 12*ilfib, fti*). The caudifemoralis brevis inserted probably on its ventral margin (text-fig. 17*A*). The internal surface of the ilium possesses distinct elevations at the points of articulation with the sacrum. The pubic and ischiadic penducles of the ilium differs very much from each other. The first one is very massive, especially at the puboiliac suture, and high-attaining about the same size (about 40 cm) as the maximum for the iliac blade. It is crescent-shaped in transverse section, the concavity being turned to the acetabulum. The ischiadic peduncle is very low. It is in fact little more than the suture surface for the joint with the ischium. Directly above this suture there is a huge tuber for the ligament of the hip joint. The second tuber of the same kind is to be seen directly below the suture (text-fig. 12*lig*) within the ischium. Both ends of the pubic peduncle are broadened in relation to the main part which forms a transverse groove indicating the course of the part of the puboischiofemoralis internus. This part (homologous to the first part of the puboischiofemoralis internus of ROMER 1923) had its origin on the sacrals, dorso-sacral, and probably on the last dorsals, as well as in the large, shallow concavities situated on the internal surfaces of the ischium and of the proximal part of the pubis (see text-fig. 17*AB*). All the fascicles inserted probably on the anterior surface of the proximal part of the femur, but their scars have not been identified in the specimen ZPAL MgD-I/48. The outward curve of the iliac blades is supposed to be connected, among others, with the character of the puboischiofemoralis internus and explicitely: (1) with the thickness of its fascicles passing between the pubic process and the anterior part of the iliac blade, on their way from the interior of the basin to the outside, (2) with the possible presence of the fascicles having their origin on the medial surface of the anterior part of the iliac blade, the curving of this blade being advantageous for their action.

Table 12

Measurements (in cm) of right acetabulum of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

	externally	medially
Horizontal diameter (from suture ilium-ischium to suture ilium-pubis	44	37
Vertical diameter	40	22
Length of ischiadic border	35	28
Length of pubic border	19	14
Breadth of the dorsal acetabular wall	22	
Breadth of sacricostal yoke in dorsal acetabular wall	10	
Breadth of ilium in dorsal acetabular wall	12	
Breadth of ilium at the pubo-iliac suture	22	

Pubis (pl. 3, fig. 6, pl. 12, fig. 1, text-figs 12, 13). The proximal part of the pubis is a massive bone plate passing distally into a shaft and medially into a symphyseal part. It faces outwards and backwards. Its external surface is slightly concave. It is bordered from the back by a longitudinal convexity extending distally over the posterior margin of the shaft. Its iliac and ischiadic parts are strongly thickened, the tuberosity for the ambiens being distinctly developed and situated directly below the pubo-iliac suture. The foramen obturator is situated near the pubo-

-ischiadic suture. The shaft of the pubis is very long (see tables 11, 17) and massive, especially so at its distal end. The external part of this end is strongly roughened for cartilage. The pubis is twisted medially to pass into the plate-like symphyseal part. The latter is directed transversally and strongly curved longitudinally so that the distal part of the pubis faces straight forwards. It is rather thin as compared with the massive shaft and with the proximal part of the pubis, but gets thicker at the suture with the ischium as well as distally. There is also a slight thickening extending along the symphysis pelvis. The following regions are identified as the places of muscle

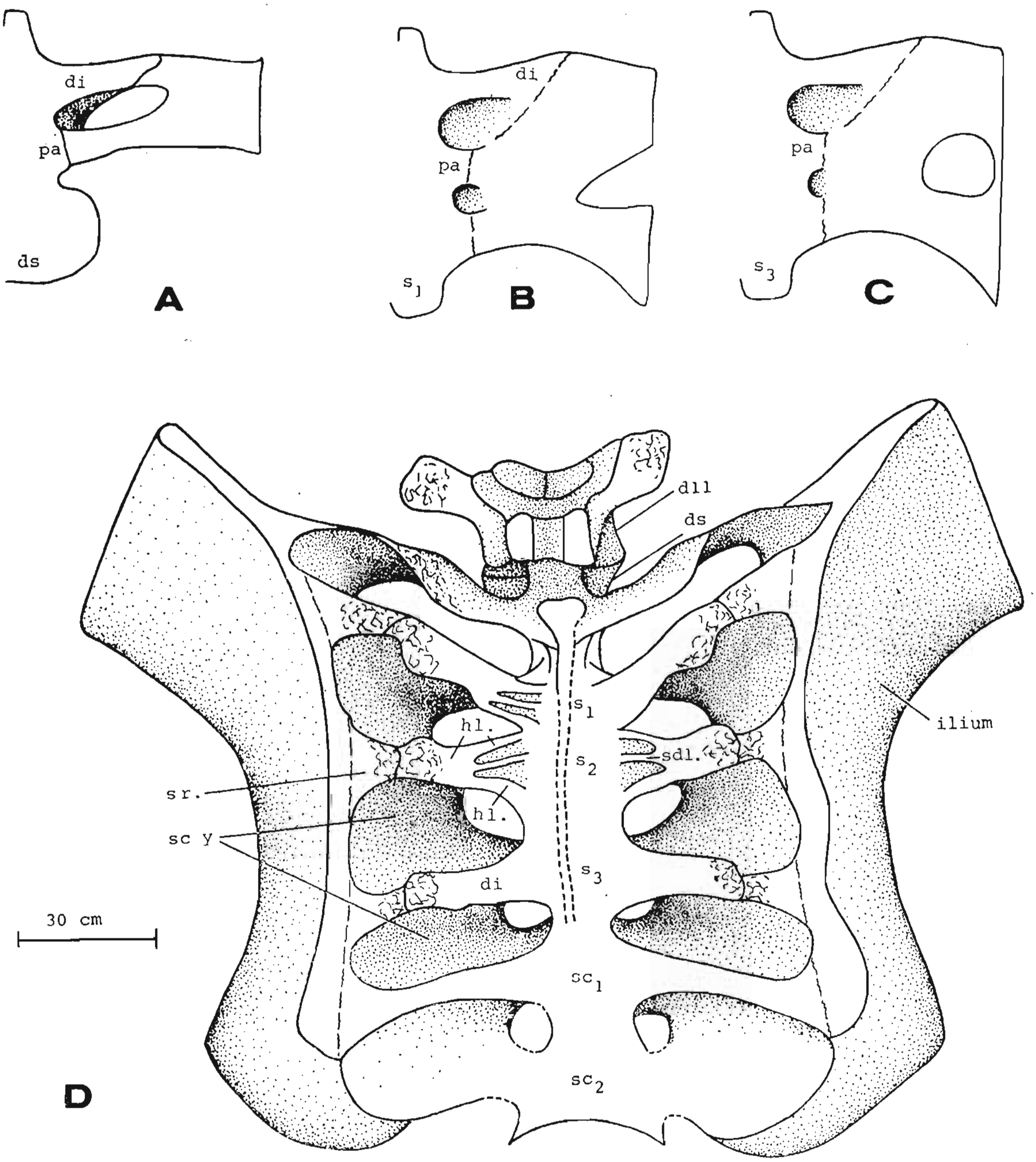

Fig. 11

Opisthocoelicaudia skarzynskii gen.n., sp.n. *A*, *B*, *C* — transverse sections of the sacrum with the transverse processes and sacral ribs in front view. *D* — sacrum and pelvis in dorsal view; anterior part of the left ilium and its union with the sacrum as well as the right half of the sacrum reconstructed. *d* — dorsal, *di* — diapophysis, *ds* — dorso-sacral, *h l* — horizontal lamina, *pa* — parapophysis, *s* — primary sacral, *sc y* — sacricostal yoke, *sd l* — supradiapophyseal lamina, *s.r.* — sacral rib.

insertions. On the internal surface of the pubis near the suture with the ischium there is a shallow concavity extending up to the foramen obturaror. It served probably as a most posterior place of the origin of these fascicles of the puboischiofemoralis internus which extended beneath the pubo-ischiadic suture (a pubic head of the puboischiofemoralis internus Russel, 1972, I division of the puboischiofemoralis externus after Romer, 1923*a* in crocodiles, III division of the puboischiofemoralis internus of Romer 1942, in lizards) to insert on the medial border of the femur in its distal part (text-fig. 15*C pifi*). The more anterior fascicles of the same part of the puboischiofemoralis internus extended probably over the whole distal part of the internal (here anterior) surface of the pubis. These two muscular surfaces could have been separated from each other as they are in aligator (see Romer 1923*a* pl. 24, inner surface). The origin of the puboischiofemoralis externus was situated on the external surface of the pubis as well as on the external part of the ischium. The pubic fascicles of these muscles were probably separated from each other as evidenced by the pubic surface. A part of them had its origin on the proximal part of the pubis in the vicinity of the foramen obturator, the second one on the concave ventral surface of the symphyseal part. A similar division of this part of the

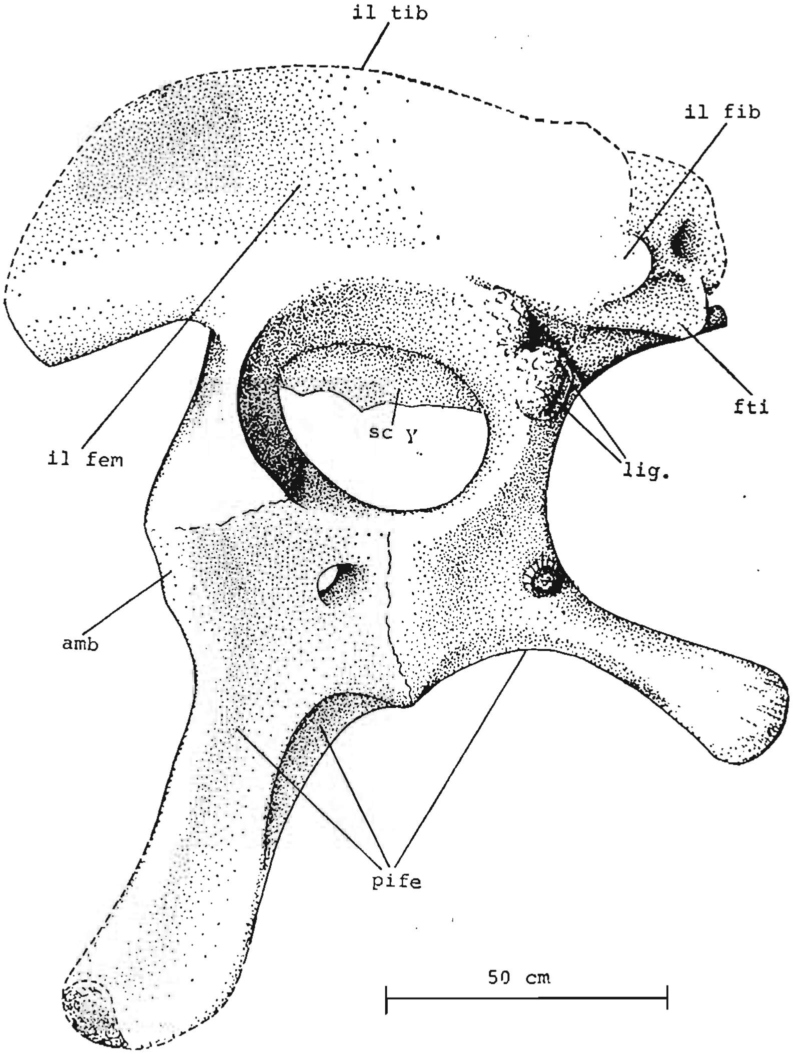

Fig. 12

Opisthocoelicaudia skarzynskii gen. n., sp. n. Pelvis. Left side view. Dorsal border of the ilium and distal part of the pubis reconstructed basing on the better preserved right side bones. *amb* — ambiens, *fti* — flexor tibialis internus, *il fem* — iliofemoralis, *il fib* — iliofibularis, *il tib* — iliotibialis, *lig* — ligamentous tuber, *pife* — puboischiofemoralis externus, *sc y*—sacricostal yoke.

puboischiofemoralis externus is stated by ROMER (1923*a*, fig. 2) in aligator. The strong development of the symphyseal part of this muscle evidenced by a large extension of the muscular field on this part of the pubis was probably advantageous as a graviportal character but it must have limited the length of stride.

Ischium (pl. 3, fig. 6, pl. 12, fig. 1*b*, *c*, text-figs 12—14). The proximal part of the ischium, the symphyseal part included, forms a subquadrangular bone plate some centimeters thick. It faces outwards in the region adjoining the acetabulum, but twists medially in its more media

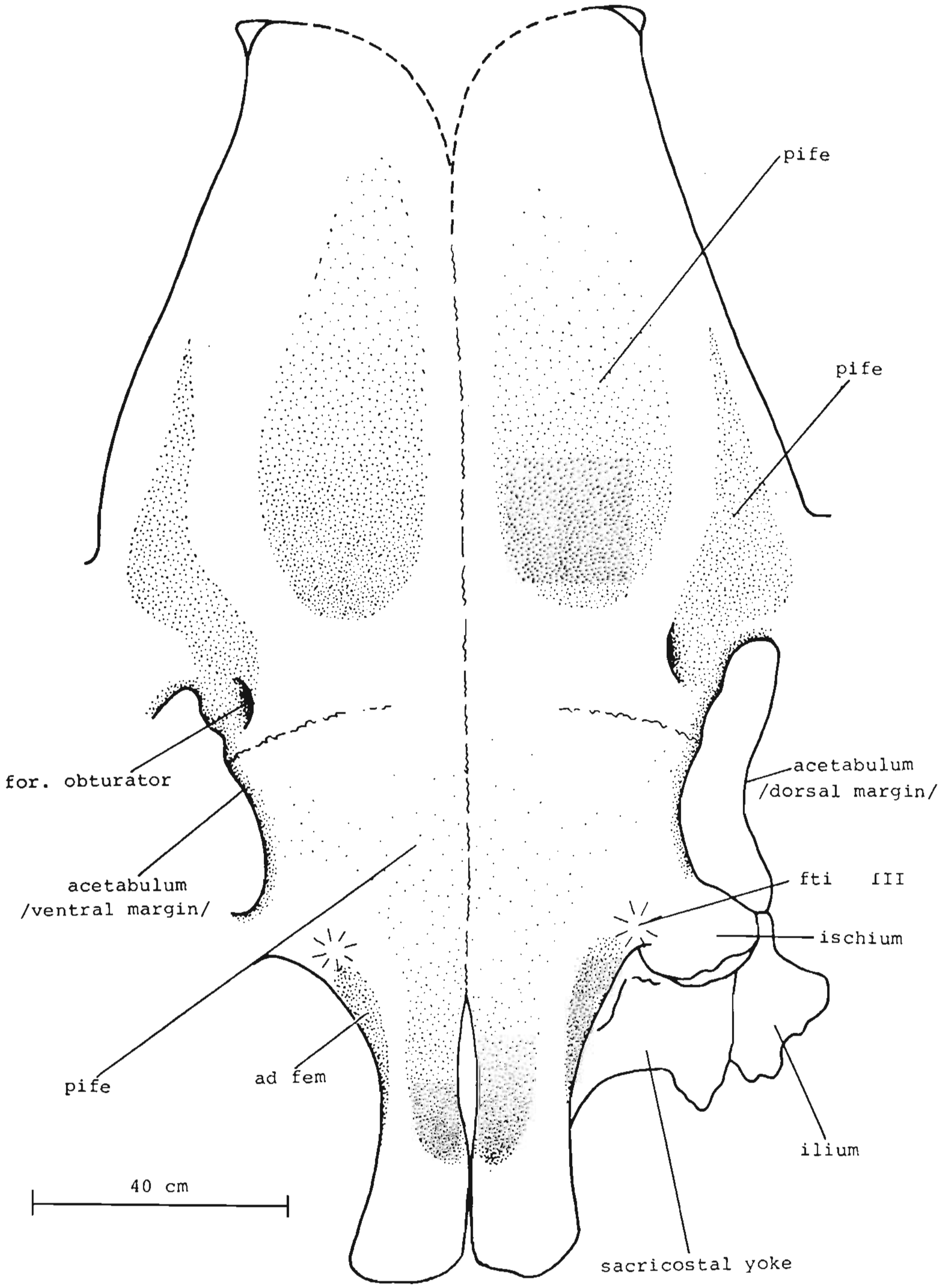

Fig. 13
Opisthocoelicaudia skarzynskii gen.n., sp.n. Pelvis. Ventral view. Schematized reconstruction after the photograph. pl. 11. fig. 1*b*. *ad fem* — adductor femoris, *fti* — flexor tibialis internus, *pife* — puboischiofemoralis externus.

and more distal regions. The shaft of the ischium is situated almost transversely (see text-fig. 14). The proximal part of the ischium is convex externally and concave medially in transverse section. But both external and medial surfaces of this part bear shallow concavities which are supposed to be connected with the muscle origins. The proximal part of the ischium is firmly coossified with the pubis, the suture region being strongly thickened, as well as with the ilium. The iliac part of the ischium which can be called iliac peduncle, because of its length, is a relatively slender bone bar subtriangular in transverse section. It constitutes in fact a whole posterior border of the acetabulum. Its dorsal end fuses with the ilium and, more medially, with the sacricostal yoke, the suture line being marked by a transverse crest. Directly underneath there is a ligamentous tuber. The shaft of the ischium is long and slender. The cross section of the shaft is subtriangular at the proximal end but strongly flattened and not much expanded at the distal end (text-fig. 14). The ischia are fused with each other in their proximal halves. The medial borders of the unfused parts of the shafts are sharp, but become thicker and roughened for cartilage at their distal ends. The tuber situated near the posterior margin of the ischium was probably connected with the flexor tibialis internus III as ROMER (1923) supposed and not with the ischiocaudalis as suggested by RUSSELL (1923) (1972). It is evidenced by the texture of this muscle scar, which does not turn posteriorly in *Opisthocoelicaudia* as distinct from Ornithominidae described by RUSSELL *(l.c.)*. The proximal part of the ischium was probably covered by the posterior parts of the puboischio femoralis externus, whereas the origin of the adductor femoris (or a part of it) was probably situated in a shallow concavity adjoining the external border of the shaft behind the origin of the flexor tibialis internus III (see text-fig. 13*adfem*).

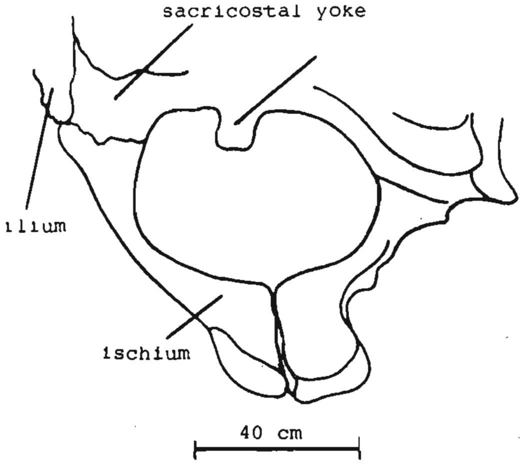

Fig. 14
Opisthocoelicaudia skarzynskii gen.n., sp.n. Pelvic canal. Posterior view. After a photograph.

HIND LIMB

Femur (pl. 8, fig. 4, pl. 13, figs 1, 2, text-fig. 15). The femur is typical of graviportal animals in having a broad shaft strongly flattened anteroposteriorly and articular surfaces almost perpendicular to the long axis of the shaft. The ratio of the anteroposterior dimension of the shaft (measured directly under the fourth trochanter) to the shaft breadth is about 1/2. The curve of the proximal part of the shaft characteristic of the most sauropods is caused not only by the medial direction of the base of the head but also by a seeming undergrowth of the external angle of the proximal extremity. This is probably the effect of the expansion of the region situated underneath. The head is almost round and distinctly convex. It is situated at the top of the medially protruding part of the shaft but it does not face medially itself. Around the well formed articular surface there is a zone of scars left by the joint capsule. The medial condyle is larger than the lateral one as regards its length and breadth. It protrudes more anteriorly and reaches farther at the posterior surface of the femur than does the lateral one. The distal surface of the lateral epicondyle is completely fused with that of the lateral condyle but it is much shorter and therefore well delimited from it (see text-fig. 15*D*). The intercondyloid fossa transmitting the common tendon of the femorotibialis, ambiens and iliotibialis is very deep. On the distal intercondyloid surface the ligaments for the menisci of the knee joint must have been attached, but the exact place of their attachment is not identified. The great trochanter is situated laterally of the head and slightly lower than it is. It was a place of insertion of the iliofemoralis, but the fascicles of this muscle inserted also underneath, on a roughened surface in the proximal 1/4 of the external wall of the femur causing the lateral expansion of this part of the bone. The low position of these fascicles increased probably its abductory action (see below). The surface of the great trochanter is slightly rugose for the muscle insertion and

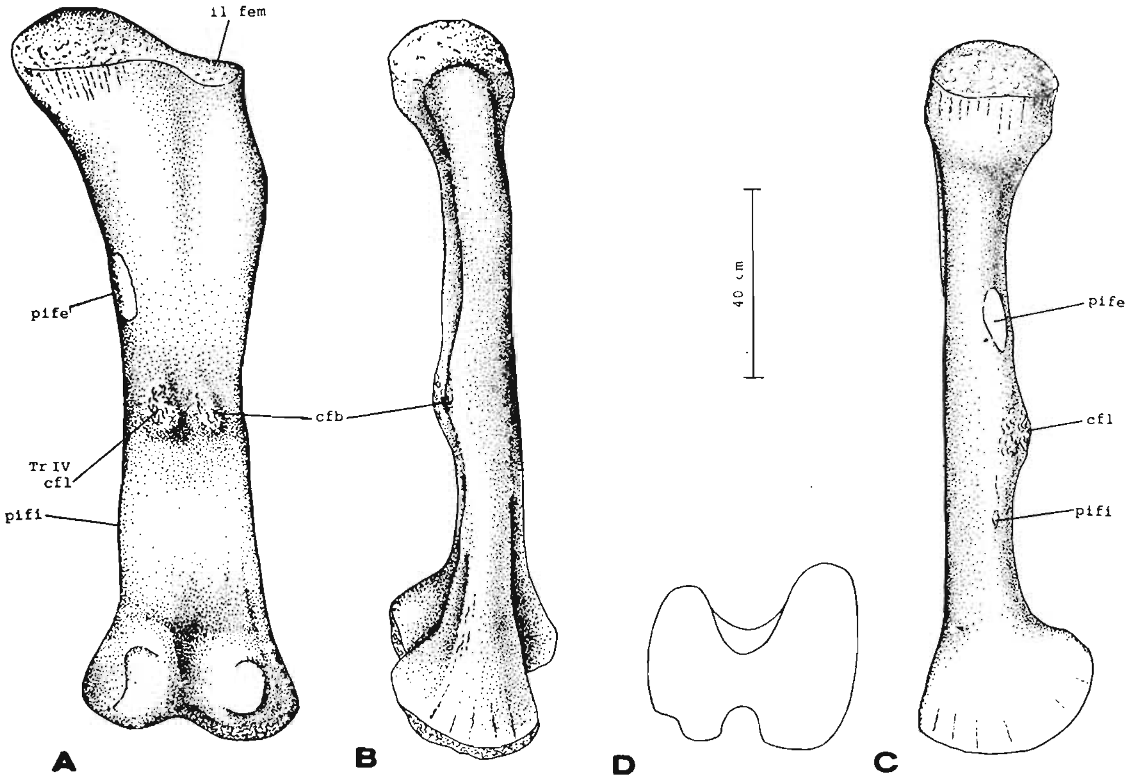

Fig. 15

Opisthocoelicaudia skarzynskii gen.n., sp.n. Right femur with trochanter major reconstructed after the left side bone. *A* — posterior view, *B* — lateral view, *C* — medial view. *cfb* — caudifemoralis brevis, *cfl* — caudifemoralis longus, *il fem* — iliofemoralis, *pife* — puboischiofemoralis externus, *pifi* — puboischiofemoralis internus, *Tr IV* — trochanter IV

Table 13

Measurements (in cm) of femur of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

	right	left
Greatest length	139.5	
Distance from trochanter IV to proximal articular surface	76	
Proximal breadth		47
Distal breadth	43	
Breadth to length of head	27/24	
Fore and aft dimension of medial condyle	40	
Fore and aft dimension of lateral condyle	32	
Least breadth of shaft	25	31
Fore and aft diameter of shaft	11	10.5

cartilage. It faces straight upwards and is not well delimitted from the head, but it is shorter in the parasagittal plane. The great trochanter is somewhat enlarged posteriorly, this part forming a swelling at its posterior margin. This was probably connected with the withdrawal of the fascicles of the iliofemoralis from the joint axis, which enabled them to rotate the joint. Most of the fascicles being inserted at the joint axis or nearby, the main role of this muscle was, however, the abduction. Such an action together with the adductory action of the puboischiofemoralis externus caused the fixation of the femoral head in the acetabulum, the effect of importance for graviportal animals. The locomotory action of the iliofemoralis was probably insignificant. An oval scar about 17 cm high and 7 cm broad occurs on the medial side of the shaft in the second third from the proximal end. The surface of this scar is very smooth. This was the probable place of insertion of the puboischiofemoralis externus. The pubic head of the puboischiofemoralis internus representing the first division of the puboischiofemoralis externus of ROMER (1923*a*, p. 542) in crocodiles and the third division of the puboischiofemoralis internus of ROMER (1942) in lizards, which according to RUSSELL (1972) inserted on the same place, is supposed to have inserted much lower in *Opisthocoelicaudia*. As shown by the curvature of the external border of the pubis this muscle should have inserted under the level of the fourth trochanter on the rugose medial wall of the femur (text-fig. 15*A*, *C*). The fourth trochanter is situated under the middle of the femur length. It is a protrudent triangular tuberosity about 14 cm high. Its texture indicating the oblique course of the muscle fascicles (from upwards inwards and backwards) is in conformity with the current opinion that it was the insertion place of the tendon of the caudifemoralis longus. The tendon of the origin of the gastrocnemius probably arose from the latter as suggested by ROMER (1923*b*). Laterally from the fourth trochanter there is a smaller tuberosity facing medially and upwards (text-fig. 15*A*, *B cfb*). The fascicles which have inserted here have been separated from the ventral parts of the pelvis by the caudifemoralis longus and therefore are supposed to have had their origins on the posterior part of the ilium or on the sacro-caudals. They can be identified with the caudifemoralis brevis, which agree with the reconstructions by ROMER (1923*b*). The localization of the adductor's insertion is unclear. All the muscles which have left the interior of the pelvis passing above the ambiens origin have inserted on the anterior surface of the proximal 1/4 of the bone, laterally from the head (the main part of the puboischiofemoralis internus, part I and part II of ROMER 1923*a*). This can be judged from the direction of the transverse furrow extending on a pubic peduncle of the ilium. The remaining part of the anterior surface of the femur was covered by the femorotibialis. Neither the puboischiofemoralis internus nor the last named muscle have left any traces on the bone surface. The origin of the extensor digitorum communis probably joined with the peroneus longus was presumably situated on the anterior surface of the lateral condyle. Such a situation results from the direction of the extensor furrow on the tibial surface (see text-fig. 16*B*).

Tibia (pl. 11, fig. 4, pl. 13, fig. 4, pl. 14, figs 1, 2, text-fig. 16*B*) is flattened bilaterally but expanded at both ends. The length of the tibia slightly exceeds a half of length of the femur. Its antero-posterior dimensions are larger than the transverse ones at all the levels except for the distal end. The proximal articular surface is an oval concavity. Its longer axis is situated almost parallel to the sagittal plane of the body. It passes laterally into a convex border situated directly under the intercondyloid surface of the femur in articulated bones. In the distal half of the bone its plane of bilateral symmetry twists outwards and forwards to make eventually an angle of about 40° with the long axis of the proximal end. In this region the antero-posterior dimension becomes in fact the transverse one. The distal end is convex as a whole but incised from the outer side and from the back. This incison cutting the distal end about a half through is destined for the articulation with the astragalus. The medial quarter of the distal surface was probably unfunctional as an articular surface. Its medial surface is more or less rugose. It was probably destined for the ligaments of the joint capsule or for the annular ligament. In the lateral part of the distal end there is an almost vertical, flat surface for the union with the fibula. The tibial crest (or cnemial crest of ROMER, 1956) strongly protrudes forwards. Its top is situated about a quarter of the tibial length from the proximal surface. The joint tendon of the femorotibialis, ambiens and iliotibialis inserted mainly on the anterior and upper rugose margin of this crest. The furrow limitted from the medial side by the tibial crest was probably occupied by the fascicles of the extensor digitorum communis (and probably the peroneus longus too) extending obliquely to the metatarsal V. The tibialis anterior covered the external surface of the tibia. To reach the dorsal surface of the metatarsal I it had to pass onto the dorsal surface of the pes. This transit occured probably slightly above the furrow of the common digital extensor (see text-fig. 16*B*) as suggested by the direction of the curvature of the external surface. The narrow posterior surface of the bone is not delimitted from the neighbouring ones. It is quite smooth and gives no indication as to the disposal of the origins of the popliteus, flexor digitorum longus and gastrocnemius which should have inserted on it. Neither is there any indication as to the situation of the insertions of the flexor tibialis internus and externus on the medial surface of the tibia.

Table 14

Measurements (in cm) of tibia and fibula of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

	Tibia		Fibula	
	left	right	left	right
Greatest length	81	81	83	83
Proximal breadth	26	24	12	12
Distal breadth	28	31.5	16	16
Least breadth of shaft	11	11	9	8
Fore and aft diameter of proximal end	36	36	21	27
Fore and aft diameter of distal end	—	20	19	21
Least fore and aft diameter of shaft	16	20	12	10
Fore and aft diameter over tuberositas tibiae	34	35		

Fibula (pl. 11, fig. 5, pl. 13, fig. 3, pl. 14, fig. 2*b*, *c* text-fig. 16*A*) is relatively slender as compared to the tibia. It is flattened bilaterally. The extremities are expanded anteroposteriorly and more massive than the shaft. The antero-posterior dimension makes 32% of the total length proximally, 25% of the same distally and only 15% in the middle of the shaft. The

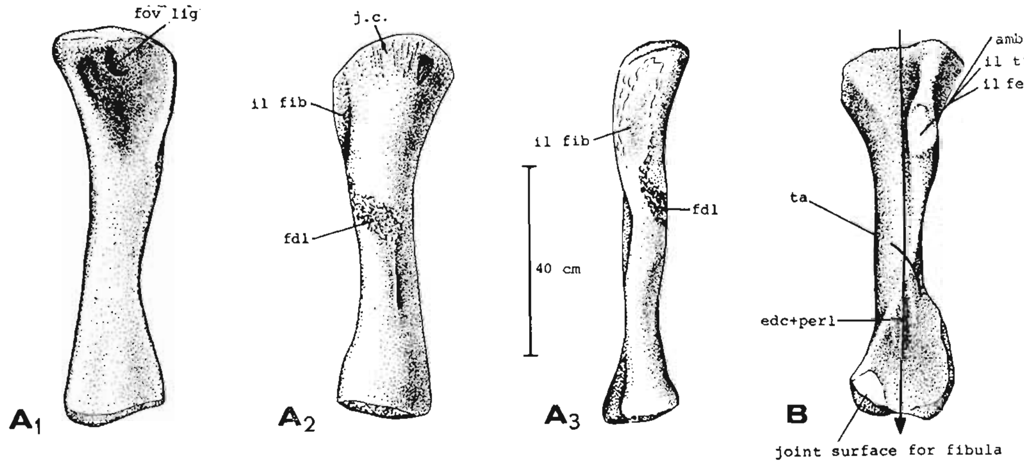

Fig. 16

Opisthocoelicaudia skarzynskii gen.n., sp.n. *A* — Right fibula, A_1 — medial view, A_2 — lateral view, A_3 — posterior view, *B* — Right tibia in antero-external view. *amb* — ambiens, *edc* — extensor digitorum communis, *fdl* — flexor digitorum longus, *fov lig* — fovea ligamentosa *il fem* — iliofemoralis, *il fib*-iliofibularis *il tib*-iliotibialis, *j.c.* — joint capsule, *perl* — peroneus longus, *ta* — tibialis anterior.

transverse dimensions make only 15%, 19% and 11% correspondingly. The shaft shows an S-shaped curvature in a parasagittal plane. The anterior border is concave proximally and straight distally, whereas the posterior one is convex proximally and concave distally (pl. 13, fig. 3). The medial surface of the bone is slightly concave, especially so in its proximal half. The two deep ligamentous foveae facing backwards and upwards occur in its proximal and anterior part (pl. 11, fig. 5, text-fig. $16A_1$). The proximal end is crescent-shaped in transverse section. The concavity of the crescent turns to the tibia, its anterior angle is blunt, the posterior one acute. The proximal surface is slightly convex and situated obliquely. It slopes down towards the tibia and to the back, and only slightly to the front. The distal articular surface is almost flat and bears traces left by cartilage. In the articulated bones the proximal end of the fibula protrudes above the level of the proximal articular surface of the tibia. This as well as the poor adjustment of the articular surface of the fibula to that of the femur indicate the presence of thick cartilaginous menisci, the thickness of which must have been at least 7 cm above the articular surface of the tibia.

The following muscle scars are to be seen on the surface of the fibula: The oval rough concave surface situated directly under the proximal articular surface on the posterior wall of the fibula (text-fig. $16A_2$, A_3) was probably the insertion place of the iliofibularis as judged from the position of this insertion in crocodiles and lizards (ROMER 1923*a* and 1956). This surface reaches down to the proximal 1/3 of the bone length, then passes on the lateral side of the bone. A strongly sculptured oval-shaped (10 cm × 2 cm) muscle trace is situated on the lateral side of the fibula about the middle of its length. Its longer axis extends obliquely forwards and downwards. About the middle of the wall it passes into a vertical, sharp crest extending distally. It has its continuation in the upwards direction too, fusing with the scar left by the iliofibularis by means of the slight rugosities. All this region could have made a place of origin of the different heads of the flexor digitorum longus. No other scars can be identified on the surface of the fibula.

Pes. *Tarsus* (pl. 14, fig. 2). Astragalus is the only ossified element of the tarsus in *Opisthocoelicaudia.* It is formed as a pyramid provided with four subtriangular surfaces. It tapers medially its distal and proximal surfaces meeting each other at its medial margin. The lateral wall situated vertically faces the distal end of the fibula. The anterior surface is regarded as the articular one for the metatarsals. The distal surface is convex and strongly rugose. It faces downwards and backwards. A small subquadrangular surface (the fifth one) occurs at the top. This surface facing bakwards, upwards and laterally is slightly concave and bears a distinct fovea for the unidentified tendon or ligament. The proximal surface constitutes the negative of the distal surface of the tibia in bearing two concavities separated from each other by a convex ridge. The lateral, higher part of the anterior surface is convex in horizontal section and fits more or less the proximal surface of the metatarsal III. It is well delimited from the distal surface by a sharp border. The medial part of the anterior surface strongly tapers medially and passes gradually into the distal surface. It neither fits the metacarpal II nor is sufficiently large for making a joint with it.

Measurements (in cm) of the right astragalus:

Maximum breadth at the anterior surface	17
Maximum fore and aft dimension	14
Height at the anterior surface	10

Metatarsus (pl. 14, figs 2—7). The metatarsals are much plumper than the metacarpals, but provided with much better articular surfaces. Their mutual relations are univocal as regards metatarsals I and II and very likely for metatarsal IV. When articulated with each other they form a flat-arched pes differing strikingly from the horseshoe-shaped manus. Such a situation of the metatarsals may suggest the subhorizontal position of the pes otherwise assertained by the situation of the articular surface for the metatarsal III on the astragalus. The metatarsal I

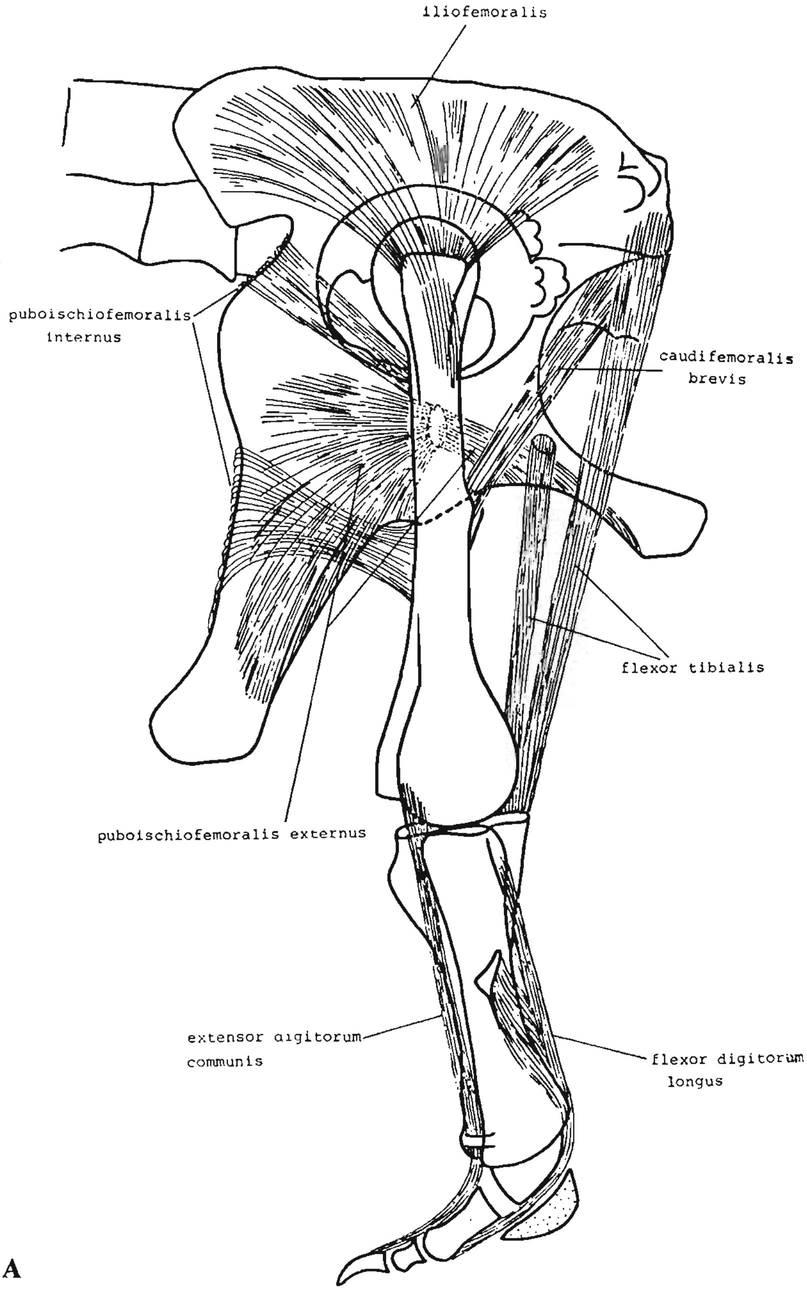

Fig. 17
Opisthocoelicaudia skarzynskii gen.n., sp.n. Reconstruction of the musculature of the pelvic girdle and limb. Lateral view. *A*, *B* — different muscle sheets.

is the most stocky and the shortest of all, its medial length being lesser than its breadth. The massiveness decreases from the metatarsal I to V. The length increases from the metatarsal I to III, the metatarsal IV being subequal to III but somewhat shorter. Metatarsal V is intermediate between the I and II as regards the length. The metatarsals are subquadrangular in transverse section all over their lengths. This makes a difference as compared to the metacarpals and is connected with the different position of the pes and manus. Their proximal ends taper slightly posteriorly (metatarsal II and IV), they are subrectangular (metatarsal III) or broadening posteriorly (metatarsal I). The proximal articular surface of the metatarsals I to III have the convex medial borders and slightly concave lateral ones. The borders of the fourth metatarsal are almost straight. The same is probably true for the metatarsal V, which is damaged to some

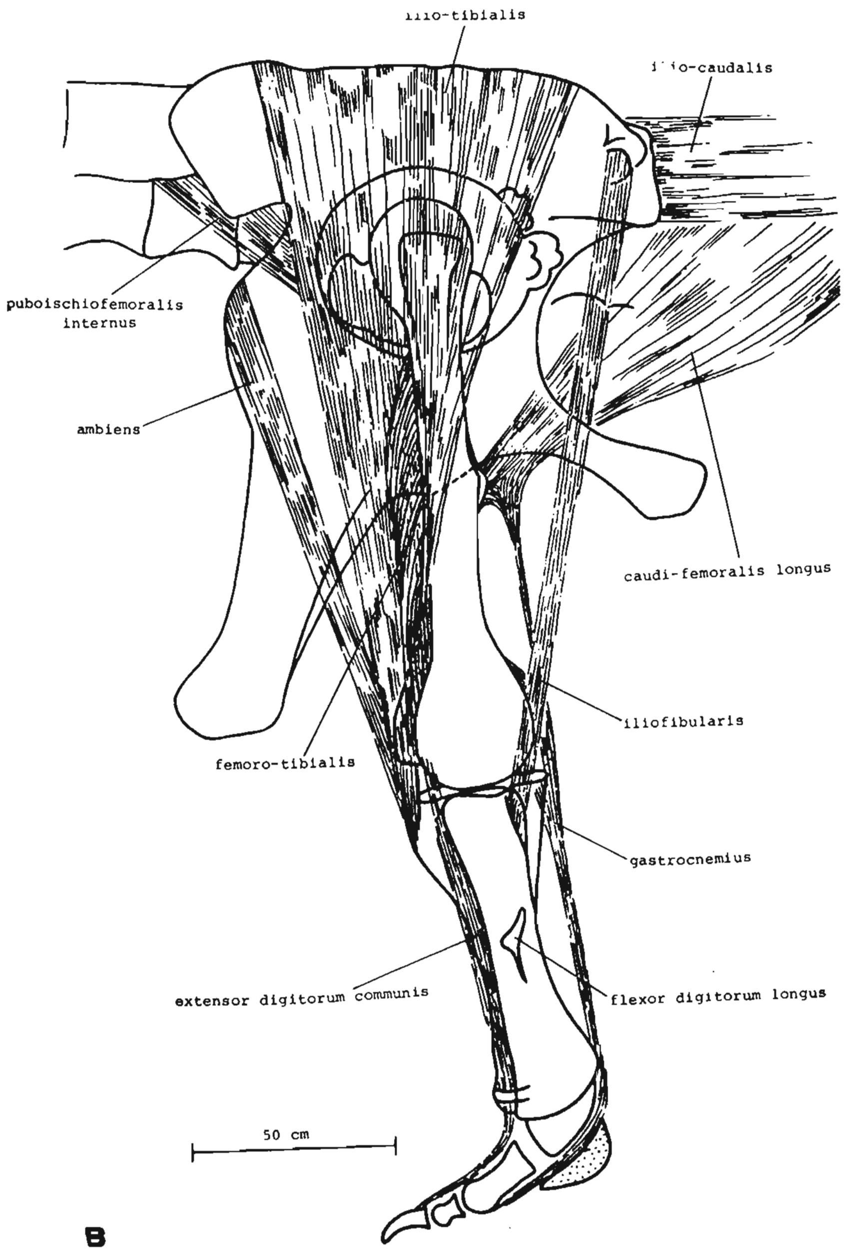

Table 15

Measurements (in cm) of right metatarsals of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

	Mt I	Mt I	Mt III	Mt IV	Mt V
Greatest length	15	18	20	18	14
Proximal breadth	12	12	11	8	9
Distal breadth	12	12	11	11	—
Least breadth of shaft	9	7	6	4	—
Proximal fore and aft dimension	16 med. 11 ext.	14	13	11	4
Least fore and aft dimension	10	8	7	10	4
Distal fore and aft dimension	11	11	10	7	—

med. medially ext. externally

extent. The proximal articular surface of the metatarsal I is convex. It is much longer in its external part than in the medial one in the way characteristic of sauropods. The proximal surface of the metatarsal II is almost flat, that of metatarsal III bears an antero-posterior concavity fitting the astragalus and bordered from both medial and lateral sides by convexities. The traces left by cartilage are to be seen over the external part of the proximal surface of the metatarsal III and over the whole convex surface of the metatarsal IV. The distal articular surfaces of the metatarsals II and III are slightly saddle-shaped and do not fit well the concave proximal surfaces of the first phalangs. They reach farther on the anterior surfaces of the metatarsals than on the posterior ones. This indicate the preponderance of the extension movements. The distal surface of the metatarsal II is asymmetrical in a similar way as that of the metatarsal I, but in lesser degree. The distal surface of the metatarsal III is almost symmetrical.

Table 16

Measurements (in cm) of phalanges of the right pes of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

	Phalanx 1				Phalanx 2 (Ungual)		
	digit I	digit II	digit III	digit IV	digit I	digit II	digit III
Greatest length	6.5 ext. 2 med.	9 ext.	8	7	15	15	11
Proximal breadth	9.5	10	11	10	6	6	5.5
Least breadth of the shaft	9	9	9	8			
Proximal fore and aft dimension	8 ext. about 1 med.	8 ext.	6	9	10		
Distal fore and aft dimension	8	6.5	5.5	4		10	7
Least fore and aft dimension	7	6.5	5	4			
Distal breadth	9	9	9.5	8.5			

med. medially, ext. externally, e. estimated

Phalanges (pl. 13, figs 5—11, pl. 14, fig. 2*ab*) are preserved in the four medial digits. The phalangeal formula is 2221. Judging from the ill formed distal articular surface of the metatarsal V the fifth digit could have been rudimentary or completely reduced. The first phalanges are characterized by a certain amount of asymmetry decreasing from the digit I to III. It manifests in a shortening of the external walls of the phalanges in relation to the medial ones. The phalanx I of the digit I is wedge-shaped tapering strongly laterally as well as posteriorly. Its posterior wall does not exist in fact, the distal and proximal surfaces adjoining each other along the acute margin. The distal articular surface faces downwards in the most extended position of the phalanx. It is slightly saddle-shaped its lateral less convex and larger part being separated from the medial one by a sagittal groove. From both parts only the first one acted probably as the articular surface for the ungual. Its axis being directed antero-medially, convergently with the axis of the medial part, it determines the position of the ungual. The anterior (dorsal) end of the articular surface of the ungual is directed medially in relation to the posterior one which is more lateral and more distal at the same time. Apart from this the long axis of the ungual is directed obliquely anterolaterally. The phalanx 1 of the digit II shows the same character as that of the digit I, but to a much lesser degree, the posterior wall being present this time although tapering laterally. The phalanx 1 of the digit III is almost symmetrical, the features described above being only slightly marked.

The unguals are strongly flattened bilaterally, and slightly crescent-shaped but truncated at both ends. The proximal articular surface occurs at one end, the second one is blunt in all the unguals. The ungual of the digit III is even roughened for cartilage at the distal end. The proximal surfaces are subtriangular, the apexes turned anteriorly (dorsally). They are differentiated into the main oval, concave surfaces and the medial convexities bordering them and fitting the sagittal furrows of the distal surfaces of the first phalanges.

RECONSTRUCTION

GENERAL REMARKS

Two elements contribute to the reconstruction of the basic body configuration in every tetrapod limb posture and axial profil. Both were extensively discussed in literature concerning sauropod. ABEL (1910) and, quite recently COOMBS (1975) in his remarakable paper gave a critical recapitulation of the previous opinions of MARSH (1883), OSBORN & MOOK (1921), HATCHER (1901), HAY (1908), TORNIER (1909) and others. JANENSCH (1929*b* and 1950) gave a modern analysis of the vertebral column architecture, the muscles and ligaments reconstruction included. The attitude of the limbs reconstructed in the present paper is in agreement with most of the previous reconstructions in being basically of the pillar-like, graviportal type. The main basis for the reconstruction of the limb posture can be afforded by its proximal segments (humerus and femur) the articulation included, the tibia and radius being subvertical both by sprawling and by erect gait. Additional indications for the limb posture may be given by other features of the limb bones and pelvis, but none of them is suitable for determination of the joint angles. The strong development of the supra-acetabular crest and perforation of the acetabulum indicate the fully improved type of limbs as CHARIG (1972) stated. The same is true for the twisted appearance of the tibia, pointed out by BONAPARTE (1969), which is also suggestive of the fully erect gait and can be likewise explained functionally. The simple type of tarsus is known in all fully improved archosaurs and therefore is suggestive of the vertical type of limb (CHARIG *l.c.*), but it has not been hitherto sufficiently explained by limb function and seems to be of importance when discussing the archosaurian phylogeny rather than when mounting skeletons. The main rule which ought to be applied when mounting the supporting limbs of the heavy tetrapods is the horizontal position of the joint surfaces mentioned by BAKKER (1971). Such a position ensures the best prop, the slipping component decreasing to zero. This rule has not been followed by some authors, which resulted in seemingly wrong reconstructions of articulations, especially the scapular one (e.g. in *Dicraeosaurus*, JANENSCH 1929*b*). In the case of a concave joint surface the plane passing through its extreme points (or GLA of BAKKER 1971), tends to be horizontal. The middle of the joint surface is evidently a fulcrum in the resting phase, because limbs characterized by one simple function (here support) tend to move like a pendulum. When moving the fulcrum passes from one extreme point to another. Its position in the resting phase is the most essential one for the mounting of skeletons, because it determines the size of the joint angles. Some difficulties in determination of this point occur in the case of the acetabulum, which is a quite circular surface and therefore has no „extreme points". Only a part of it, no doubt, acts as a real articular surface, this part having of course its extreme points. The rest of the acetabulum is merely a completion of the articulation acting as a mechanical strengthening of the pelvis as well as the insertion place of the joint capsule. The problem is to distinguish the two functionally different parts of the acetabulum as they are not differentiated morphologically. The difference in the thickness of the acetabular walls may be and indication here. Whether the thickening of the acetabular wall does always indicate the propping function of this wall is, however, unclear. It may be connected with the great dimensions of the contributing bones as well. The problem may be solved in sauropods on the basis of the presence of a sacricostal yoke. This develops on demand for the increase of the support efficiency and therefore must be situated within the supporting part of the acetabulum. As it extends over the whole length of the acetabulum in *Opisthocoelicaudia* (the length of its diameter) its center may be regarded as a fulcrum in a resting phase and its extension as that of the articular part of the acetabulum in a quadrupedal position of the animal. The solution of the problem of support of the pelvic region is decisive for the reconstruction of the skeleton as a whole, because the direction of the pelvis and sacrum determines the slope of the vertebral column in that region. It can be thus treated as an issue for the mounting of the remaining parts of the vertebral column.

Table 17

Selected anatomic ratios of *Opisthocoelicaudia skarzynskii* gen. n., sp. n.

	right	left
Total length of fore limb to total length of hind limb		74%
Least breadth to distal breadth of scapula	75%	73%
Angle between glenoid axis (G) and scapular blade axis (SB) (measured directly at the specimen)	about 40°	
Length of humerus to length of femur	72%	
Length of radius to length of humerus	63%	64%
Greatest length of metacarpus to length of humerus	30%	
Length of sternal plate to length of humerus	75%	
Length of pubis to length of ischium	156%	
Length of pubis to length of ischium in acetabulum	58%	
Length of tibia to length of femur	58%	
Breadth of astragalus to distal breadth of tibia	54%	
Greatest length of metatarsus to length of femur	12%	
Least circumference of shaft to its length:		
humerus	59%	54%
femur	49%	
radius	57%	57%
ulna	60%	54%
tibia	60%	60%
fibula	40%	

FORE LIMBS

Based on the above rules the angle of the scapular blade to the horizontal plane can be determined as about 40°, while the posterior angle of the scapular joint is approximately 100°. It can be expected that the first of these angles (i.e. the position of the scapula in the mounted skeleton) could be determined from the scapulocoracoid alone, the axis of the glenoid cavity being regarded as a horizontal one. This angle is, however, very difficult to measure, because the bones of the girdle extend in several planes; it can be used therefore only as a general indication. The basic configuration of the forearm bones is designated by the structure of the joint surfaces of the elbow articulation described above (p. 26), the radius lying in front, the ulna behind. Such a position is very mammal-like but there is no indication of the crossing-over of the bones. The relation of the metacarpals to each other is very well determined too. In the articulated position they interlock at their proximal ends forming a semicircle, their shafts being situated almost vertically. This would result in a lateral direction of the anterior (dorsal) surface of the manus if the sagittal plane of the limb as a whole were parallel to that of the main body. A rather broad cross-section of the thorax must have caused a somewhat oblique position of the limb as a whole, the elbow joint being directed slightly outwards and the anterior surface of the manus forwards and outwards. Such a position of the manus would better agree with the known sauropod footprints (HAUBOLD, 1974) than the laterally facing one. The manus is subject to a strong reduction there being no carpal bones at all and probably practically no phalanges. It is possible that the carpals and phalanges have been lost during the excavation. However, the decrease of the relative size of the astragalus as compared to other sauropods, indicates that the progress in reduction of the ossification did occur in the distal parts of the posterior limbs of *Opisthocoelicaudia*. So we can deal with a similar process in the fore limbs as well. Such a reduction being known from the very beginning of the sauropod history, although to a lesser degree, we can consider the manus of *Opisthocoelicaudia* as a progressive stage of the same evolutionary process. The proximal surfaces of the metacarpals were probably covered by cartilage (cartilaginous carpale or carpals). At the distal ends the metacarpals could have been lengthened by connective tissue.

The total height of the mounted fore limb is 2.74 m, when measured up to the highest point of the scapula, and 1.87 m to the proximal end of the humerus. The latter forms 74% of the total height of the mounted hind limbs (2.46 m). These relations give an indication that the vertebral column was situated relatively high in the anterior part of the thorax, but it does not determine precisely the level of the vertebral column in that region. Another indication of the reconstruction of the backbone position may probably be given by the shape of the scapulocoracoid itself, namely by the bend of the scapular blade in relation to the proximal part of the girdle. The well known differences between sauropod genera as regards this bend should be connected with the position of the chest, the latter being in its turn closely connected with the position of the dorsal part of the vertebral column. There exists probably an optimum angle between the ribs and the posterior scapular margin (text-fig. 18*A*) supporting them by means of the serratus superficialis. If the thorax is lowered this angle would increase seriously (text-fig. 18*B*), thus causing the appearance of component forces twisting the ribs. In order to fix this angle the scapular blade would have to be lifted up (text-fig. 18*C*) in relation to the proximal part of the girdle, the horizontality of the glenoid being retained. The reverse process would be true when the thorax (i.e. the vertebral column) is raised. That is probably why the arched-backed sauropods such as *Dicraeosaurus* and *Diplodocus* have more upwardly bent scapular blades than the straight-backed ones do *(Camarasaurus)*. As a conclusion of the above more upwardly bent scapular blades may be regarded as suggestive of the low position of the anterior dorsalsand conversely. Of course, this can be only treated as a general indication. The shape of the scapulocoracoid indicates a rather high position of the thorax and backbone in *Opisthocoelicaudia*, which is in agreement with the limbs' length ratios.

HIND LIMBS

The articular surfaces of the femur are perpendicular to its long axis, which indicates a vertical position of the femur. The same is true for the proximal articular surface of the tibia. All this causes a straight column-like appearance of the hind limb in resting position. The proximal extremity of the fibula protrudes over a proximal articular surface of the tibia. It does not fit well to the articular condyles of the femur. Its surface faces obliquely medially and upwards, contacting with the cartilaginous menisci, which probably adjusted the articular surfaces of the knee joint as usually. Their presence in the knee joint of *Opisthocoelicaudia* is evidenced by the position of the ligamentous foveae which are situated on the medial wall of the proximal end of the fibula (see text-fig. 16*A*) facing the interior of the joint capsule. There is also a difference of the levels between the distal ends of the fibula and tibia in their parts adjoining each other (see pl. 14, fig. 2). The tibia, which is shorter of the two, is lengthened in its external part by the addition of the astragalus. The latter is longer laterally than medially. No other articulation of the described skeleton is so badly adjusted as the tarso-metatarsal joint. The distal end of the fibula as well as the postero-distal surface of the astragalus bear traces of being covered by cartilage. There existed probably some more cartilages independent from

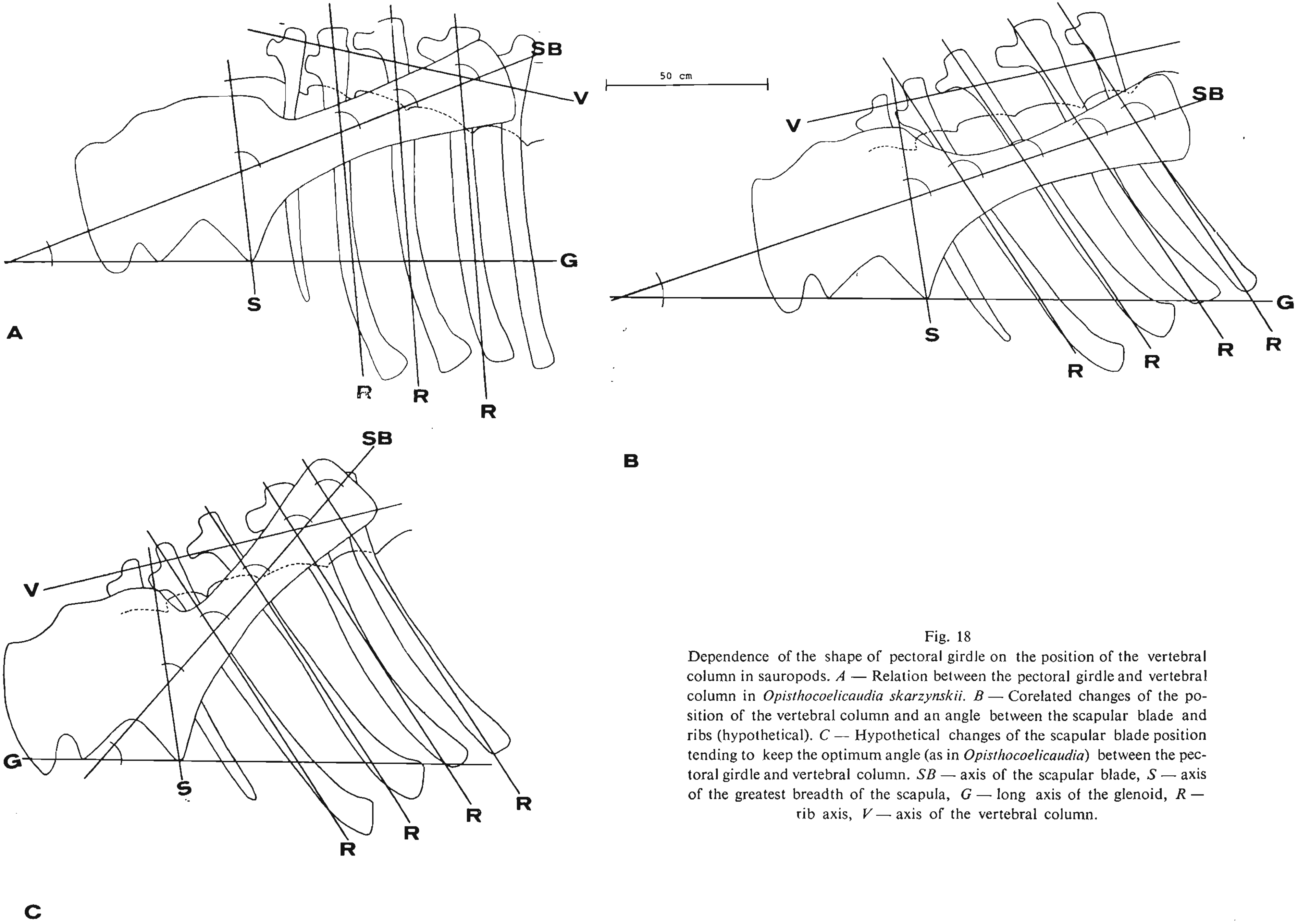

Fig. 18
Dependence of the shape of pectoral girdle on the position of the vertebral column in sauropods. *A* — Relation between the pectoral girdle and vertebral column in *Opisthocoelicaudia skarzynskii*. *B* — Corelated changes of the position of the vertebral column and an angle between the scapular blade and ribs (hypothetical). *C* — Hypothetical changes of the scapular blade position tending to keep the optimum angle (as in *Opisthocoelicaudia*) between the pectoral girdle and vertebral column. *SB* — axis of the scapular blade, *S* — axis of the greatest breadth of the scapula, *G* — long axis of the glenoid, *R* — rib axis, *V* — axis of the vertebral column.

the bone surfaces which filled up the joint, making suitable articular surfaces for the metatarsal. These cartilages would correspond to unossified tarsals. The only surface of the astragalus, which can make an articulation with the metatarsal is its anterior surface, facing forwards and slightly downwards. The external part of this surface fits to the proximal surface of the metatarsal III, constituting thus a basis for the reconstruction of the foot in a semiplantigrade position. The medial part of the astragalus is neither large enough to make a joint surface for the whole metatarsal II, nor fits to a part of it. All metatarsals but metatarsal III articulate proximally by means of a thick cartilage (or cartilages); so their position can be deduced only from their mutual relations, and especially from their relation to the metatarsal III. As their proximal surfaces are rather subrectangular than wedge-shaped as in metacarpals, they form a very flat arch when articulated. Both proximal and distal articular surfaces are distinctly formed, the distal ones being much more suitable for the articular purpose than those in metacarpals. Their slightly spool-like surfaces face farther dorsally than ventrally indicating a preponderance of extension movements. Certain features of a bilateral symmetry about the digit III can be observed as regards the length of the digits; otherwise the pes is asymmetrical. The asymmetry is manifested in the thickness of the metatarsals, in the development of unguals in the digits I—III only, and in the shape of the phalanges themselves (see p.44). The asymmetry of the phalanges causes the oblique position of the unguals, their antero-posterior plane slanting both from sagittal and from vertical planes; their distal ends are directed antero-laterally, while their medial walls face slightly downwards. The mobility of the unguals was probably rather small, their resting position being slightly flexed in relation to the phalanges.

VERTEBRAL COLUMN

Presacral and sacral parts. The position of the sacrum fused with the pelvis is determined by the position of the acetabulum, as mentioned above. In *Opisthocoelicaudia skarzynskii* the sacrum is inclined at an angle of about 10° to the horitzontal plane. No change of direction of the backbone axis can be noticed when passing from the sacrum to the dorsal series. The dorsal part of the vertebral column is basically of the straight type in *Opisthocoelicaudia.* It is caused by the position of the articular surfaces of the centra, which are perpendicular to their axis in dorsals 5—11. The articular surfaces both central and zygapophyseal show a very limited mobility of the dorsal series in a sagittal plane. A very slight downward flexion of this part of the backbone is, however, possible. Such a flexion is desirable when mounting the skeleton on account of the position of the scapula, which should not be very far away from the vertebral column, although their mutual relation is not strictly determined. Despite their poor preservation, the dorsals numbered 1—3 provide some interesting data concerning the anterior part of the vertebral column. Their reduced lengths indicate not very long cervicals, at least in the posterior part of the neck, whereas the articular surfaces of their centra show a certain flexion of the vertebral column in this region. The ball of the dorsal 3 faces slightly upwards indicating the predominance of the upwards motions, whereas the downwardly turned ball of the dorsal 1 could simply indicate the downward direction of the neck (and a predominance of downward motions), otherwise evidenced by the stucture of the metapophyses. The ligamentum nuchae extended between two rows of the metapophyses (as reconstructed by JANENSCH, 1929*b* in *Dicraeosaurus*) to insert on the anterior surface of the sacral spine. Such a posterior insertion of the ligamentum nuchae indicates a not very short neck. The shortening of the first dorsals and presumably also of the last cervicals was perhaps connected rather with an increased mobility of this region. The groove between the metapophyses corresponds to the shape and volume of the ligamentum nuchae in the posterior part of the dorsal series from about dorsal 7. More anteriorly it seems to be too wide and too deep to be filled with the ligamentum, its considerable volume being rather an adaptation to the lateral movements of the much narrower ligamentum. The medial walls of the metapophyses are quite even, there being no traces of the ligamentary insertions. In the posterior part of the dorsal series, beginning from dorsal 7 the ligamentum nuchae could have fused with the interspinal ligamentum, being thus fixed to the underlying vertebra in the interspinal regions. In the anterior dorsals the ligamentum nuchae was probably completely free, there being neither spinal nor interspinal insertions; the prespinal and postspinal laminae are very feeble or lacking. Extending along the vertebrae and not attaching to them, ligamentum nuchae is able to work only over the straight vertebral column or over a convex one, which means a horizontal or downwardly curved neck. Otherwise it fails to function. If the reconstruction of the ligamentum nuchae in *Opisthocoelicaudia* is right, the neck of this reptile must have been horizontal or curved downwards with the repponderance of downward movements.

Tail. No other part of the skeleton awakes so many problems as the tail in *Opisthocoelicaudia*. The base of the tail is somewhat lifted in relation to the sacrum, thus turning the axis of the vertebral column from one descending posteriorly at an angle of 10° into a more horizontal one. This initial direction seems to be kept all over the length of the tail or to be slightly flexed upwards in resting position. So the tail profile would have been horizontal or bent upwards, dorsally concave. The evidence for such a position of the tail includes the absence of the wedge-shaped or downwardly flexed centra in the caudal series as well as heamapophyses firmly fused with the centra in caudals 6—17. All centra have approximately the same slope of the articular surfaces in relation to the axis of the centra; the angle is a little more than 90° in the anterior half of the tail (ending with caudal 11), the posterior articular surfaces facing very slightly upwards, while the anterior ones respectively slightly downwards. Such an obliquity would have caused a downward slope of the tail, in spite of the absence of the wedge-shaped centra, only if the posterior articular surface of the sacrum were vertical or faced downwards, which was, however, not the case. In the posterior part of the tail, beginning from the caudal 12, the articular surfaces of the centra are perpendicular to their axis. The ossified chevrons 6—16 checked, no doubt, the downward movements of the tail indicating at the same time that no appreciable downward bending of the tail axis could occur in this region. The mobility was also very limited in the more posterior region of the tail, the centra from 22 to 28 being probably coossified, though the region between 16 and 22 was perhaps more mobile. It is difficult to imagine the animal being unable to touch the ground with its tail, but it is equally difficult to show how it could do so. Perhaps it managed this by summing up the small flexions possible between the first five caudals having loosely articulated chevrons, but it was by no means its resting position. The upward flexion of the tail between caudals 3 and about 20 and especially from 6 to 15 was probably more easy than the downwards one and seems to be more natural in *Opisthocoelicaudia*. The opisthocoelous centra of the anterior half of the tail constitute a very characteristic feature of the tail in *Opisthocoelicaudia*.

TAIL'S FUNCTION AND PROBABLE HABITS IN *OPISTHOCOELICAUDIA*

The well known rule that the convex articular surface turns to the region of the increased mobility as compared to the concave one, suggests that the opisthocoelous tail could have served as a support or as an anchor. The opisthocoelous caudals occur very seldom, but the known examples confirm this suggestion. They are known in some groups of Chelonia such as Baenidae, Chelydrinae and Platysterniinae. The available data concerning these groups (MŁYNARSKI & WERMUTH, 1971 and MŁYNARSKI personal communication) are as follows: Platysternon is a fresh-water form living in streams. It anchors with its tail struggling against a current. Chelydra can walk on the ground being supported on its semierect limbs as well as on its opisthocoelous tail. The use of the tail of *Opisthocoelicaudia* as an anchor is quite impossible, but the tail working as a prop seems more probable. Of course it could not have been a supporting tail in sense of Abel (1910) working as such, while the animal stood on its four limbs. Occasional bipediality is therefore strongly suggested. It is, however, not a matter of briefly assuming a bipedal stance as possible in most of the tetrapods. If the bipedal stance was really familiar to *Opisthocoelicaudia* it must have been connected with some important part of its life activity, most probably, in my opinion with a way of taking food. The animal must have been stable in this position; otherwise this posture would not have left such distinct traces in the skeleton architecture. Features supporting the hypothesis of the Megatherium-like habits of *Opisthocoelicaudia* are as follows:

1. The acetabulum is strongly deepened all along the iliac part of it. Its thickened wall is completed by the sacricostal yoke in the whole upper part of the acetabulum regarded as an articular surface in a quadrupedal position (see above), but consists of the ilium alone in its anterior part. The extent of the movements in acetabulum can be estimated from the above at almost 180°, with the strong preponderance of retraction. Such a strong retraction would have been unnecessary in a quadrupedal posture. In the most retracted position the femur would have been almost parallel to the axis of the tail base, which meant the erect position of the body. Whether the thickening of the acetabular wall really means such a big extension of movements is unclear (see above). The problem needs further investigation.

2. The architecture of the tail as a whole as well as the biological sense of this organ can be fairly well explained, if one assumes the familiarity of the "tripodal posture" in this genus. The possibility of the dorsal flexion of the anterior half of the tail would have been useful in the erect position of the body when the tail touched the ground with its posterior part and the anterior one made a tripod with the hind limbs. The maximum curve of the tail ought to be situated then at a distance from the fulcrum approximately equal to the length of the hind limb. The caudal 12 is situated at such a distance from the fulcrum in *Opisthocoelicaudia* and it is really within the region of the increased dorsal flexibility. Neither dorsal nor ventral flexibility should have been necessary in the posterior part of the propping tail, which lay on the ground; so the centra of the caudals 22—28 are partly coosified in *Opisthocoelicaudia*. The very oblique position of the first five chevrons seems to be an adaptation to the strong downwards flexion of the tail, which would have been possible only in the erect position of the body in *Opisthocoelicaudia*. Of course it could have been an adaptation to laying eggs as well. There is, however, a striking difference between *Opisthocoelicaudia* and other known sauropods in the position of the chevrons at the tail base, *Brachiosaurus* with its strongly sloping tail being the most similar in this regard. The tail problem needs also further investigation, and particularly the revision of the previous reconstructions of the position of the tail (e.g. in *Camarasaurus*) as well as the position of the chevrons which sometimes may be wrong. This is, however, not possible within the scope of the present paper. As regard the use of the tail, *Opisthocoelicaudia* should not be treated separately from other sauropods, the tail problem being open in the whole group.

3. Such features of the pelvis as the outward bend of the iliac blades and the fused symphysis pubis could be, in my opinion, connected with the bipedal posture, serving as a support for the viscera. The outward bend of the ilium could be also an adaptation to the increased lateral mobility of the dorsal part of the vertebral column.

The data which seemingly disagree with the hypothesis of the Megatherium-like habits of *Opisthocoelicaudia* are as follows:

1. The fore limbs are relatively long and heavy and the pectoral girdle as well as sternal plates are very massive, whereas the whole fore limbs are reduced in dimensions in most of the bipedal and in the occasionally bipedal animals. However, the Megatherium-like habits would have more likely appeared within a group feeding from high vegetation that in one looking for low plants. In sauropods which are typical quadrupeds such differences in feeding habits were probably closely connected with the length of the fore limbs, which would have been relatively longer in high vegetation feeders. So the relatively considerable length of the fore limbs

of *Opisthocoelicaudia* is probably not contradictory to the hypothesis of its Megatherium-like habits.

2. In bipedal animals the vertebral column may be regarded as a beam supported by one end only (SLIJPER, 1946), so the demands made on the spinal ligaments and epaxial musculature would be greater here as compared with quadrupeds. Therefore relatively higher spines could be expected in bipedal or in the occasionally bipedal animals, which is not the case in *Opisthocoelicaudia*. However, the height of spines depends also on some other factors, such as the direction of the vertebral column in the stable phase of bipedality. The demands on spinal ligaments and muscles and respectively the height of the spines would probably decrease as this direction becomes more vertical. If *Opisthocoelicaudia* was really occasionally bipedal its posture would have been near verticality. This question, however, must still be a subject of more detailed investigations.

CONCLUSIONS

The limbs of *Opisthocoelicaudia* were basically of a pillar-like, graviportal type. The position of the humerus and that of the elbow joint was mammal-like. That of the more distal part of the fore-limb was reminiscent of the reptilian situation in displaying the uncrossed antebrachial bones and the manus not fully turned forwards. The possible antero-lateral and not lateral position of the manus was probably caused by the outward turn of the fore-limb as a whole. Both manus and pes are characterized by a strong reduction of the ossification, carpals and digits being unossified and tarsus markedly reduced in dimensions.

The dorsal part of the vertebral column together with the sacrum formed a straight line sloping posteriorly at an angle of about 10°. As shown by the reconstruction of the nuchal ligament, the neck was probably of medium length (about 5 m or so) and was carried low. The tail was carried in a horizontal position not touching the ground, as evidenced by the structure of caudals. Such uncommon features of the caudals as the opisthocoelous centra together with some additional characters of the caudals and some characters of the pelvis (acetabulum, iliac blade, symphysis pelvis) could be explained fairly well by an ability of assuming a tripodal position. This might be connected with the feeding habits.

The stream-line shaped body of the animal and the horizontal position of its tail, as reconstructed, text-fig. 19, are slightly suggestive of the aquatic life, but they do not prove it. Even when submerged sauropods remained still basically walking animals. That is why their anatomy gives no decisive arguments for the solution of the problem of their habitat, as already shown by COOMBS, 1975.

SYSTEMATIC POSITION

Three main facts should be taken into account when considering the problem of the systematic position of the described postcranial skeleton of *Opisthocoelicaudia skarzynskii*.

1. The skeleton comes from the Nemegt Formation, the locality Altan Ula IV. The skull of *Nemegtosaurus mongoliensis* (NOWIŃSKI, 1971) was found in the same formation in the locality of Nemegt. Other sauropod remains known from this formation (ZPAL MgD-I/25c) are identical with *Opisthocoelicaudia*. This may suggest that the both forms are conspecific.

2. The axial skeleton, which is widely held to be the most important part of the postcranial skeleton from the point of view of systematics in sauropods, reveals striking similarities to that of *Camarasaurus* in its dorsal part. This and some other features of *Opisthocoelicaudia* may indicate its relation to the Camarasauridae.

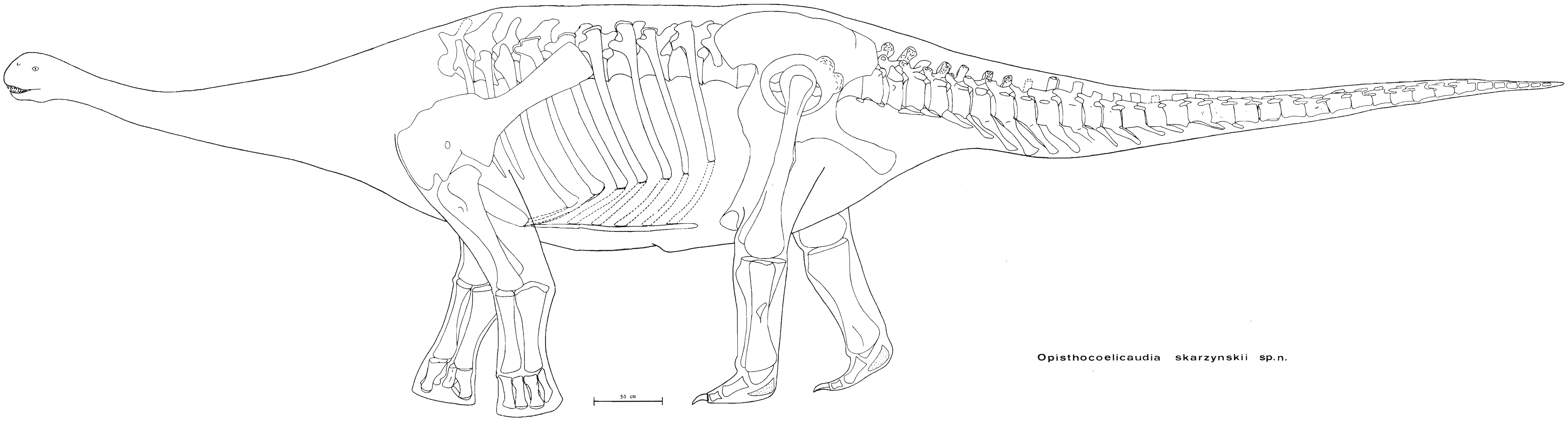

Fig. 19
Reconstruction of the skeleton and restoration of *Opisthocoelicaudia skarzynskii* gen.n., sp.n.

3. The close resemblance of some other features of *Opisthocoelicaudia* to those of the Titanosaurinae, together with the Upper Cretaceous age of the specimen may indicate its belonging to this subfamily.

Before making a choise between these possibilities it is necessary to consider them in detail.

CONGENERITY OF *NEMEGTOSAURUS* AND *OPISTHOCOELICAUDIA*

The occurence of both *Opisthocoelicaudia* and *Nemegtosaurus* in the same formation does not support in any way the supposition of their congenerity. The common occurrence of several genera of these huge animals in the same formation and even in the same locality is possible, as shown by very well known examples of the Tendaguru beds (*Barosaurus africanus*, *Brachiosaurus brancai*, *Tornieria robusta*, *Dicraeosaurus sattleri* — Oberer Horizont des Saurier-mergels after JANENSCH, 1929*a)* as well as Morisson Formation (*Apatosaurus louisae*, *Barosaurus* sp., *Camarasaurus lentus*, *Diplodocus longus*, *Astrodon* sp., — Dinosaur National Mon. Quarry, Utah, after GILMORE, 1936 and others). This can be partly caused by an accumulation of allochtonous remains, which is, however, less possible in case of sauropods. More likely this may be caused by the chronostratygraphical differences within formations as well as by the ecological differentiation of the animals occurring in the same locality. The bone material present in the Nemegt Formation seems to be autochtonous (GRADZIŃSKI, 1970) and the significant differences of stratigraphic age of the specimens coming from the localities of Nemegt and Altan Ula seem improbable because of a possibly very rapid accumulation (GRADZIŃSKI *l.c.*). The differences between the specimen from Nemegt and that from Altan Ula caused by ecological factors seem possible instead. The geological evidence neither contradicts nor confirms the supposition of the specific and generic identity of the specimens coming from the Nemegt Formation, whreas the anatomical features of *Opisthocoelicaudia* preclude its assignement to Dicraeosaurinae to which *Nemegtosaurus* appertains.

COMPARISON OF *OPISTHOCOELICAUDIA* WITH *CAMARASAURUS* AND WITH SOME OTHER REPRESENTATIVES OF THE CAMARASAURIDAE

The vertebral column of *Opisthocoelicaudia* resembles *Camarasaurus* in having very low spines divided into two metapophyses overlaping the postzygapophyses. In the sacral region there are undivided spines, which are simlarly low and tuberous at the tops in both genera. Both have simple transverse processes of caudals and unforked chevrons. The dorsal part of the backbone is straight, its anterior portion being situated relatively high. This has to be correlated with the limb length ratios, but corresponding data are missing or very unprecise. In Sauropoda as in many fossil groups the exact data concerning the ranges of the intergeneric variation are missing which makes it impossible to ground the assignements on the numerical data. The data concerning the mutual relations of the different bones within one individual are especially poor, because of the scarcity of the completely preserved specimens. The pectoral girdle of *Opisthocoelicaudia* resembles that of *Camarasaurus* and *Brachiosaurus* in a small size of the angle between the glenoid axis and the long axis of the scapular blade, but differs from them in other features. The subquadrate shape of the coracoid which makes a difference between the type specimen of *Opisthocoelicaudia skarzynskii* and representatives of *Camarasaurus* seems to be a subject to individual changes, as shown by the specimen ZPAL MgD-I/25c (pl. 8, fig. 1) representing the individual younger than the type specimen.

From about 9 sauropod genera occurring in Central Asia only one, *Euhelopus*, known from the Lower Cretaceous of Shantung (China) belongs probably to the Camarasauridae. This supposed Camarasaurid of *Brachiosaurus*-like appearance is distinguished from the other representatives of the family by a somewhat intermediate type of skull. Otherwise it is typical of the family. *Euhelopus* resembles *Opisthocoelicaudia* in some features of the pelvis such as a fused symphysis pelvis, a strongly curved anterior part of the ilium as well as in a much elongated sacrum comprising 5 vertebra. All these features are supposed to represent a certain stage of the evolutionary tendency to the strengthening of the pelvis, characteristic of both genera but not of the other Camarasauridae. This is the only positive evidence of the close relationship between *Euhelopus* and *Opisthocoelicaudia*; other common features of both genera bear on the camarasaurid-like character of the dorsal vertebral series. Some important differences can be stated between these two forms as well. These are: a relatively short pubis in *Euhelopus* and a considerable shortening of the last three dorsal ribs. It is difficult to comment upon the relationship of the two forms without an adequate knowledge of their osteology. Some important parts of the skeleton preserved in one of them (the skull and cervicals of *Euhelopus* and the tail in *Opisthocoelicaudia*) are unknown in the second one, or their assignement to the genus is uncertain (the pectoral girdle and humerus described by YOUNG, 1935 as belonging to *Euhelopus*).

THE MEANING OF THE *CAMARASAURUS*-LIKE FEATURES

The *Camarasaurus*-like character of *Opisthocoelicaudia* appears in a set of features connected with the animal posture and hence with its habits. The complex of features consisting of the backbone structure and pectoral girdle character is more plastic and therefore more differentiated in sauropods than the remaining postcranial features, the limbs of those par exellence graviportal animals having only very limited possibility to change. The skull being unpreserved very often, this complex is regarded as a main basis for systematics in sauropods. It will be handeled below. The straight course of the dorsal portion of the vertebral column, reconstructed (p. 49) from the articulated dorsals, is probably correlated with the low spines and may be deduced from them. The close relation between the neural spine heights and the backbone curvature which is the basis of the above statement is, however, denied by SLIJPER (1946). After this author the construction of the trunk skeleton which is that of the bow-and-string is balanced chiefly by the weight of intestines combined with the constructive qualities of this arrangement itself. The elasticity of the bow which is, of course, necessary for the proper action of this construction, depends mainly on the shape of the transverse sections of the centra, the epaxial musculature and ligaments playing merely a second-rate role in this respect. The neural spines which form the insertion places for these muscles and ligaments are therefore not affected by the demands of the bow-and-string construction. Their height and inclination depends on the type of the mobility of the body axis which is caused by the epaxial musculature, the strength and direction of these muscles being very essential this time. So the features of the neural spines are determined by dynamic function of the trunk skeleton and not by static one, which can be therefore neglected as SLIJPER (1946) considered. All this is probably true in the case of the small animals because the maintenance of the back-bone elasticity gets easier with the decreasing size of the body; it is also true for those characterized by straight body axes because the demands on the elasticity of the bow decrease with the decreasing curvature. But it is probably not true for the animals characterized by very big dimensions, especially if connected with the arched back-bone, as known in sauropods. Besides the bow-and-string construction of the trunk skeleton, which can be expected in reptiles must differ very much from that present in mammals, because of the presence of the strong tail as well as of its great importance to the backbone architecture. This construction is probably elongated as compared to mammals, the anterior part of the tail (the one on which the ilioischiocaudal muscles insert) being included in the bow, whereas the caudal muscles and aponeuroses make an elongation of the string. The demand on elasticity of such an enormous bow would probably involve the increase of the neural spines. This increase would be more marked the more pronounced the curvature of the backbone. The demands of the ligamentum nuchae supporting the neck and, to some extent, those of the supraspinal and interspinal ligaments supporting the tail constitute the second factor of importance for the development of the neural spines. The longer are those protruding parts of the body (neck and tail) the more effective the ligaments must be. Their effectiveness depends not only on their strength but also on the situation of their attachments, the higher neural spines being advantageous in this regard (angle of insertion of GREGORY, 1912). Both factors, the axial skeleton curvature and the ligament requirements cause the same effects and sometimes it is difficult to discern, which is more important.

The comparison of the huge long-necked and long-tailed forms such as *Diplodocus* and *Apatosaurus*, provided with high spines with relatively short-necked forms with low spines as *Camarasaurus* suggests that the spines are developed chiefly for the support of the neck or both neck and tail from the sacrum which is the best buttressed region of the body. The symmetry of the neural spines about the sacrum correspond with the symmetry of the length of the neck and tail about the middle of the trunk in the high spine forms. The place of maximum length of spines is shifted from about the last dorso-sacrals to the middle of the dorsal series in Brachiosaurus which has a much shortened tail together with a very long neck. However, if one compares the relatively smaller short-necked but arched-backed forms such as *Dicraeosaurus* provided with huge spines with much bigger straight-backed forms as *Camarasaurus* and *Opisthocoelicaudia* with low spines and *Euhelopus* with long neck and low spines the architectonic role of neural spines seems to be obvious.

The ligamentum nuchae acts on the high spines of arched-backed forms as well as on the low spines of straight-backed ones causing their further variation. As JANENSCH (1929*b*) stated in its comprehensive study of the vertebral column of *Dicreosaurus*, the main reason for sagittal incision of spines is the tendency to lower the position of the ligamentum nuchae in order to increase the downwards mobility of the neck; the high spines are advantageous for the efficiency of the ligamentum nuchae but they check the downwards movements, the more so the higher they are. The forked spines occur where the necessity of the habitual lowering of the neck is in conflict with the demands of the bow-and-string construction of the trunk vertebral column. As evidenced by the first dorsals of the best known sauropod genera (text-fig. 3) most of which have the forked spines, the preponderance of downwards movements is very common in sauropods, only few making exceptions. These are *Brachiosaurus*, *Euhelopus*, *Tornieria* and probably some other representatives of the Titanosaurinae, which lack the metapophyseal grooves — evident traces of ligamentum nuchae running close to the vertebral axis.

The forked spine dorsals of different sauropods differ from each other first of all in their height, the abrupt lengthening of metapophyses being seen when passing from Camarasauridae to Atlantosauridae (see text-fig. 3). Secondly they differ by the rate of fusing of the metapophyses, while going down the dorsal series (text-fig. 3). The last dorsals have single spines as a rule, *Opisthocoelicaudia* making an exception in this regard. The rate of fusing of the metapophyses may be connected with the length of the neck and the type of its mobility; these connections must be, however, complex and are not hitherto sufficiently understood. The dorsals of the forked spine type differ as well in the presence or absence of the tubercule on the bottom of the metapophyseal groove; otherwise they are very similar. The last named tubercule acts as a substitute for the undivided neural spine (or it is its homologue) making the insertion place for the ligamentum nuchae. Such a tubercule is to be seen on the first dorsals of *Diplodocus* (text-fig. 3*F*) or *Tornieria robusta* and in all the dorsals of *Euhelopus zdanskii* (text-fig. 3*C*). The very upper part of the prespinal lamina of the posterior dorsals in *Camarasaurus* can be probably treated as the same. Other sauropods such as *Opisthocoelicaudia*, *Camarasaurus* (in anterior part of its dorsal series) *Apatosaurus* and to some extent *Dicraeosaurus* (between presacral vertebra 12 and 16) have no intermetapophyseal tubercule. The division of the anterior sauropod dorsals into two types may be proposed, the one of which, provided with two metapophyses or with undivided spine has no insertion place for ligamentum nuchae, the second with metapophyses or with undivided spines has a distinct trace of the ligamentum nuchae insertion. This difference must be, in my opinion, connected with the way of carrying head and neck, the lack of nuchal ligament insertion together with the development of the metapophyseal groove indicating the low position of the head, the presence of the insertion trace in the metapophyseal groove or undivided spine suggesting the habitual lifting or permanent upper position of the neck correspondingly. Such a division runs across the well known division into forked and unforked type of spines thus indicating that we are dealing with a mosaic of spine features, all of them fairly well explained by function.

The character of the chevrons which is an auxilliary diagnostic feature in Sauropoda is probably connected with the tail attitude. It can be therefore regarded as a „posture feature" just like the spine architecture of the dorsals.

It is worth noticing, that the simple chevrons of *Opisthocoelicaudia* occur in the tail, which was no doubt, carried clear off the ground by gait, whereas the biramous type of chevrons is known in the posterior parts of the tails in *Diplodocus* and *Dicreaosaurus*. The tail was probably dragged by gait or laid on the ground in the resting position in *Dicreaosaurus*, as evidenced by the shape of caudal centra *(Dicreaosaurus hansemanni*, caudals 3—6 JANENSCH 1929b Taf III, *Dicraeosaurus sattleri*, at least caudals 5 and 6 JANENSCH *l.c.* Taf. VII), but the evidence concerning *Diplodocus* is not so clear. The caudals of *Camarasaurus* figured by OSBORN & MOOK (1921) show in my opinion no distinguished regions of flexion. All caudals are equilateral in lateral aspect being similar to those of *Opisthocoelicaudia* in this respect and they are provided with simple chevrons. It seems probable that *Camarasaurus* was similar to *Opisthocoelicaudia* in the overall attitude of its tail too, and so the reconstruction of COPE figured by OSBORN and MOOK (1921 pl. 82) was more correct than that of OSBORN and MOOK (1921 pl. 83 and 84) in this regard. I would assume that the type of chevrons is correlated with the tail's overall attitude, the biramous type occurring only in dragged tails [2]. However the problem remains open until new evidence comes.

A highly behavioural character of discussed features together with their plasticity make it possible for them to appear repeatedly in different groups of these animals, the more so that the connection and mutual correlation of the features are rather simple. Whether we really deal with convergence, or with a set of derivative camarasaurid-like features (synapomorphic features of HENNING, 1965) is a difficult question. It may be answered, rather arbitrary, basing on all other available evidence concerning the problem.

COMPARISON OF *OPISTHOCOELICAUDIA* WITH THE ATLANTOSAURIDAE MARSH 1877

The limb bones and the pelvic girdle of *Opisthocoelicaudia* are reminiscent of the atlantosaurid type rather than of the camarasaurid one in the following features:

1. A not much expanded distal end of scapula (see table 17).
2. The development of the processus ambientis.
3. The ischium forming a relatively larger part of the acetabulum; its shaft is shorter as compared to the shaft of the pubis.
4. Metacarpals I and V are the strongest of all.
5. The sternal plates of considerable length (see table 17) and of the same shape as in *Alamosaurus sanjuanensis*.

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[2] The correlation between the biramous type of chevrons and the dragged type of tails was often explained by the necessity of a better protection of the blood vessel in the region contacting with the earth than in the regions kept off the ground.

6. A straight external edge of the humerus.
7. A strong pectoral scar.
8. A comparatively distinct olecranon.
9. Relatively great length of the caudals.
10. A posterior situation of the neural arch upon the centrum.

The features numbered 1—3 are characteristic of both the Atlantosaurinae and the Titanosaurinae most of the features (4—10) are limited to the Titanosaurinae NOPCSA 1928. In spite of these similarities *Opisthocoelicaudia* cannot be assigned to the Atlantosauridae because of its opisthocoelic tail, procoelic caudals being regarded as a diagnostic feature of the whole family Atlantosauridae from the very beginning of their history. The existence of the independent family might be therefore suggested. This would be characterized by the atlantosaurid and titanosaurid features combined with the overall attitude of the skeleton similar to the Camarasaurinae. However, no one of the atlantosaurid features, of *Opisthocoelicaudia* seems to be sufficiently important to justify a foundation of such a taxon. At least four of these features, the ones numbered 2, 5, 7 and 8 may be regarded as progressive in sauropods. They can be therefore expected in the Late Cretaceous sauropods representing the final stage of the evolutionary tendencies in this infraorder, irrespective of what family they belong to. The same is probably true of the relative contribution of the ischium and pubis to the formation of the pelvis. The differences between the Jurassic Camarasauridae and Atlantosauridae in this regard may be a matter of the rate of evolutionary changes in these families; Atlantosauridae evolved probably more rapidly. The process of increasing of the acetabular part of ischium in relation to the acetabular part of pubis is probably common for the whole infraorder, as mentioned by STEEL (1970). It should be also noticed that this problem eludes an accurate consideration because of the scarcity of the exact numerical data. The lengthening of the shaft of pubis, which is said to be correlated with the decrease of its share in the formation of the acetabulum in the Atlantosauridae, may be also a sign of a more general tendency. The overlengthening of this bone (see table 17) in *Opisthocoelicaudia* may be, however, a generic feature as well, supposed to be connected with the adptation to the habitual verticality, if it really existed. The degree of extension of the distal end of scapula seems to be a generic feature rather then one of the higher systematic rank; in any case it seems to be invalid as a feature of familial rank.

CONCLUSIONS

Since the titanosaurid and atlantosaurid characters of *Opisthocoelicaudia* seem to indicate something else than its close relationship to the Atlantosauridae there is no objection to assigne it to the Camarasauridae. The group of camarasaurid features is thus decided to be of synapomorphic character and not caused by convergence. The development of the camarasaurid-like group by convergence from the atlantosaurid stock is the less probable, as this family is represented itself in Central Asia. *Opisthocoelicaudia* is tentatively assigned to the Euhelopodinae based on the similarities cited above and on the fact, that it is one of the only two comprehensively known representatives of the Camarasauridae in Central Asia. The most outstanding generic features of *Opisthocoelicaudia* are its opisthocoelous caudals and the relatively long vertebral centra of both dorsal and caudal vertebrae.

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EXPLANATION OF PLATES

Photo: W. Skarżyński

PLATE 1

Opithocoelicaudia skarzynskii gen. n., sp. n. ZPAL MgD-I/48

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia

Dorsal vertebrae (see also pls 2 and 3, figs 1—5 and 7—9, pl. 4, fig. 4 pl. 12, fig. 4).

1. Dorsal 1: anterior view, stereophotographs.
2. Dorsal 2: anterior view.
3. Dorsal 4: anterior view, stereophotographs.
4. Dorsal 3: anterior view.
5. Dorsal 5: anterior view.
6. Dorsal 9: anterior view, stereophotographs.
7. Dorsal 7: anterior view, stereophotographs.
8. Dorsal 8: anterior view.
9. Dorsal 10: anterior view.

All × 1/10

PLATE 2

Opisthocoelicaudia skarzynskii gen. n., sp. n. ZPAL MgD-I/48

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia

Dorsal vertebrae (see also pls 1 and 3, figs 1—5 and 7—9, pl. 4, fig. 4, pl. 12, fig. 4).

1. Dorsal 2: posterior view, stereophotographs.
2. Dorsal 3: posterior view.

3. Dorsal 5: posterior view, stereophotographs.
4. Dorsal 7: posterior view.
5. Dorsal 6: posterior view, stereophotographs.
6. Dorsal 10: *a* left side view, *b* posterior view, stereophotographs.
7. Dorsal 9: posterior view.

All ×1/10

PLATE 3

Opisthocoelicaudia skarzynskii gen. n., sp. n. ZPAL MgD-I/48

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia

1—5, 7—9 dorsal vertebrae (see also pls 1, 2 and 4, fig. 4, pl. 12, fig. 4)
1. Dorsal 7: left side view, stereophotographs.
2. Dorsal 8: left side view.
3. Dorsal 9: stereophotographs *a* left side view, *b* right side view.
4. Dorsal 6: right side view.
5. Dorsal 8: right side view, stereophotographs.
7. Dorsal 1: left side view.
8. Dorsal 2: left side view.
9. Dorsal 4: left side view.

All dorsals × 1/10

6. Pelvis (see also pl. 12, fig. 1), medial view, stereophotographs, ×1/20)

PLATE 4

Opisthocoelicaudia skarzynskii gen. n., sp. n. ZPAL MgD-I/48

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia

Caudal vertebrae (see also pls 5, 6)
1. caudals 1—2, stereophotographs: *a* ventral view, *b* left side view, *c* caudal 1, anterior view, *d* dorsal view.
2. caudals 3—5: *a* left side view, stereophotographs, *b* ventral view.
3. fused centra of sacro-caudals 1 and 2; the anterior part of the first one lacking, right side view.
4. Dorsal 3, right side view (see also pl. 1, fig. 4., pl. 2, fig. 2.)

All ×1/10

PLATE 5

Opisthocoelicaudia skarzynskii gen. n., sp. n. ZPAL Mg-I/48

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia

Caudal vertebrae (see also pl. 4, fig. 1, 2 and pl. 6)
1. caudals 3—5, stereophotographs: *a* dorsal view, *b* caudal 3 anterior view, *c* caudal 5 posterior view.
2. caudals 6—8 (see also pl. 6, fig. 4.), stereophotographs: *a* left side view, *b* ventral view, *c* caudal 6 anterior view.

3. caudal 2, posterior view, stereophotographs.
4. sacro-caudal 2, posterior view, stereophotographs.
5. caudals 9—10 (see also pl. 6, fig. 5.), left side view.

All ×1/10

PLATE 6

Opisthocoelicaudia skarzynskii gen. n., sp. n. ZPAL Mg-I/48

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia

Caudal vertebrae (see also pl. 4, figs 1, 2 and pl. 5)

1. caudals 16—20: *a* dorsal view, *b* left side view.
2. caudals 20—24; *a* dorsal view, *b* left side view.
3. caudals 24—28; *a* dorsal view, *b* left side view.
4. caudals 6—8 (see also pl. 3, fig. 2): *a* caudal 8, posterior view, stereophotographs, *b* dorsal view.
5. caudals 9—10 (see also pl. 5, fig. 5.): *a* anterior view, stereophotographs, *b* posterior view, stereophotographs, *c* ventral view, stereophotographs, *d* dorsal view.
6. caudals 29—34 left side view.
7. caudals 11—15: *a* left side view, stereophotographs, *b* dorsal view.

All × 1/10

PLATE 7

Opisthocoelicaudia skarzynskii gen. n., sp. n. ZPAL MgD-I/48

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia

1. right scapula and coracoid, stereophotographs, ×1/15: *a* antero-dorsal view, *b* lateral view, *c* medial view, *d* postero-ventral view.
2. right sternal plate (see also pl. 11, fig. 1.), stereophotographs, ×1/10: *a* anterior view, *b* posterior view.
3. left metacarpals I—III, dorsal view, ×1/9.
4. right radius (see also pl. 9, fig. 2.), medial view, stereophotographs, ×1/11.
5. right radius and ulna (see also pl. 11, fig. 3.), proximal view, ×1/8.

PLATE 8

Opisthocoelicaudia skarzynskii gen. n., sp. n. ZPAL MgD-I/48 except fig. 1

Upper Cretaceous, Nemegt Formation, Altan Ula I, Gobi Desert, Mongolia

1. Right scapula and coracoid ×1/15: *a* lateral view, stereophotographs, *b* medial view.
   ZPAL MgD-I/25c, Altan Ula IV.
2. Left scapula and coracoid, medial view, stereophotographs, ×1/12.

3. Right humerus (see also pl.. 9, fig. 3.), distal view, posterior surface of the bone faces upwards; the transverse line visible on the medial side of the bone is a fracture and not a line of division into medial and lateral condyles, stereophotographs, ×1/9.
4. Left femur, (see also pl. 13, fig. 2.), proximal view, posterior surface of the bone faces upwards, stereophotographs, ×1/9.
5. Right ulna (see also pl. 7, fig. 5., pl. 9, fig. 1., pl. 11, fig. 3.), medial view, ×1/12.
6. Right astragalus (see also pl. 14, fig. 8.), postero-distal view, stereophotographs, ×1/10.

PLATE 9

Opisthocoelicaudia skarzynskii gen. n., sp. n. ZPAL MgD-I/48

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia

1. Right ulna (see also pl. 7, fig., 5., pl. 8, fig. 5.), stereophotographs, ×1/12: *a* anterior view, *b* lateral view.
2. Right radius (see also pl. 7, figs 4, 5.), ×1/12: *a* posterior view, stereophotographs, *b* lateral view, stereophotographs, *c* anterior view.
3. Right humerus (see also pl. 8, fig. 3.): *a* lateral view, stereophotographs, ×1/12, *b* anterior view, stereophotographs, ×1/12, *c* posterior view, ×1/12, *d* medial view, stereophotographs, ×1/12, *e* proximal view, posterior surface of the bone faces upwards, stereophotographs, ×1/10.

PLATE 10

Opisthocoelicaudia skarzynskii gen. n., sp. n. ZPAL MgD-I/48

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia

Right ribs (see also pl. 11, fig. 6.)

1. rib 2: *a* anterior view, *b* lateral view.
2. rib 3: *a* anterior view, *b* lateral view.
3. rib 4: *a* anterior view, *b* lateral view.
4. rib 5: *a* anterior view, *b* lateral view.
5. rib 6: anterior view.
6. rib 7: anterior view.

All stereophotographs, ×1/13

PLATE 11

Opisthocoelicaudia skarzynskii gen. n., sp. n. ZPAL MgD-I/48

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia

1. Right sternal plate (see also pl. 7, fig. 2.), stereophotographs, ×1/13: *a* ventral view, *b* dorsal view.
2. Left metacarpus (see also pl. 7, fig. 3.), *a* proximal articular surfaces, ×1/8, *b* posterior view, ×1/9, *c* metacarpals III, IV, V. dorsal surfaces, stereophotographs, ×1/9.

3. Right radius and ulna, distal view, (see also pl. 7, fig. 5., pl. 9, figs 1, 2., pl. 8, fig. 5.), stereophotographs, ×1/8.
4. Left tibia with fused astragalus, lateral view, stereophotographs, ×1/12.
5. Right fibula, medial view, stereophotographs, ×1/12.
6. Rib 4, (see also pl. 10, fig. 3.), medial view, stereophotographs, ×1/13.

PLATE 12

Opisthocoelicaudia skarzynskii gen. n., sp. n. ZPAL MgD-I/48

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert Mongolia

1. Pelvis, stereophotographs, ×1/20 (see also pl. 3, fig. 6.): *a* anterior view, *b* ventral view, *c* left side view.
2. Dorsal 7 (see also pl. 1, fig. 7., pl. 2, fig. 4., pl. 3, fig. 1.), right side view, ×1/10.
3. Sacrum with a part of iliac blade, stereophotographs left side view, ×1/20.
4. Dorsal 5 (see also pl. 1, fig. 5., pl. 2, fig. 3.), right side view, ×1/10.
5. Right femur (see also pl. 13, fig. 1.), distal view, ×1/8.

PLATE 13

Opisthocoelicaudia skarzynskii gen. n., sp. n. ZPAL MgD-I/48

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia

1. Right femur, (see also pl. 12, fig. 5.), stereophotographs, ×1/14; *a* lateral view, *b* anterior view, *c* medial view, *d* posterior view.
2. Left femur, (see also pl. 8, fig. 4.), stereophotographs, ×1/14, lateral view.
3. Right fibula, (see also pl. 13, fig. 12., pl. 11, fig. 5., pl. 14, fig. 2*b*, *c*), lateral view, ×1/12.
4. Left tibia somewhat distorted in the distal part with fused astragalus (see also pl. 11 fig. 4.), posterior view, ×1/12.
5. Phalanx II_1, phalanges of the pes, *a* proximal view, *b* posterior view
6. Ungual II in medial view
7. Phalanx I_1, *a* proximal view, *b* posterior view
8. Ungual I in medial view
9. Phalanx IV_1 in posterior view
10. Phalanx III_1 in posterior view
11. Ungual III in medial view

   5*b*, 6, 7*b* and 8—11 stereophotographs. All ×1/8
12. Right tibia, fibula and astragalus, distal view, ×1/8.

PLATE 14

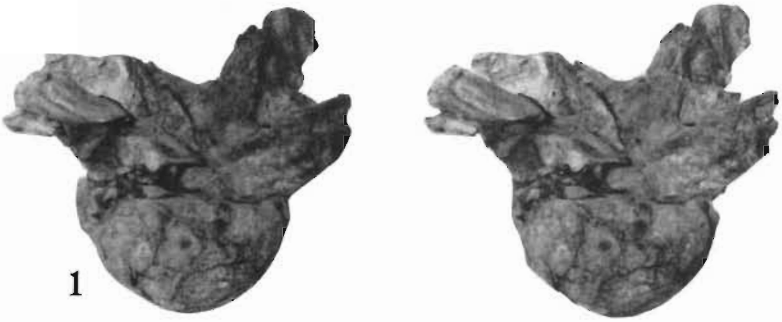
Opisthoelicaudia skarzynskii gen. n., sp. n. ZPAL MgD-I/48

Upper Cretaceous, Nemegt Formation, Altan Ula IV, Gobi Desert, Mongolia

1. Right tibia, stereophotographs, antero-medial view, ×1/12.
2. Right crus and pes, stereophotographs, ×1/12: *a* medial view, *b* anterior view, *c* posterior view.

   Right metatarsals ×1/8, posterior view.

3. Metatarsal I, stereophotographs.
4. Metatarsal II, stereophotographs.
5. Metatarsal IV, stereophotographs.
6. Metatarsal V.
7. Metatarsal III, stereophotographs.
8. Right astragalus (see also pl. 8, fig. 6.), stereophotographs, × 1/10.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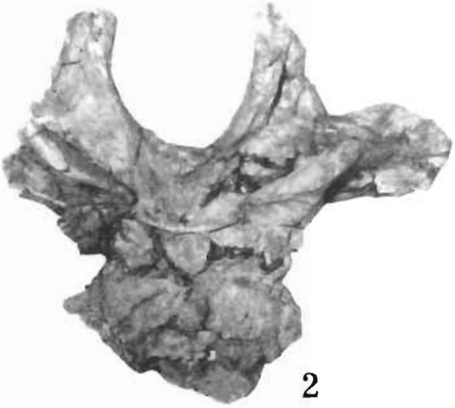
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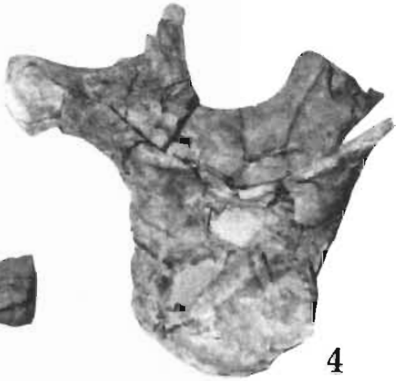
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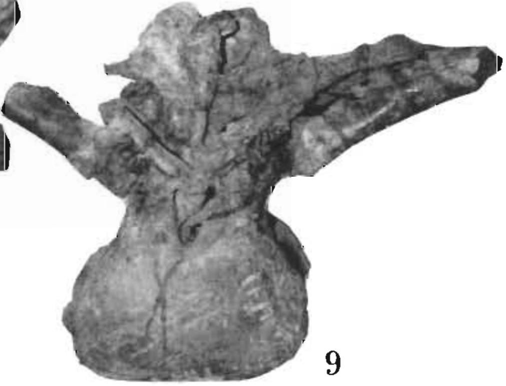
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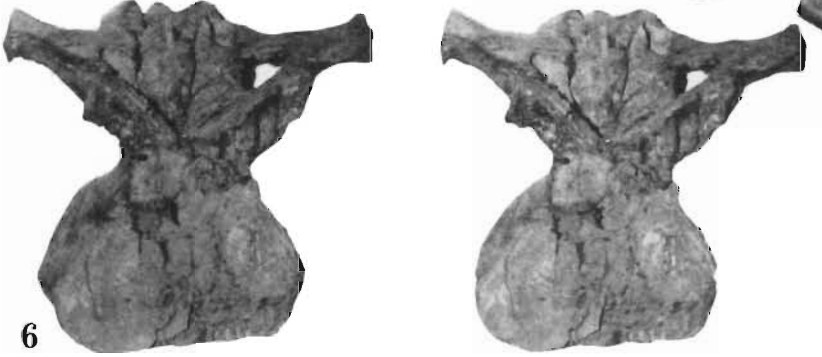
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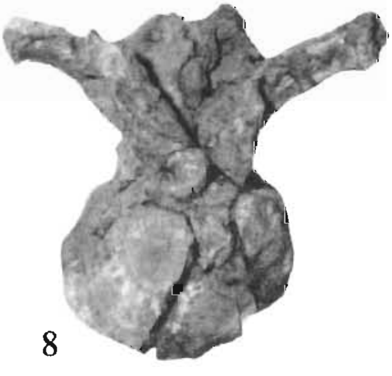
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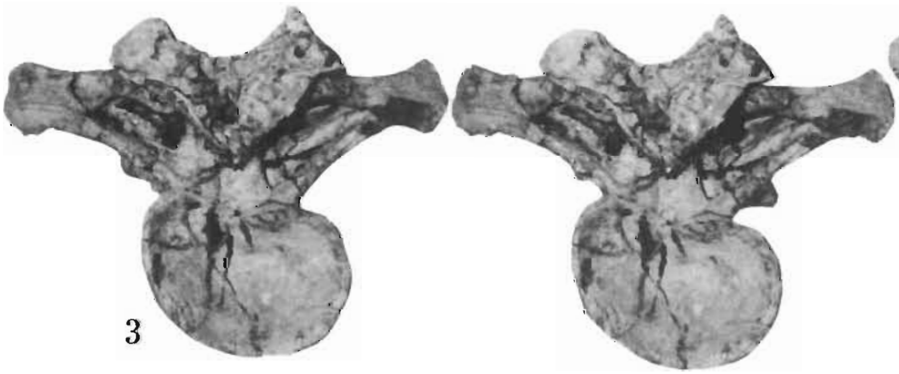

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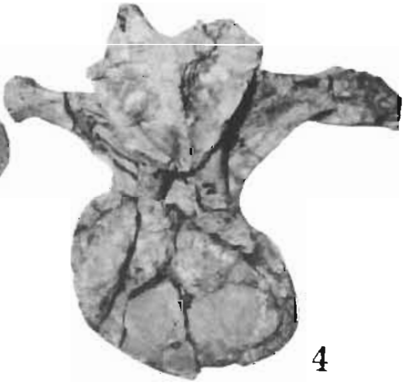

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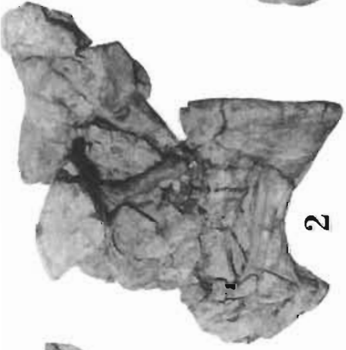
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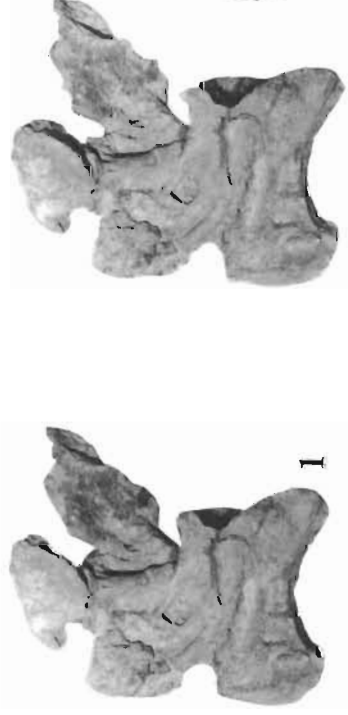
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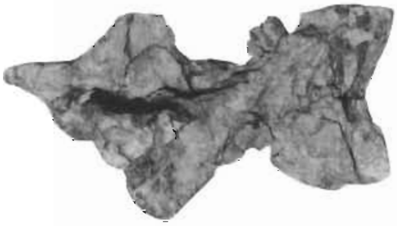
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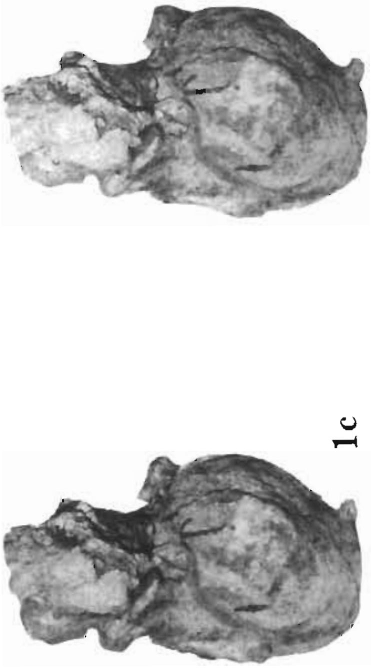

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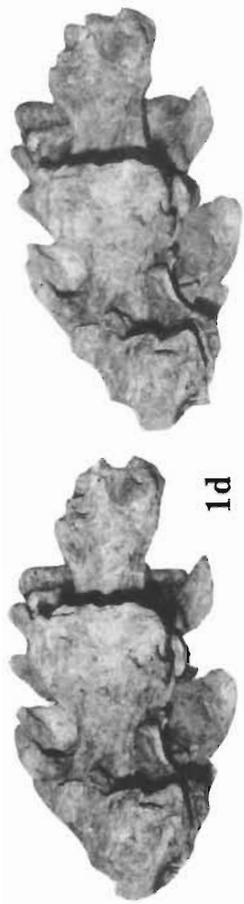

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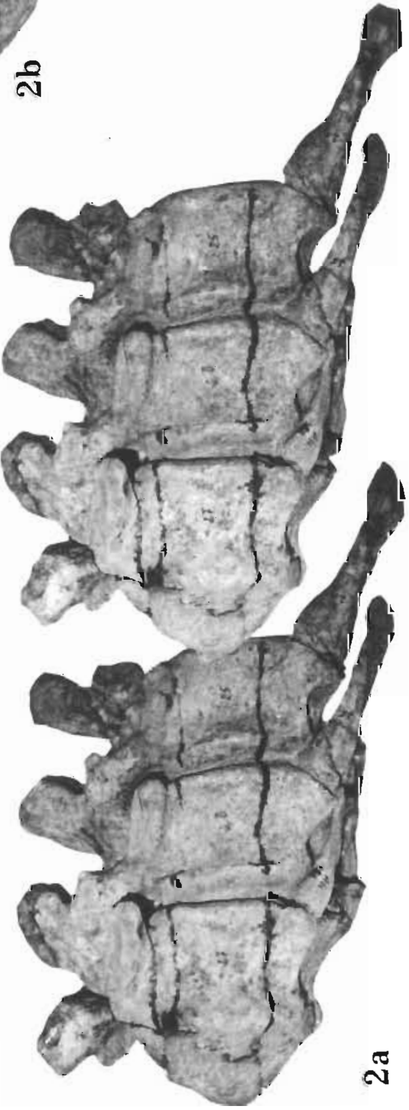

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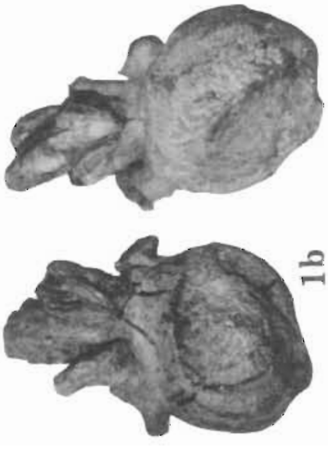

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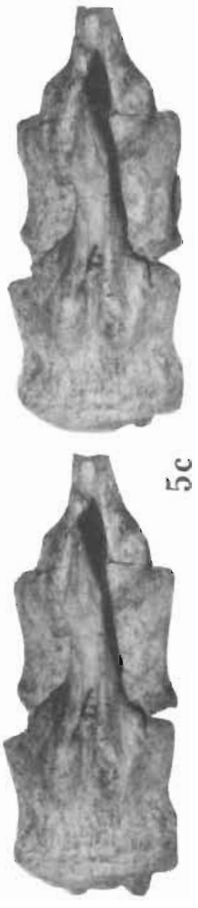
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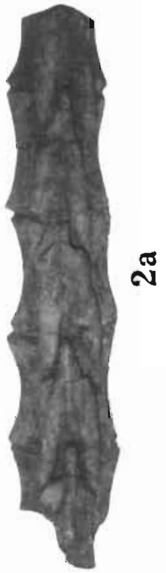
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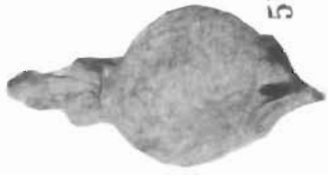
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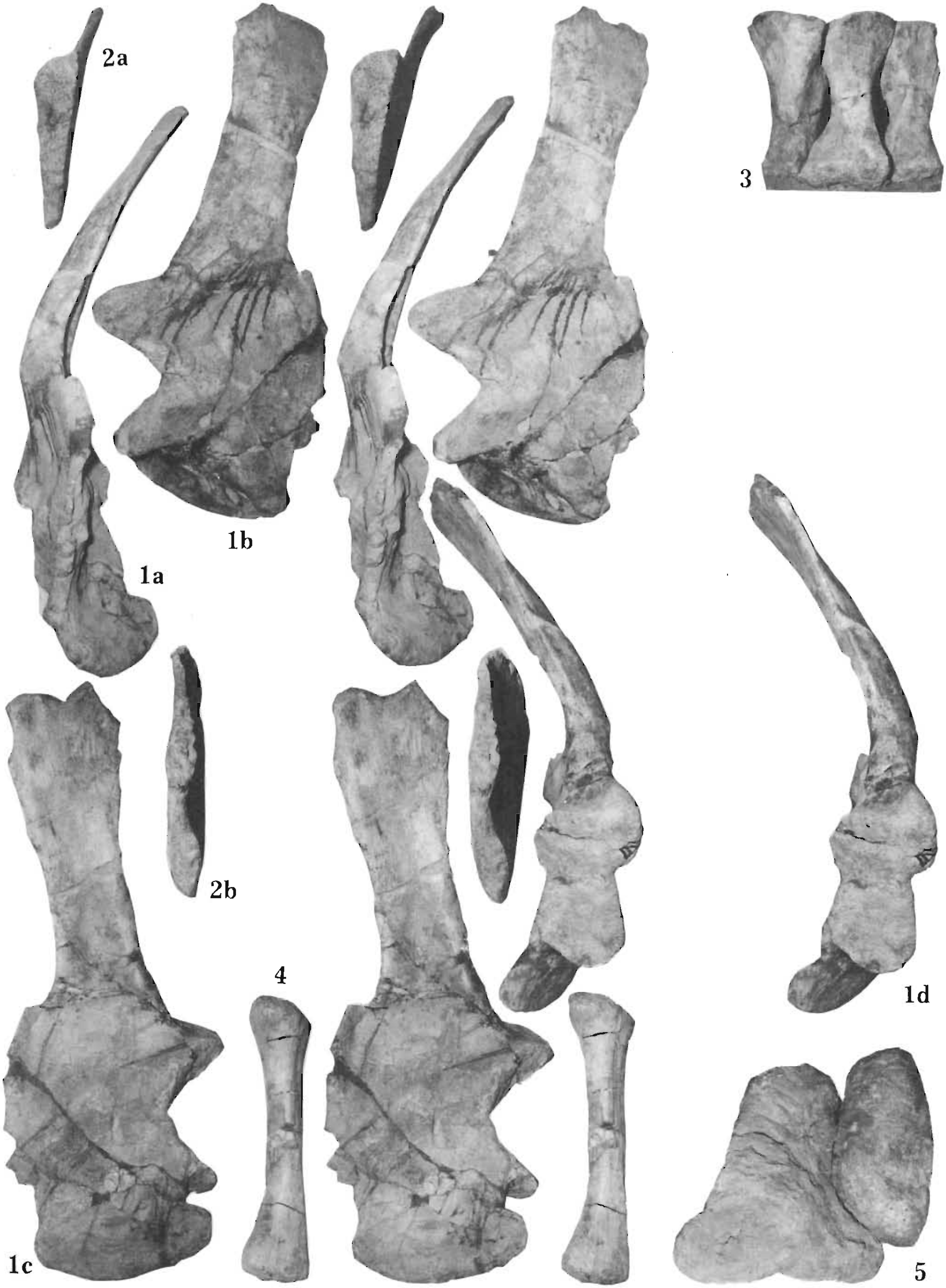
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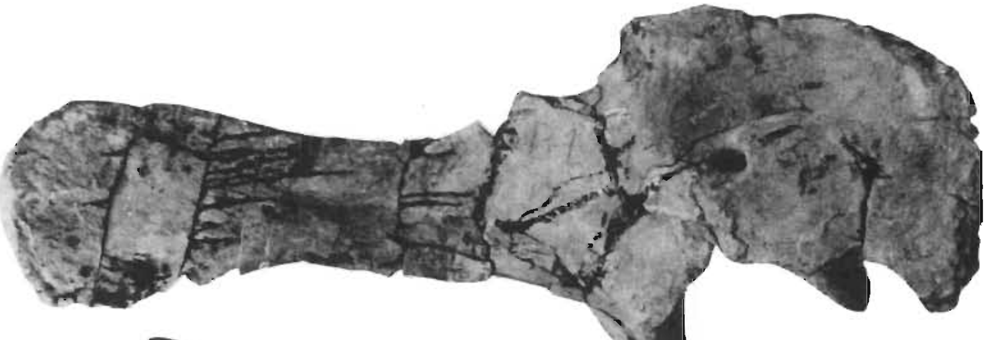

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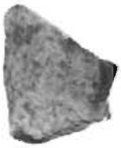

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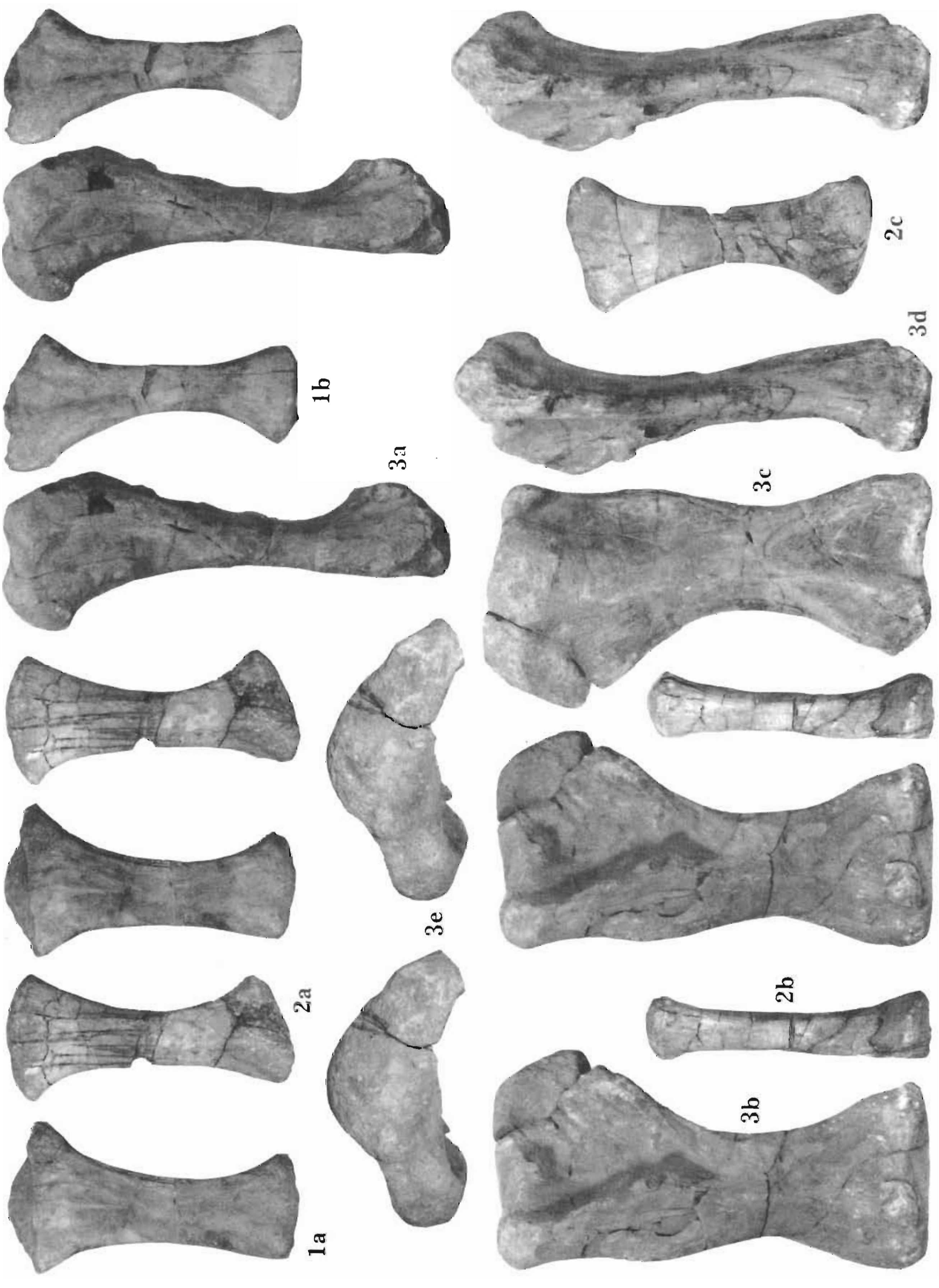
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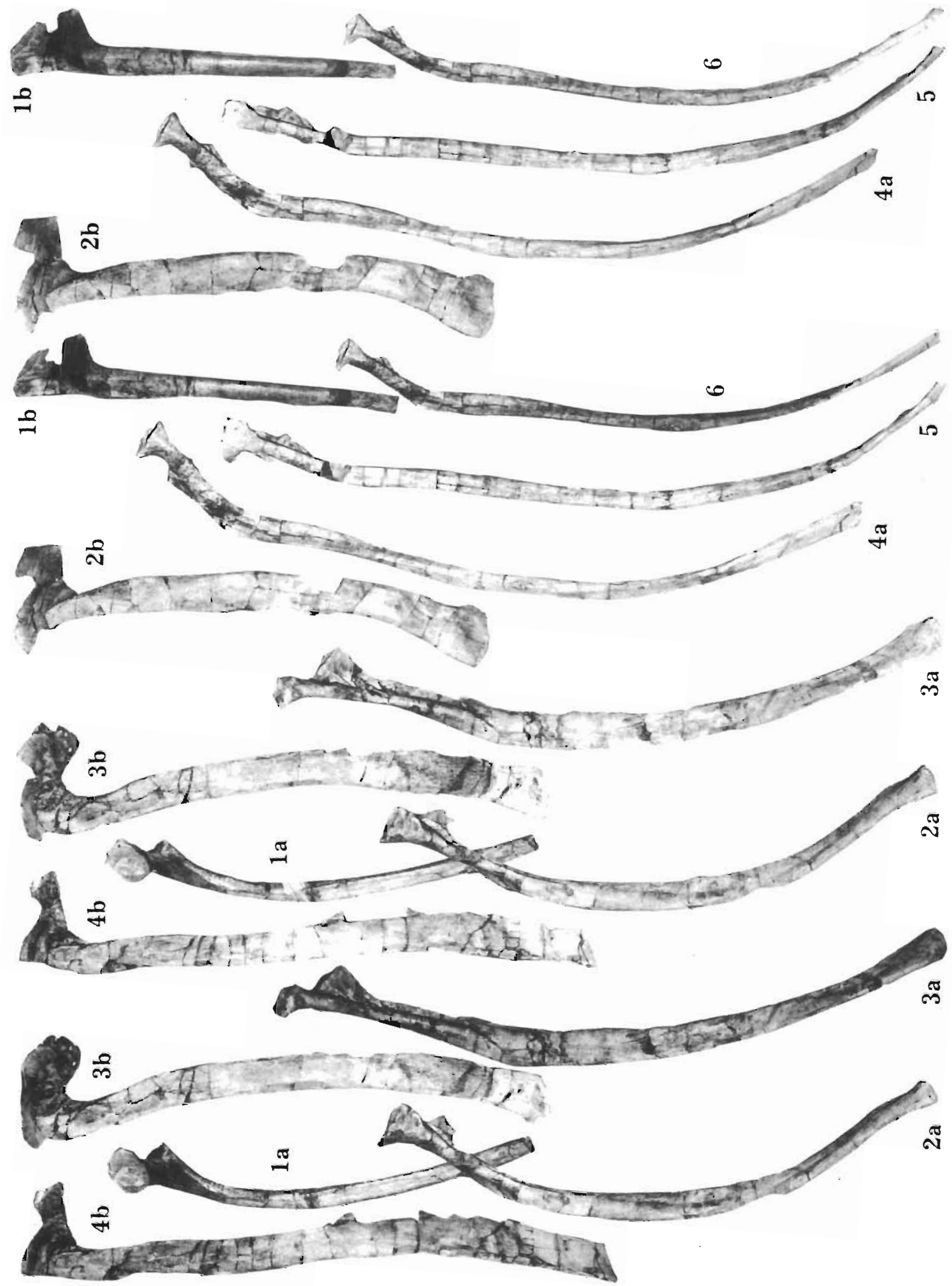
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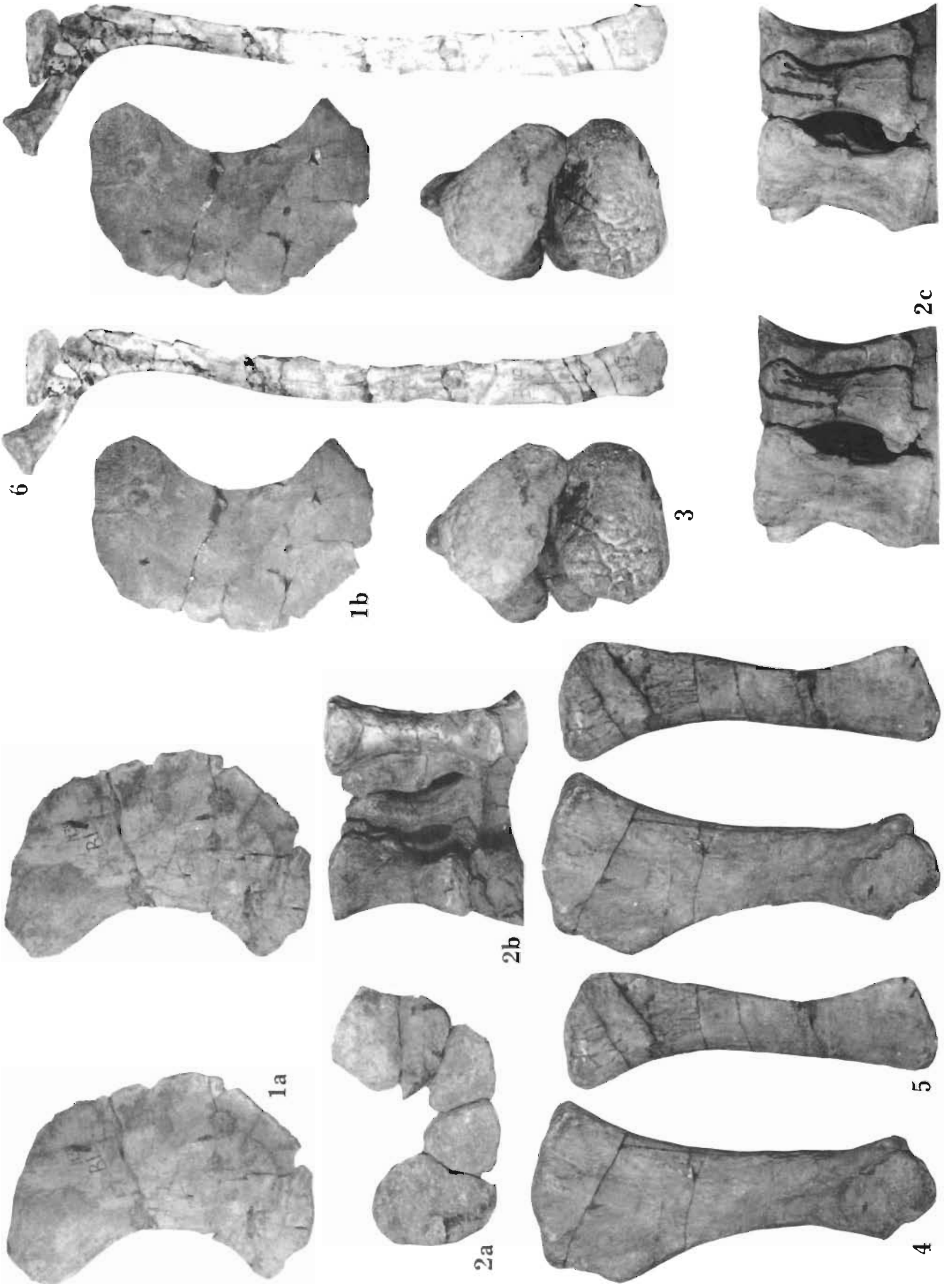
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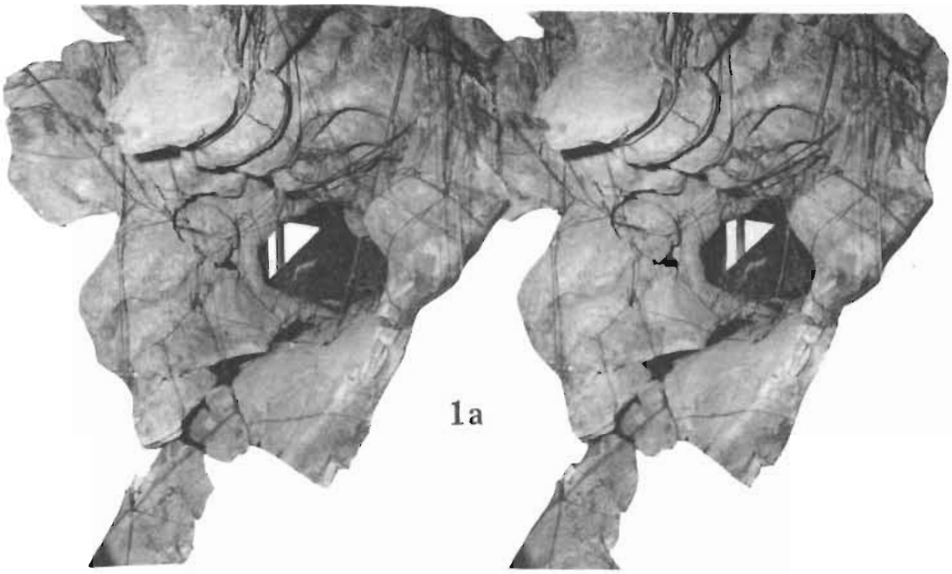
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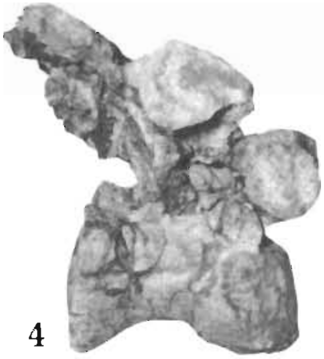
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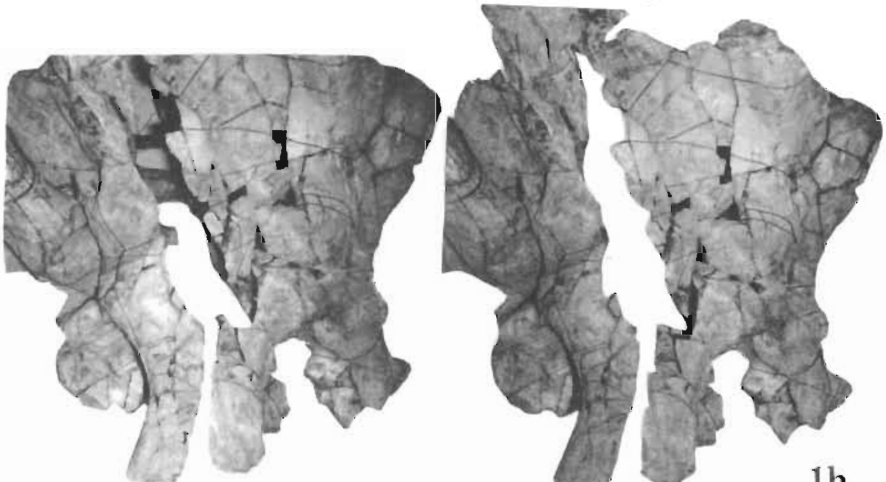
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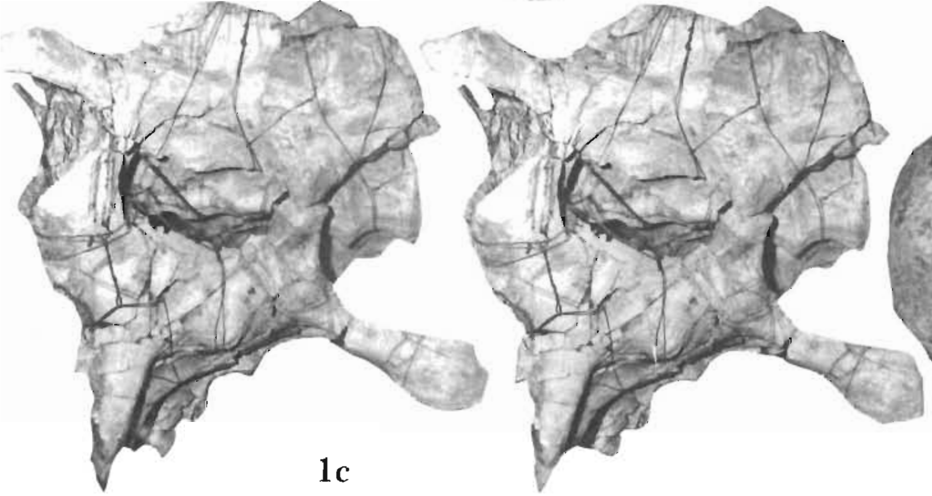
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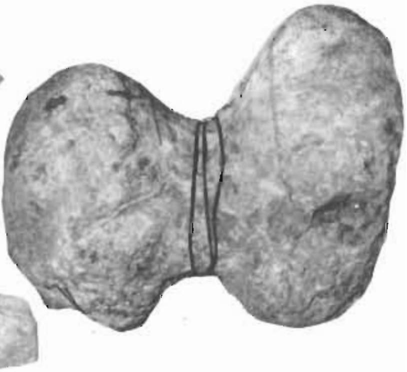

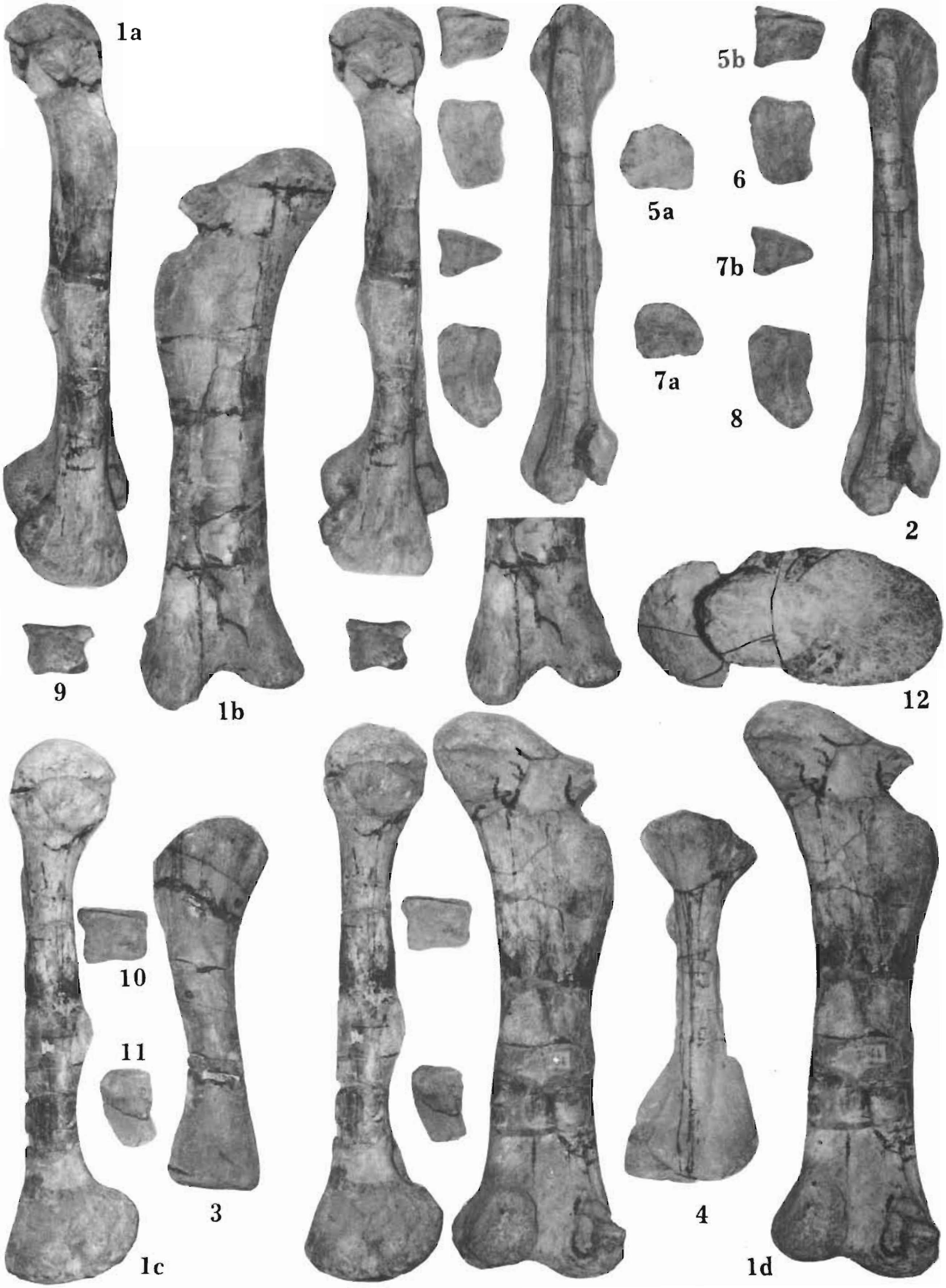
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M. Borsuk-Białynicka: New camarasaurid sauropod