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# An early prosauropod dinosaur from the Upper Triassic of Nordwürttemberg, West Germany

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With 5 plates, 4 figures and 1 table

Summary

A partial skeleton of a prosauropod dinosaur is described from the Lower Stubensandstein (Upper Triassic, Middle Norian) of Ochsenbach, Stromberg, Nordwürttemberg. It is referred to *Sellosaurus gracilis* v. HUENE, the well represented prosauropod taxon from the overlying Middle Stubensandstein. The third sacral rib is roughly T-shaped in lateral view as in the holotype of *Sellosaurus gracilis* rather than squarish as in *Plateosaurus* from the overlying Knollenmergel.

Apart from several disarticulated prosauropod bones (destroyed in World War II) probably coming from the Lower Burgsandstein near Nürnberg of approximately the same age, and originally referred to the rauisuchid thecodontian *Teratosaurus suevicus* v. MEYER, this partial skeleton represents the earliest record of a prosauropod from Europe. The supposedly earlier records from Europe are based on bones of the lacertilian *Tanystropheus* and of carnivorous archosaurs (rauisuchid thecodontians and theropod dinosaurs). The earliest records of prosauropods are isolated bones from the Carnian of North Africa and North America plus articulated bones from the Lower Elliot Formation (Carnian or Lower Norian) of South Africa.

Zusammenfassung

Aus dem Unteren Stubensandstein (Obertrias, Mittel-Nor) von Ochsenbach im Stromberg, Nordwürttemberg, wird das unvollständige Skelett eines prosauropoden Dinosauriers beschrieben. Es gehört zu *Sellosaurus gracilis* v. HUENE, dem recht gut bekannten Prosauropoden aus dem überlagernden Mittleren Stubensandstein. Die dritte Sacralrippe ist, von lateral betrachtet, eher annähernd T-förmig wie jene des Holotyps von *Sellosaurus gracilis*, als ungefähr quadratisch wie bei *Plateosaurus* aus dem überlagernden Knollenmergel.

Von einigen isolierten Prosauropoden-Knochen (im 2. Weltkrieg vernichtet) abgesehen, die vermutlich aus dem etwa gleichaltrigen Unteren Burgsandstein bei Nürnberg stammen und ursprünglich dem rauisuchiden Thecodontier *Teratosaurus suevicus* v. MEYER zugeschrieben wurden, ist dieser Skelettrest der älteste Prosauropoden-Fund in Europa. Die angeblichen älteren europäischen Belege sind Einzelknochen des Lacertiliers *Tanystropheus* und carnivorer Archosaurier (rauisuchider Thecodontier und theropoder Dinosaurier). Der früheste Nachweis von Prosauropoden stützt sich auf isoliert gefundene Knochen aus dem Karn von Nordafrika und Nordamerika, sowie Skeletteile aus der unteren Elliot-Formation (Karn oder Unter-Nor) von Südafrika.

## 1. Introduction

The remains of prosauropod dinosaurs are well known from the Stubensandstein of the Stromberg region north of Ludwigsburg, Nordwürttemberg. This material was described as several species of *Sellosaurus* (later *Plateosaurus*) and *Teratosaurus* by v. Huene (1908, 1932). However, apart from the holotype maxilla of *Teratosaurus suevicus* v. Meyer 1861 (and similar isolated teeth), which probably represents a rauisuchid thecodontian rather than a carnivorous dinosaur (Bonaparte 1981), all this material is now referred to the herbivorous prosauropod *Sellosaurus gracilis* v. Huene 1908 (Galton, in prepn.).

Nearly all this material came from the Middle Stubensandstein and the only evidence for a prosauropod from the Lower Stubensandstein is a partial skeleton, the hindlimbs of which were illustrated by Berckhemer (1938) in a review of the vertebrates from the Stubensandstein of the Stromberg region. This partial skeleton, which lacks the skull, most of the cervical and all of the dorsal vertebrae, was discovered by O. Linck in April 1936 and it came from the southeastern part of the abandoned former Gotsch Quarry 375 m northwest of the church of Ochsenbach (R 3498500, H 5431825; Topographische Karte 1:25000, sheet 6915 Güglingen). Berckhemer (1938, fig. 57) provided a photograph of the site and noted that the skeleton was found 3 m above the lower sandstone in a 4 m thick layer of red marl. Brenner (1978 : 116, Profil 8) gives a stratigraphic section for north of Ochsenbach; the skeleton probably came from layers 18 to 20 (R. Wild, personal communication). Linck (1938 : 179, fig. 2) noted that there are 25 to 30 m of marly beds (with the limy Ochsenbachschicht in the upper part, see also Bachmann & Gwinner 1971, fig. 11) between the lower and middle sandstones; so this skeleton was found about 22 to 27 m below the Middle Stubensandstein. Consequently, this is the earliest record of an associated skeleton of a prosauropod from West Germany and, as will be discussed below, it is also the earliest from Europe. However, nothing has been published on the important specimen since the brief note by Berckhemer (1938).

The purpose of this paper, which is the first in a series that will revise the dinosaur remains from the Stubensandstein, is to provide a description of this prosauropod skeleton from the Lower Stubensandstein and to evaluate other early occurrences of prosauropods. Institution names for cited specimens have been abbreviated as follows:

BMNH: British Museum (Natural History), London; MNHN: Muséum National d'Histoire Naturelle Paris; PU: Museum of Geology, Princeton University, N.J.; IGS GSC: Institute of Geological Sciences – Geological Society Collection, London; SMNS: Staatliches Museum für Naturkunde in Stuttgart; WM: Warwickshire Museum, Warwick, England.

## 2. Description and Comparisons

SMNS 17928 (Fig. 1A) consists of 46 vertebrae (2 cervicals, 1 dorsal, 3 sacrals, 40 caudals with parts of 23 chevrons), the right scapula, coracoid, humerus and most of the manus, the left ulna, proximal end of radius and parts of the manus plus both pelvic girdles and hindlimbs. The principal measurements of the bones of the appendicular skeleton are given in Table 1.

Vertebral column. – The two cervical vertebrae are tentatively identified as the third and fourth (Pl. 1, Figs. 1–4) by comparison with a complete neck of *Plateosaurus* (SMNS 13200; v. Huene 1926, pl. 2, fig. 1). The third is the least well preserved with a midventral length of 96 mm for the centrum. This measurement is 101 mm for

| | L | Wp | Wd | | |
|---|---|---|---|---|---|
| Scapula, r | 382 | – | – | 49[a] | |
| Coracoid, r | 170 | 51 | – | | |
| Humerous, l | 323 | – | – | 200[b] | |
| Ulna, r | 219 | – | – | | |
| Metacarpal I, r | 58.6 | – | 39[l] | 87.8[c,l] | 51[d,l] |
| ,, II, r | 90.8 | – | – | 78.6[c,l] | 40[d,l] |
| ,, III, r | 85.7 | – | – | | |
| ,, IV, r | 56.2 | – | – | | |
| Ilium, l | 268 | 172[e] | 156[f] | 86[g] | |
| Pubis, r | 372 | | 85 | | |
| Ischium, l | 343 | 95 | 40 | | |
| Femur, l | 487 | 110 | 111 | 226[h] | |
| ,, , r | 495 | 98 | 102 | 229[h] | |
| Tibia, l | 422 | 103 | 86 | 460[i] | 95[j] |
| ,, , r | 435 | 120 | 97 | 460[i] | 92[j] |
| Fibula, l | 426 | 64 | 56 | | 32[k] |
| ,, , r | 425 | 54 | – | | 32[k] |
| Metatarsal I, l | 103 | – | 34.3 | 80.5[c] | 28.5[d] |
| ,, II, l | 175 | – | – | 76.8[c] | 28.8[d] |
| ,, III, l | 206 | – | 54 | 67[c] | 30.8[d] |
| ,, IV, l | 180 | 43.5 | – | 56.5[c] | 24[d] |
| ,, V, l | 89.3 | – | 26.8 | | |
| ,, I, r | 123 | 41 | – | 79.1[c] | 42.3[d] |
| ,, II, r | 180 | – | 51 | 72.2[c] | 30[d] |
| ,, III, r | 208 | – | 58.6 | 64.2[c] | 27.3[d] |
| ,, IV, r | 186 | 62 | 42 | 51.5[c] | 18.3[d] |
| ,, V, r | 108 | 47 | – | | |

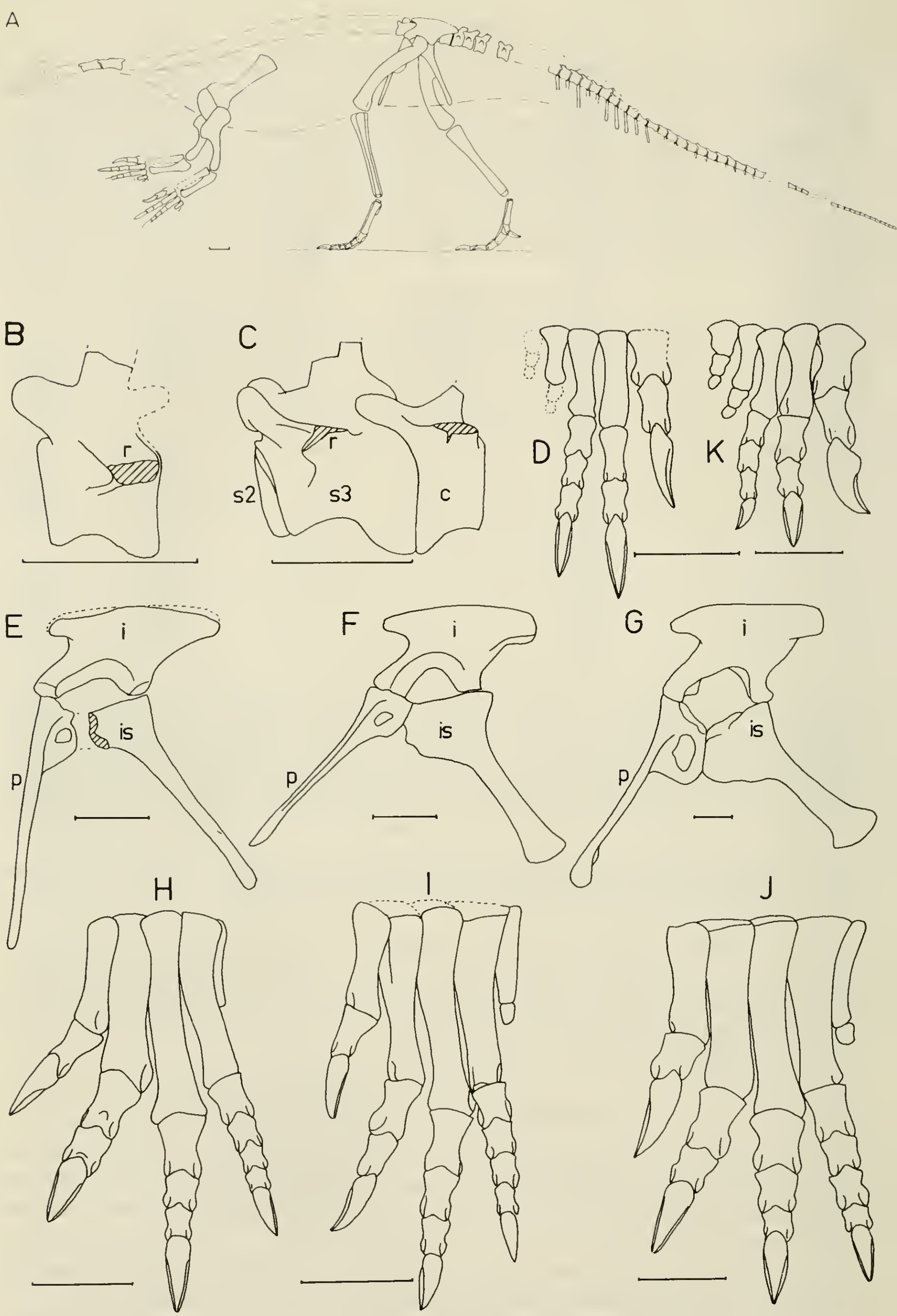
a = minimum width of blade; b = head to apex of deltopectoral crest; c = maximum length of ungual; d = maximum proximal width of ungual; e = pubic to ischiadic peduncles; f = maximum height above ischiadic peduncle, g = maximum transverse width of acetabulum; h = minimum distance from head to apex of fourth trochanter; i = maximum length of tibia plus astragalus; j = maximum length of astragalus; k = maximum length of calcaneum; l = left; L = maximum length; r = right; Wd = maximum distal width; Wp = maximum proximal width.

Tab. 1. Measurements of postcranial bones of *Sellosaurus gracilis* (SMNS 17928) from Lower Stubensandstein of Ochsenbach, Nordwürttemberg.

the fourth centrum, the maximum dorsal length of which is 110 mm, and the maximum pre- to postzygapophysis distance is 142 mm. The incomplete neural spine is low, the ends of the centra are obviously concave, and the proximal end of a rib is still attached on the right side (Pl. 1, Fig. 4).

Only the last dorsal vertebra is preserved; it is attached by matrix to the sacrum (Pl. 1, Fig. 8; Pl. 2, Figs. 1–3). Comparisons with the situation in *Plateosaurus* and *Sellosaurus* (see v. HUENE 1926, 1932) indicate that this is the fifteenth dorsal vertebra. A lateral view is visible of the right side (Pl. 2, Fig. 2) and only the base of the transverse process is preserved (Pl. 1, Fig. 8; Pl. 2, Fig. 1). In ventral view (Pl. 2, Fig. 2), the posterior part of the centrum is expanded transversely, and there is a prominent median ridge.

The sacrum consists of three vertebrae, the first two of which are attached together (Pl. 2, Fig. 3) whereas the third is united to the first caudal by matrix (Pl. 2, Figs. 1, 2, 5, 6). The form of the first two sacrals in dorsal view (Pl. 2, Fig. 1) is similar to that of the holotype of *Sellosaurus gracilis* (SMNS 5715; Pl. 3, Fig. 3) and of *Plateosaurus* (e.g. SMNS 13200; v. HUENE 1926). The first transverse process and sacral rib are very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robust and the distal part extends anterolaterally whereas these parts are more slender and extend posterolaterally in the second sacral. The third sacral rib is slender and dorsoventrally thin with a subvertical butressing sheet (Pl. 2, Figs. 2,7); so it is roughly T-shaped in lateral view (Pl. 2, Figs. 5,6). As preserved, the process is not close to the ilium but comparisons with the sacra of *Sellosaurus* (Pl. 3) and *Plateosaurus* (v. HUENE 1926) indicate that the ilium has shifted anteriorly with respect to the sacrum and that originally the anterior end of the first centrum was approximately below the apex of the angle formed by the anterior process and the pubic peduncle of the ilium (Pl. 1, Fig. 7), rather than level with the middle of the acetabulum as preserved (Pl. 2, Fig. 2). v. HUENE (1908, pl. 72, fig. 4) illustrated (Fig. 4C) the first caudal vertebra of *Sellosaurus* (SMNS 5715) with the posterior part of the centrum of the preceding vertebra still attached and this is identified as part of the third sacral (v. HUENE 1908 : 179). However, this piece of centrum fits perfectly against the incomplete posterior end of the second sacral, so the first caudal is actually the third sacral (Pl. 3). The roughly T-shaped form of the transverse process of this vertebra in lateral view (Fig. 3C; Pl. 3, Figs. 1,2) is similar to that of SMNS 17928 (Figs. 1 B, C) and it is in marked contrast to its subsquare and block-like form in *Plateosaurus* (see v. HUENE 1908, 1926, 1932). In ventral view (Pl. 2, Fig. 2), the centrum of the first sacral vertebra of SMNS 17928 is poorly preserved, but the centra obviously decrease in massiveness and length for each vertebra; the median lengths are 74, 64 and 55 mm, respectively.

The first caudal is still attached to the last sacral (Pl. 2, Figs. 1, 2, 5, 6), the remaining caudals are tentatively identified as shown (Pl. 1, Figs. 5, 6; Pl. 2, Fig. 8), and the series is similar to those of *Sellosaurus* (SMNS 5715; v. HUENE 1908, pl. 72, figs. 4, 5; pl. 73) and *Plateosaurus* (v. HUENE 1926). Only the bases of the neural spines are preserved as is also the case for the transverse processes, the last traces of which are on caudal vertebra 25.

The chevrons or hemal arches are preserved to a varying degree (Pl. 1, Figs. 5, 6; Pl. 2, Figs. 5, 6); a small piece of bone between the centra of the last sacral and the first caudal vertebra (Pl. 2, Fig. 5) represents part of a rudimentary first chevron as has been illustrated for *Plateosaurus* by v. HUENE (1926, pl. 2, fig. 2). The total number of chevrons was probably about 35.

Pectoral girdle and forelimbs. – The scapula and coracoid (Figs. 2 A, B) plus the humerus (Figs. 2 C–F), ulna (Figs. 2 G, H) and proximal end of the radius (Figs. 2 I, J) are similar to those of *Sellosaurus* (see v. HUENE 1932, pls. 17, 23; GALTON

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Fig. 1. *Sellosaurus gracilis*, referred specimen SMNS 17928 from Lower Stubensandstein of Ochsenbach, Nordwürttemberg (A,B,D,E,H) and specimens from the Middle Stubensandstein of Nordwürttemberg (C,F,I) plus *Plateosaurus* from the Knollenmergel of Trossingen (G,J,K).
A: skeletal reconstruction; B: sacral vertebra 3 in left lateral view; C: as B for SMNS 5715 plus the centrum of sacral 2 and the first caudal vertebra, after v. HUENE (1908, pl. 72, fig. 4); D: reconstructed right manus in anterior view; E: reconstructed right pelvic girdle in lateral view; F: as E for SMNS 12354; G: as E for SMNS 13200, after v. HUENE (1926); H: reconstructed left pes; I: as H for SMNS 12222; J: as H for SMNS 13200; K: reconstructed right manus of SMNS 13200 (at same scale as J).

c = caudal vertebra 1; i = ilium; is = ischium; p = pubis; r = sacral rib of sacral vertebra 3; s2 = posterior end of entrum of sacral vertebra 2; s3 = sacral vertebra 3.

Scale lines represent 10 cm.

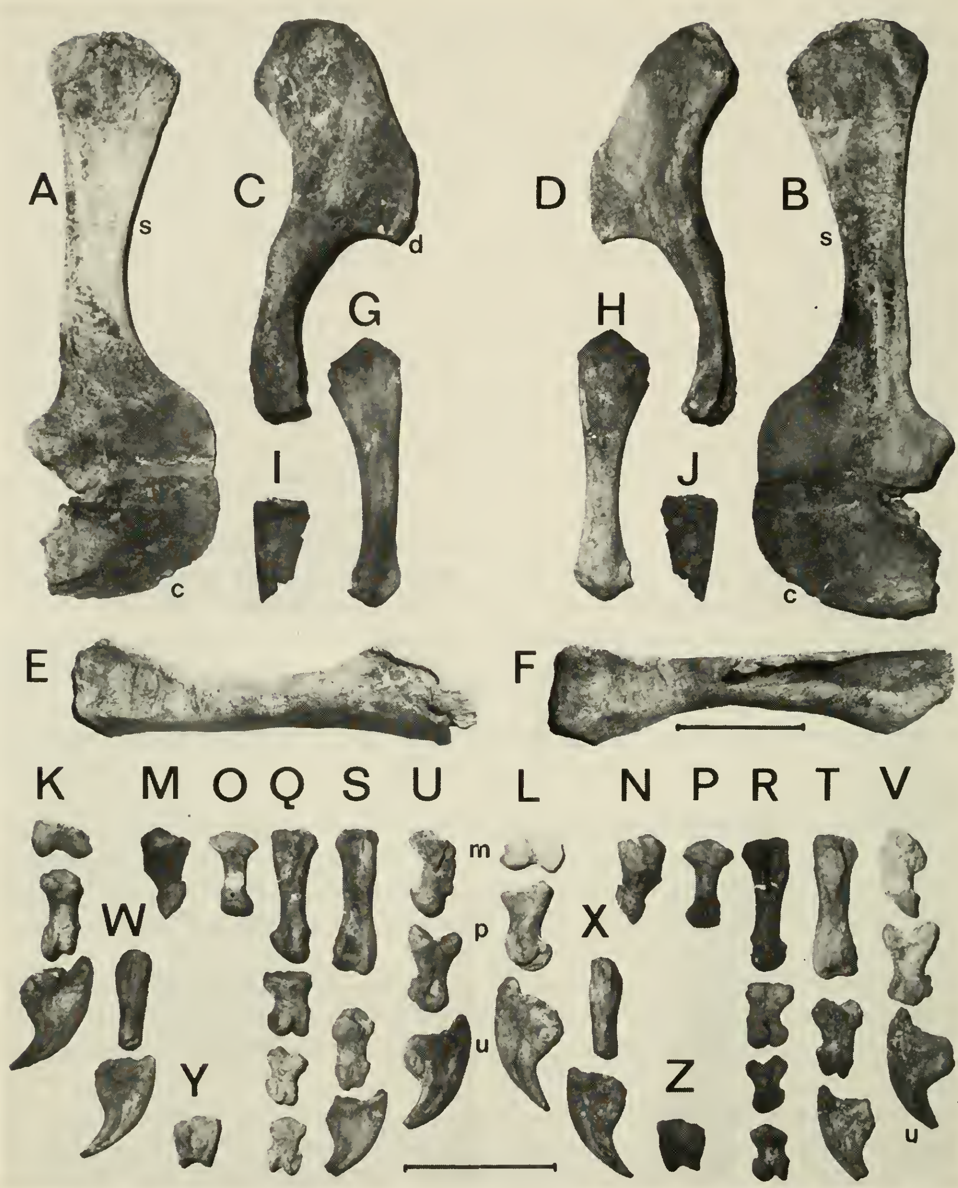


Fig. 2. Shoulder girdle and forelimb of *Sellosaurus gracilis*, referred specimen SMNS 17928 from Lower Stubensandstein of Ochsenbach, Nordwürttemberg.
A,B: left scapula and coracoid in A: lateral and B: medial views, x 1/6; C–F: left humerus in C: medial; D: lateral; E: posterior and F: anterior views, x 1/6; G,H: right ulna in G: lateral and H: medial views, x 1/6; J: proximal end of right radius in I: lateral and J: medial views, x 1/6; K–Z: bones of left and right manus x 0.2; K,L: left digit I, metacarpal I in K: anterior and L: distal views, first phalanx in K: anterior and L: medial views, and ungual in K: lateral and L: medial views; M,N: right first phalanx digit II in M: lateral and N: medial views; O,P: right metacarpal IV in O: dorsal and P: ventral views: Q,R: right metacarpal III in Q: lateral and R:

1973, figs. 6–8). The scapula and coracoid have been restored to some extent in plaster (including filling in the coracoid foramen); there is a rugose region to the glenoid at the scapular-coracoid junction that was originally filled in with cartilage. The humerus is somewhat distorted, especially distally and in the region of the deltopectoral crest that is transversely compressed (Fig. 2 F).

The bones of the left and right manus have been tentatively identified as shown (Figs. 2 K–Z) and reconstructed (Fig. 1 D) by comparison with the articulated manus of *Plateosaurus* (SMNS 13200; Fig. 1 K). Unfortunately the manus is very poorly represented for larger individuals of *Sellosaurus* (see v. HUENE 1932) and those of juvenile individuals were rather badly distorted during preservation (see BERCKHEMER 1938, fig. 39; GALTON 1973, figs. 9, 10). Metacarpal I is represented by the medial half of the right and the distal articular end of the left (Figs. 2 K, L, U, V). However, both phalanges are preserved and the ungual is large and very trenchant (Figs. 2 K, L, U, V). This is characteristic of all prosauropods (see GALTON & CLUVER 1976, fig. 7), as is the relative shortness of metacarpal I with its broad asymmetrical distal articular surface and the asymmetrical form of the distal condyles of the first phalanx. Digit II (Figs. 2 S, T) is complete but the first phalanx is poorly preserved, digit III (Fig. 2 Q, R) only lacks the ungual phalanx, digit IV (Figs. 2 O, P) is only represented by the metacarpal, and digit V is not preserved.

Pelvic girdle and hindlimb. – The complete pelvic girdle is preserved (Fig. 1 E); it is typically prosauropod in form, being similar to those of *Sellosaurus* (Fig. 1 F; GALTON 1973, v. HUENE 1908, 1932) and *Plateosaurus* (Fig. 1 G, v. HUENE 1926, 1932). The ventral ends of the pubic and ischiadic peduncles are damaged (Pl. 2, Fig. 2) and most of the dorsal margin is missing (Fig. 1 E; Pl. 1, Fig. 7). The acetabulum appears to be wider transversely in ventral view (Pl. 2, Fig. 2) than it is in *Sellosaurus* (Pl. 3, Fig. 4), but this is probably an artifact resulting from the incompleteness of the medial edge of the acetabulum in SMNS 5715 and, in addition, SMNS 17928 appears to have been distorted a little by dorsoventral compression (Pl. 1, Fig. 8; Pl. 2, Fig. 4).

The pubis (Figs. 3 D–G) is similar to those of *Sellosaurus* and *Plateosaurus* except that in SMNS 17928 the obturator foramen (with maximum anterior width of 22 mm, maximum depth of 26 mm) is proportionally smaller and the dorsal outline of the proximal third to half is gently convex (Figs. 1 E, 3 D, E), instead of being gently concave; so the proximal part curves upwards toward the ilium (Fig. 1 F). However, this difference may be the result of compression during preservation because it is impossible to articulate the pubis with the ilium and ischium (Fig. 1 E). The central part of the more medial part is restored in plaster and more proximally the medial edge is incomplete (Figs. 3 F, G) as are parts of the distal end.

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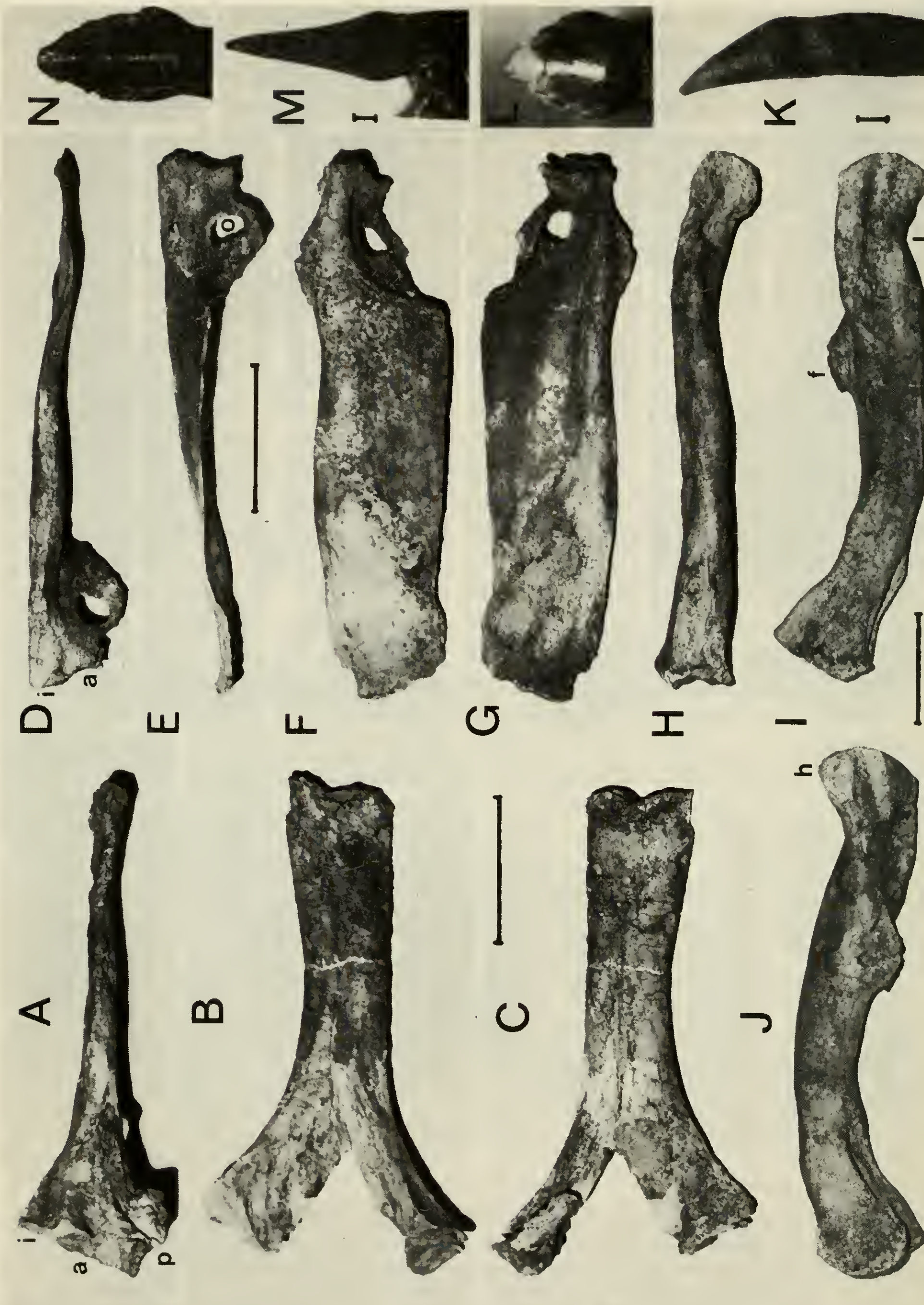
medial views plus phalanges 1 to 3 in Q: anterior and R: posterior views; S,T: right metacarpal II and second phalanx in S: anterior and T: posterior views plus ungual in S: lateral and T: medial views; U,V: right metacarpal I in U: anterior and V: posterior views plus first and ungual phalanges in U: lateral and V: medial views; W,X: left metacarpal II in W: anterior and X: posterior views; Y,Z: proximal end of left metacarpal III in Y: medial and Z: lateral views.

c = coracoid; d = deltopectoral crest; g = glenoid; m = metacarpal; p = phalanx; s = scapula; u = ungual phalanx.

Scale lines represent 10 cm.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The more complete right ischium (Fig. 3 A–C; Pl. 2, Fig. 9) is a little incomplete at both ends. The proximal end appears to be proportionally less expanded than it is in *Sellosaurus* (Figs. 1 E, F) and *Plateosaurus* (Fig. 1 G) but at least some of this difference is a result of crushing that is particularily marked proximally (Fig. 3 A; Pl. 2, Fig. 9).

Both hindlimbs are complete with the right femur (Figs. 3 H–J) separate from the lower leg and pes (Pl. 4, Figs. 1, 2) whereas the left pes (Pl. 5, Figs. 3, 4) can be attached back onto the rest of the limb (Pl. 4, Figs. 3, 4). The form of all of the bones is similar to those of *Sellosaurus gracilis* (v. HUENE 1908, 1932; GALTON 1973).

The form of the femur is typically prosauropod with an obliquely inclined head (Figs. 3 I, J; Pl. 4, Fig. 4), a curved ridged lesser trochanter (Fig. 3 I, J; Pl. 4, Fig. 3), and a large proximally placed fourth trochanter (Figs. 3 I, J; Pl. 4, Fig. 4). The distal part of the left femur is a little distorted by compression (Pl. 4, Fig. 3) but the form of the condyles is much better preserved (Pl. 4, Figs. 3, 4) than it is on the right femur, the distal end of which is transversely compressed (Figs. 3 H–J).

Although preserved in contact, it should be noted that the left lower leg has rotated through about 90° with respect to the femur (Pl. 4, Figs. 3, 4) and that the right pes and distal tarsals have been displaced proximally over the astragalus, calcaneum and the distal ends of the tibia and fibula (Pl. 4, Figs. 1, 2; Pl. 5, Figs. 1,2). Distally the fibula contacts the tibia, the astragalus and the small calcaneum (Pl. 4, Figs. 3, 4; Pl. 5, Fig. 2). Each astragalus is firmly attached to the tibia so the relative height of the ascending process of the astragalus cannot be determined.

Two distal tarsals are poorly preserved on the right side (Pl. 5, Fig. 1) but both pedes are well preserved except for the crushed and possibly incomplete distal end of metatarsal V (Pl. 5, Figs. 2, 4). As in all prosauropods except *Anchisaurus* (GALTON 1976), the distal end of metatarsal I is relatively broad and the first ungual phalanx is the longest on the pes (Figs. 1 H–J, Pl. 4, Figs. 2–4).

On the basis of its overall similarity in form, the partial skeleton from the Lower Stubensandstein of Ochsenbach is tentatively referred to *Sellosaurus gracilis* v. HUENE 1908, the prosauropod taxon from the overlying Middle Stubensandstein of the Stromberg region of Nordwürttemberg.

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Fig. 3. *Sellosaurus gracilis*, referred specimen SMNS 17928 from Lower Stubensandstein of Ochsenbach, Nordwürttemberg.

A–C: ischia in A: left lateral; B: dorsal and C: ventral views, x 0.2; D–G: right pubis in D: lateral; E: medial; F: dorsal and G: ventral views, x 0.2; H–J: right femur in H: anterior; I: lateral and J: medial views, x 0.15.
K,L: Fabrosaurid ornithischian tooth MNHN ALM 509, x 4, from mid-Carnian of Atlas Mountains, Morocco, in K: lateral or medial and L: anterior or posterior views; M,N: prosauropod *Azandohsaurus laarousi* tooth MNHN ALM 508 x 3 from mid-Carnian of Atlas Mountains, Morocco, in M: anterior or posterior and N: lateral or medial views.
a = acetabulum; f = fourth trochanter; h = head; i = surface for ilium; is = surface for ischium; l = lesser trochanter; o = obturator foramen; p = surface for pubis.

Scale lines represent 1 mm (K–N) or 10 cm.

### 3. Earlier European Record of Prosauropods

The Lower Stubensandstein is Middle Keuper (Upper Triassic) and probably equivalent to rocks of Middle Norian age in the Alpine series. However, prosauropods have been reported from beds in Europe that are equivalent to earlier Alpine stages: the underlying Carnian (lower Upper Triassic) and the two stages of the Middle Triassic, the Ladinian and the underlying Anisian. The earlier records of prosauropods from Europe need to be reviewed and this will be done in ascending order of occurrence.

The original material of *Thecodontosaurus antiquus* MORRIS 1843, the type species of the genus *Thecodontosaurus* RILEY & STUTCHBURY 1836, came from the Magnesian Conglomerate of Durdham Down near Bristol, England. This taxon is undoubtedly a prosauropod dinosaur (see v. HUENE 1908, GALTON & CLUVER 1976), the age of which is now considered to be Rhaetic (upper Upper Triassic; MARSHALL & WHITESIDE 1980). However, several species based on non-prosauropod material from beds of a much earlier age have been incorrectly referred to this genus.

*Thecodontosaurus primus* v. HUENE 1908 consists of two incomplete dorsal vertebrae (see v. HUENE 1908: 217–218; pl. 92, figs. 8, 9) from the Lower Muschelkalk (Wellenkalk, Anisian) near Gogolin, Upper Silesia, Poland. COLBERT (1970:32) discussed these vertebrae and concluded that "they may be dinosaurian, but they can perfectly well be pseudosuchian vertebrae, and most probably are." However, v. HUENE (1931) reidentified these vertebrae as coming from the lacertilian *Tanystropheus* and WILD (1973:151) refers them to *Tanystropheus antiquus* v. HUENE 1908 with *T. primus* (v. HUENE) as a junior synonym.

*Thecodontosaurus latespinatus* v. HUENE 1908 consists of several vertebrae (v. HUENE 1908:218–223, figs. 237–243; pl. 91, figs. 1–8; pl. 92, figs. 1–7) from the Upper Muschelkalk (early Ladinian, Middle Triassic) of Lunéville (France), of Bayreuth, Crailsheim, Göttingen (West Germany) and Thüringen (East Germany). These vertebrae are also discussed by COLBERT (1970, as non-dinosaurian), v. HUENE (1931, as *Tanystropheus*) and WILD (1973 : 149) who lists these vertebrae under *Tanystropheus conspicuus* v. MEYER with *T. latespinatus* (v. HUENE) as a junior synonym.

v. HUENE (1908) described several isolated limb bones and vertebrae of *Thecodontosaurus antiquus* from the Bromsgrove Sandstone Formation of Bromsgrove and Warwick, England, the age of which is now considered to be equivalent to the upper part of the German Muschelkalk or Early Ladinian (Middle Triassic: WALKER 1969; PATON 1974). However, WALKER (1969) points out that most of the material referred to *Thecodontosaurus* from the English Midlands represents a poposaurid. An examination of much of this material (WM) in 1983 confirmed its poposaurid, non-prosauropod nature, and it is currently being redescribed (GALTON & WALKER in prepn.). The family Poposauridae was removed from the Saurischia and referred to the Thecodontia by GALTON (1978); it is now included in the thecodontian family Rauisuchidae by BONAPARTE (1981). The only specimens that WALKER (1969) retained in *Thecodontosaurus* were a cervical vertebra and a tooth from Warwick. However, this cervical vertebra (BMNH 2628) is definitely not prosauropod; it is from an indeterminate archosaur. The tooth (IGS GSC 4873; Pl. 4, Figs. 5, 6) is that of a small carnivorous archosaur, not a prosauropod. The fine serrations are perpendicular to the cutting edge (Pl. 4, Figs. 5, 6) as illustrated (Fig. 4 D) by MURCHINSON & STRICKLAND (1840, pl., 28, fig. 7 a) and not at 45° to it as in the inaccurate copy of this figure (Fig. 4 E) given by

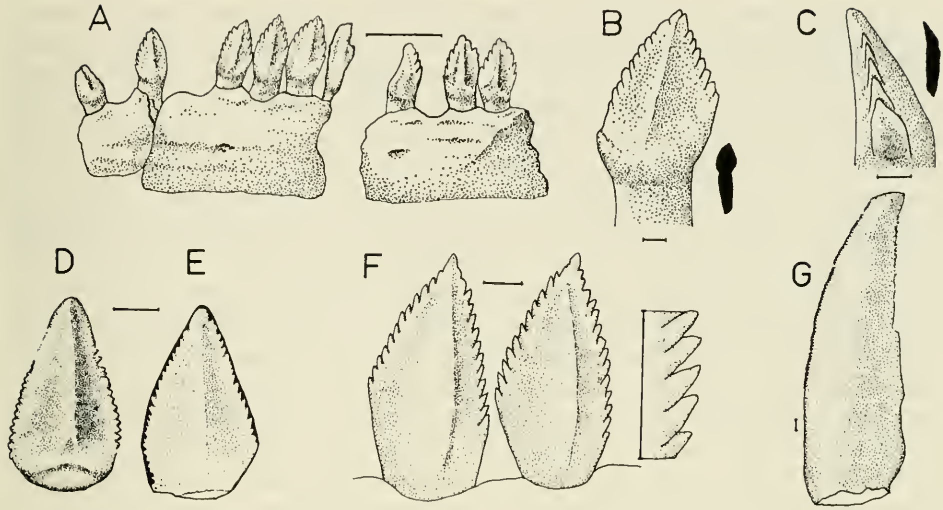


Fig. 4. A–C: anterior end of left dentary (A: MNHN MTD XVI 1, x 1) and an isolated tooth (B: MNHN MTD XVI 2, x 3) in lateral view of prosauropod *Azandohsaurus laaroussi* DUTUIT 1972 plus fabrosaurid ornithischian dinosaur tooth (C: MNHN MTD XVI 3, x 4.5) in anterior or posterior view from the mid-Carnian (Upper Triassic) of Argana Valley, Atlas Mountains, Morocco, from GALTON (in press) after DUTUIT (1972).
D,E: tooth of carnivorous archosaur IGS GSC 4873, x 6, from Bromsgrove Sandstone Formation of Warwick, England. – D: after MURCHINSON & STRICKLAND (1840, pl. 28, fig. 7a) and E: after V. HUENE (1908, fig. 265).
F: two teeth x 5 with detail of anterior edge, x 20, of *Thecodontosaurus antiquus* from the Magnesian Conglomerate (Rhaetic) of Durdham Down near Bristol, England, after V. HUENE (1908, fig. 207).
G: holotype SMNS 52456, x 1.5, of *Thecodontosaurus subcylindrodon* V. HUENE 1908 from the Lower Keuper Schilfsandstein of Stuttgart, after V. HUENE (1908, fig. 268).

Scale lines represent 10 mm (A) and 1 mm.

V. HUENE (1908, fig. 265), who did not locate this specimen. In *Thecodontosaurus*, as in all other prosauropods (see GALTON, in press), the serrations are proportionally larger (high notches or "Spitzkerbung" of V. HUENE 1926); they are set at an angle of 45° to the cutting edge (Fig. 4 F) and, in addition, the widest part of the crown is not at the root-crown junction but more apically on the main part of the crown (see also Fig. 3N).

*Thecodontosaurus subcylindrodon* V. HUENE 1908 is based on a tooth (V. HUENE 1908:241–242, fig. 268) from the Schilfsandstein (Middle Keuper, Upper Triassic) of Stuttgart. This tooth (SMNS 52456; Fig. 4 G) has a tapering, slightly recurved form with very fine serrations set perpendicular to the cutting edge so it is probably from a carnivorous archosaur; it is certainly not from a prosauropod.

V. HUENE (1908:169–171) referred to *Teratosaurus suevicus* several isolated postcranial dinosaur bones from the "Fränkischer Semionotus-Sandstein" (V. HUENE 1908:169) of Günthersbühl near Nürnberg, West Germany. According to HÄNEL (1974:12) in Günthersbühl there is exposed the Feuerletten, and in its surroundings the Upper Burgsandstein. The latter never has yielded reptile bones or *Semionotus*.

Only in the Lower Burgsandstein in the region of Nürnberg were found vertebrates, mainly *Semionotus*. The Lower Burgsandstein corresponds with the Upper "Semionotensandstein" sensu THÜRACH (1889, according to EMMERT 1964 : 108). So I suspect that either v. HUENE'S or the collector's data regarding the bones from Günthersbühl are wrong. The cervical vertebra (v. HUENE 1908, pl. 25, fig. 6) is similar to the fifth or sixth cervical vertebra of *Plateosaurus* (SMNS 13200; v. HUENE 1926, pl. 2, fig. 1). It is undoubtedly prosauropod. The anterior caudal vertebra, a chevron and the distal end of a humerus (v. HUENE 1908, fig. 179; pl. 25, figs. 7, 8) are probably prosauropod, too. The distal end of a femur and a complete but damaged tibia were described but not figured. However the femur was similar to the femur of *Pachysaurus*, a junior synonym of *Plateosaurus*. And the latter was similar to tibiae of *Plateosaurus* from the Upper Keuper; so both bones probably represent prosauropods. Unfortunately, none of this material can be restudied because the collection of the Naturhistorische Gesellschaft Nürnberg was destroyed during World War II (R. WILD, personal communication). Additionally the question remains open if the material was collected in the Burgsandstein or – what seems to be more probable – came from the overlying Feuerletten, from the bone-bearing Feuerletten-Konglomerat.

The remaining prosauropod dinosaurs described from Europe are from the Middle Stubensandstein of West Germany (v. HUENE 1908, 1932) plus the overlying Knollenmergel of West and East Germany and the Rhät of West Germany (v. HUENE 1908, 1926, 1932), and from beds of an equivalent age in England, France and Switzerland (v. HUENE 1908, 1932). Consequently, the partial prosauropod skeleton from the Lower Stubensandstein of Nordwürttemberg is the earliest record (Middle Norian) of the group from Europe.

### 4. Carnian Prosauropods from outside of Europe

In addition to the typical prosauropod families Anchisauridae and Melanorosauridae, COOPER (1980, 1981) referred the family Herrerasauridae BENEDETTO 1973 (in which he included Staurikosauridae GALTON 1977) to the Prosauropoda. *Herrerasaurus* REIG 1963 is a carnivorous form with a proportionally large skull and a short neck from the Ischigualasto Formation (Upper Triassic, Carnian) of Argentina (see also BENEDETTO 1973; BONAPARTE 1978, fig. 149 for photograph of mounted skeleton). *Staurikosaurus* COLBERT 1970 is a similar form with much more gracile proportions and a more elongate tibia from the Santa Maria Formation (Carnian or possibly upper Ladinian) of Brazil (see also GALTON 1977). These genera were included in the Prosauropoda by COLBERT (1970) and VAN HEERDEN (1978). They were regarded as having theropod affinities but classified as Saurischia incertae sedis by BENEDETTO (1973) and GALTON (1973, 1977), and referred to the Theropoda by BONAPARTE (1978). In both genera the teeth are tapering and slightly recurved with fine serrations set perpendicular to the edge which, as noted above, is in marked contrast to the form of the teeth of all prosauropods sensu stricto (Figs. 3 N, 4 A, B, F). Consequently I agree with BONAPARTE (1978) in refering these two genera to the Theropoda.

*Thecodontosaurus gibbidens* COPE 1878 from the New Oxford Formation (Carnian, Upper Triassic) of the Gettysburg Basin, Pennsylvania, U.S.A., consists of a premaxillary tooth plus a few cheek teeth (see v. HUENE 1921 : 571, figs. 14, 15) of an ornithischian dinosaur and similar teeth of a Carnian age are known from North Carolina, U.S.A., and Nova Scotia, Canada (GALTON 1983; GALTON & OLSEN, in prepn.).

*Azandohsaurus laarousi* DUTUIT 1972 is based on a dentary with teeth plus two loose teeth (Figs. 4 A-C) from the Upper Triassic of the Argana Valley in the Atlas Mountains, Morocco. This taxon was described as an ornithischian dinosaur but, as was first pointed out by THULBORN (1974), it is a prosauropod dinosaur. From the material the tooth MNHN XVI 3 (Fig. 4 C, cf. Figs. 3 M, N) should be removed as a cotype because it is not straight in anterior view (as in prosauropods, Fig. 3 M); it is from a fabrosaurid ornithischian dinosaur (see GALTON 1978). Additional fabrosaurid material includes loose teeth (Figs. 3 L, M) and maxillae with teeth that will be described by DUTUIT (personal communication). *Azandohsaurus* was found with metoposaurid amphibians, a large kannemeyrid dicynodont and a rauisuchid thecodontian (? *Ticinosuchus*); from that material the age was deduced as uppermost Middle Triassic (upper Ladinian) or lowermost Upper Triassic (lower Carnian) by DUTUIT (1980). However, these beds may not be as early as this because pollen studies on equivalent rocks south of Marrakech (125 km east of fossil locality in Argana Valley) give an age of Middle Carnian (COUSMINER & MANSPEIZER 1976).

Undescribed prosauropod teeth (PU) have been reported by BAIRD (1972) from the Wolfville Formation of the Fundy Basin, Nova Scotia, Canada, the age of which is Carnian (OLSEN & GALTON 1984).

Associated postcranial bones of the prosauropods *Euskelosaurus* and *Melanorosaurus* have been described from the Lower Stormberg Series (Lower Elliot Formation) of South Africa (HAUGHTON 1924, VAN HEERDEN 1979), the age of which is Carnian and/or lower Norian from a review of the vertebrate fauna represented by bones and footprints (OLSEN & GALTON 1984).

The remaining prosauropods are either clearly from the Norian (upper Los Colorados Formation of Argentina, see OLSEN & GALTON 1984) or from the Lower Jurassic, as in the case of the Glen Canyon Series of Western U.S.A., the upper part of the Newark Supergroup of eastern U.S.A., the upper Stormberg Series (Upper Elliot and Clarens formations) of southern Africa, and the upper Lower Lufeng Series of Yunnan, China (OLSEN & GALTON 1977; 1984).

From the above, it is apparent that the earliest records of prosauropods are from the Carnian (lower Upper Triassic) of Morocco and Nova Scotia plus possibly South Africa. However, whether the Lower Elliot Formation is Carnian or Lower Norian, it represents the earliest record of naturally associated remains of prosauropods reported to date.

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Plate 1

*Sellosaurus gracilis*, referred specimen SMNS 17928 from Lower Stubenstandstein of Ochsenbach, Nordwürttemberg.

Figs. 1, 2. Cervical vertebra 3 in lateral view. 1: from left; 2: from right. – x 1/3.

Figs. 3, 4. Cervical vertebra 4 in lateral view. 3: from left; 4 from right. – x 1/3.

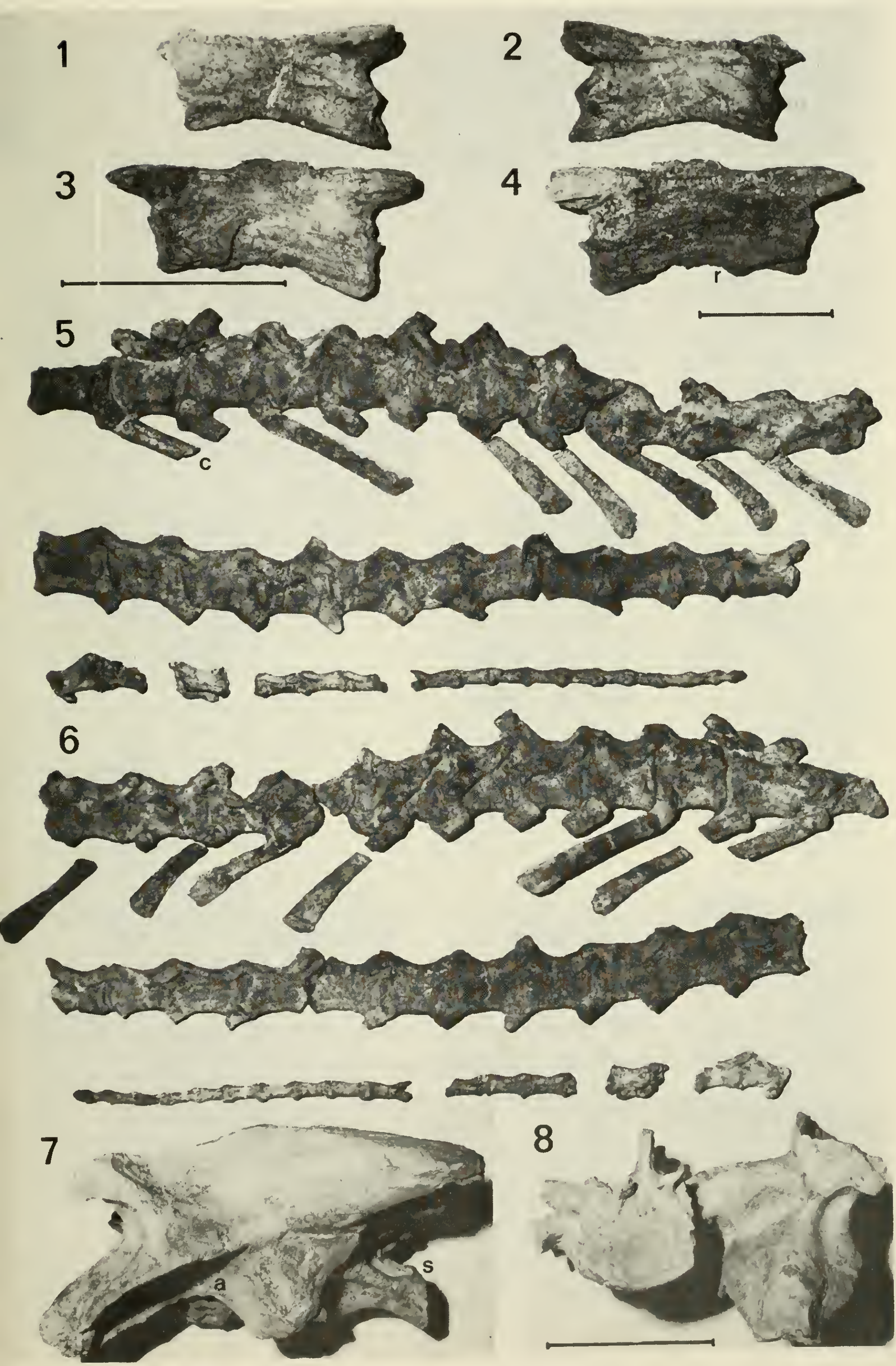
Figs. 5, 6. Caudal vertebrae and chevrons from about caudal 10 to 55 in lateral view. 5: from left; 6: from right. – x 0.2.

Fig. 7. Left ilium in lateral view. – Approx. x 0.25.

Fig. 8. Left ilium and dorsal vertebra 15 in anterior view. – Approx. x 0.25.

a = acetabulum; c = chevron; r = cervical rib; s = second sacral vertebra;
10–55 = position of vertebrae in tail.

Scale lines represent 10 cm.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## Plate 2

*Sellosaurus gracilis*, referred specimen SMNS 17928 from Lower Stubensandstein of Ochsenbach, Nordwürttemberg.

Figs. 1, 2. Dorsal 15, sacral 1 to 3 and caudal vertebra 1 in 1: dorsal and 2: ventral views. – Approx. x 0.25.

Fig. 3. Dorsal 15 and sacral vertebrae 1 and 2 in right lateral view. – Approx. x 0.25.

Fig. 4. Left ilium and sacral vertebra 2 in posterior view. – Approx. x 0.25.

Figs. 5, 6. Sacral 3 and caudal vertebrae 1 to 3 in lateral view. 5: from left; 6: from right. – Approx. x 0.25.

Fig. 7. Sacral vertebra 3 in anterior view. – x 0.25.

Fig. 8. Anterior caudal vertebra in left lateral view. – x 0.25.

Fig. 9. Proximal end of left ischium in proximal view. – x 0.2.

a = acetabulum; c = chevron; cl – caudal vertebra 1, d = dorsal vertebra 15; i = surface for ilium; p = surface for pubis; r 1,2,3, = sacral ribs 1,2, and 3; s2,3 = sacral vertebrae 2 and 3.

Scale lines represent 10 cm.

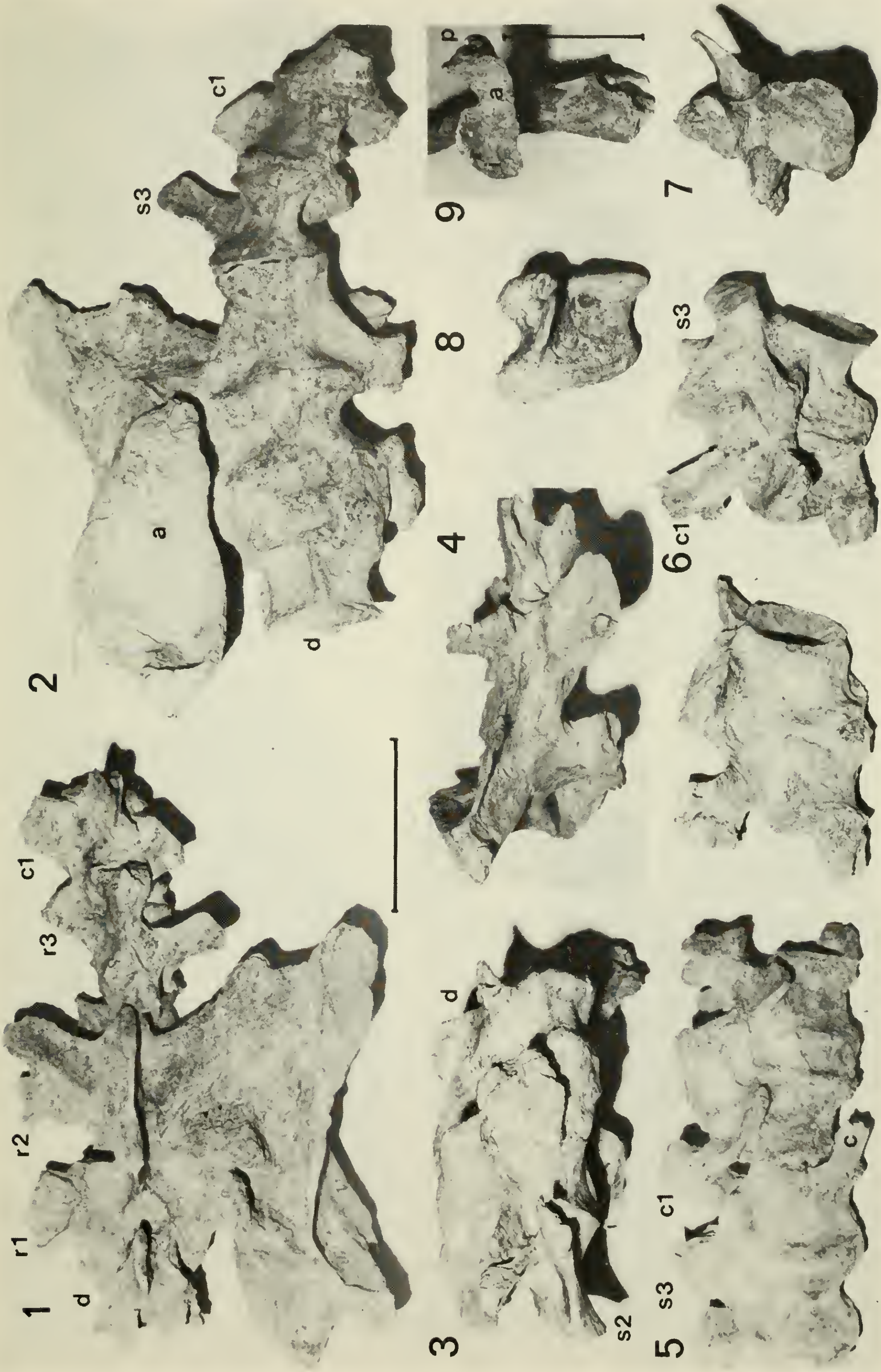
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Plate 3

*Sellosaurus gracilis* v. HUENE 1908, part of holotype SMNS 5715 from the Middle Stubensandstein of Heslach in Stuttgart.

Figs. 1–4. Sacral vertebrae 1 to 3 and caudal vertebra 1 plus right ilium in 1: left lateral; 2: right lateral; 3: dorsal and 4: ventral views. – Approx. x 0.25.

c = caudal vertebra 1; s1,3 = sacral vertebrae 1 and 3.

Scale line represents 10 cm.

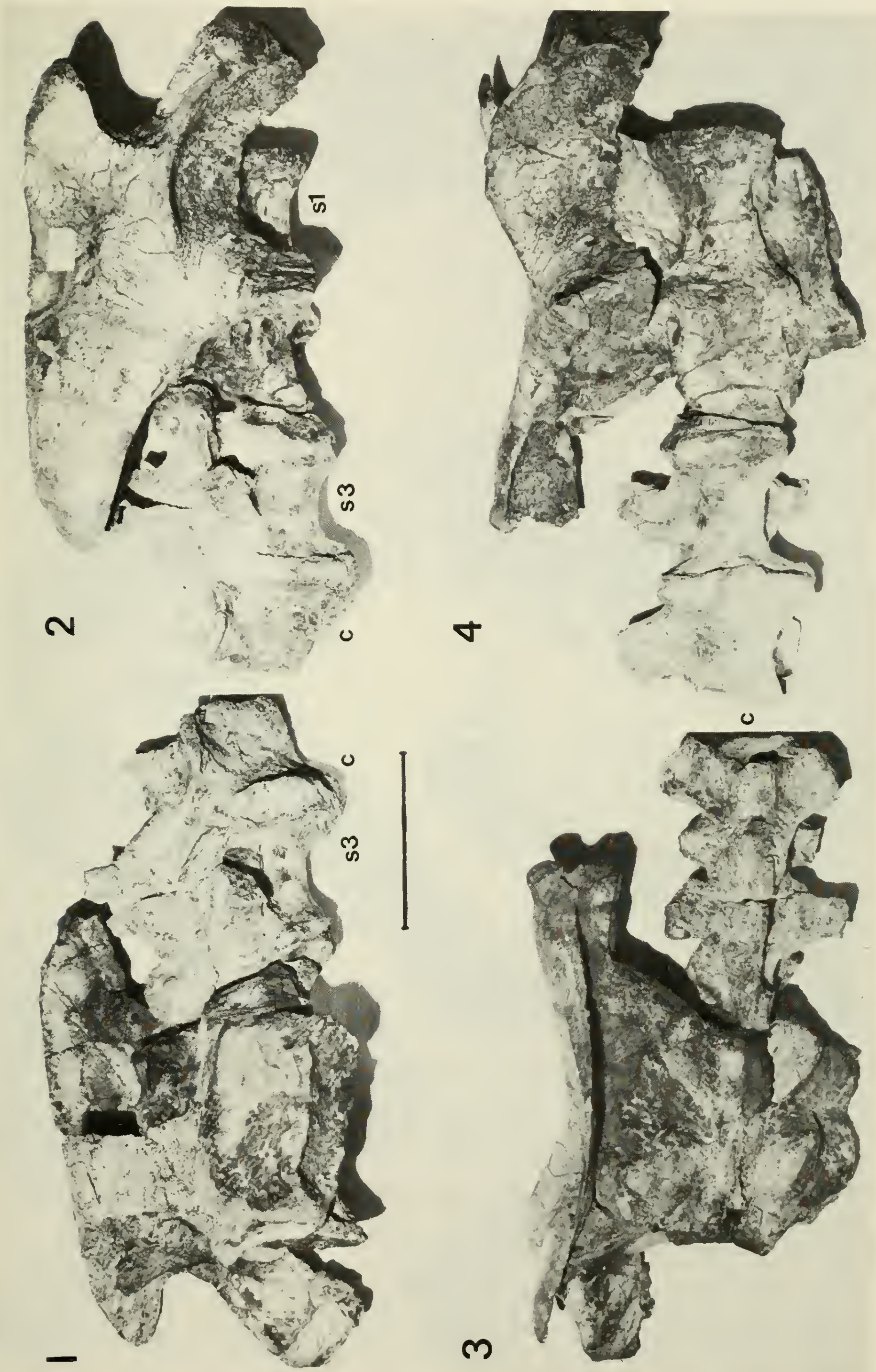
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Plate 4

*Sellosaurus gracilis,* referred specimen SMNS 17928 from Lower Stubensandstein of Ochsenbach, Nordwürttemberg.

Figs. 1,2. Right tibia, fibula, astragalus, calcaneum, distal tarsals and pes in 1: anterior and 2: posterior views. – x 0.15.

Figs. 3,4. Left femur in 3: lateral and 4: medial views with left tibia, fibula, astragalus and calcaneum in 3: posterior and 4: anterior views. – x 0.15.

Tooth of carnivorous archosaur from Bromsgrove Sandstone Formation of Warwick, England, IGS GSC 4873.

Fig. 5. Crown in lateral view. – x 5.

Fig. 6. Detail of anterior edge. – x 15.

a = astragalus; c = calcaneum; d = distal tarsal; f = femur; fi = fibula; ft = fourth trochanter; h = head; l = lesser trochanter; m = metatarsal; t = tibia; 1–4 = digits.

Scale line represents 1 mm (5, 6) and 10 cm.

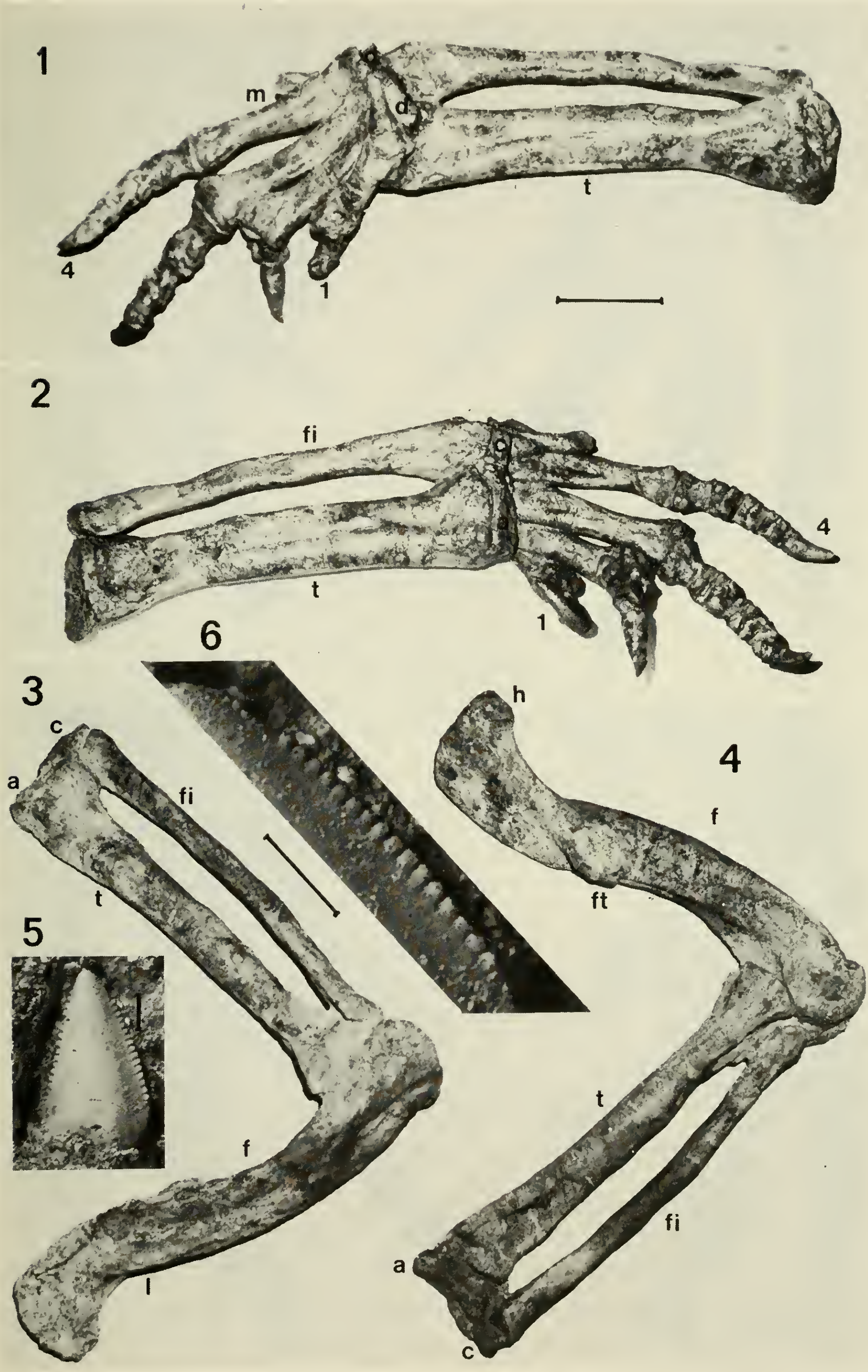
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Plate 5

*Sellosaurus gracilis*, referred specimen SMNS 17928 from Lower Stubenstein of Ochsenbach, Nordwürttemberg.

Figs. 1,2. Right pes in 1: anterior view with distal tarsals and 2: posterior view with astragalus, calcaneun and distal ends of tibia and fibula. – x 0.25.

Figs. 3,4. Left pes in 3: anterior and 4: posterior views. – x 0.25.

a = astragalus; c = calcaneum; dl = lateral distal tarsal; dm = medial distal tarsal; f = fibula; m = metatarsal; t = tibia.

Scale line represents 10 cm.


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