OSTEOLOGY OF THE JURASSIC LIZARD *ARDEOSAURUS BREVIPES* (MEYER)

by NIALL J. MATEER

ABSTRACT. A description is given of a new and well-preserved specimen of *Ardeosaurus brevipes* from the Solnhofen facies of the Kimmeridgian of Bavaria, Germany. The specimen is in the Paleontological Museum of Uppsala University (PMU.R58). The type of *A. brevipes* is missing and only a cast represents the poorly preserved original. The new specimen has characters exemplifying the similarities between the two species of *Ardeosaurus*: *A. brevipes* and *A. digitatellus*. Differences between *Ardeosaurus* and a similar genus *Eichstaettisaurus* are clarified and emphasized. The specimen is compared with other Jurassic lizards also probably belonging to the Gekkota: *Yabeinosaurus*, *Bavarisaurus*, and *Palaeolacerta*.

A NEW specimen of the Jurassic lizard *A. brevipes* was recently discovered in the collections of the Paleontological Museum in Uppsala, previously having been labelled as *Homeosaurus*. The genus *Ardeosaurus* is known only from the Kimmeridgian of Germany, and the present specimen is from Solnhofen. Nothing is known of the purchase or collection of this specimen by the museum.

Three other specimens represent this genus, one of which, the type for *Ardeosaurus*, is apparently lost and is represented only by a cast. The other two specimens, both from Solnhofen, have been referred to the species *A. digitatellus* (Cocude-Michel 1963) and *A.* cf. *digitatellus* (Grier 1914). All three of these specimens are poorly preserved and do not reveal much osteological detail. However, a closely related genus, *Eichstaettisaurus* from Eichstätt, is well-preserved and provides a useful comparison with the present specimen. A review of the taxonomic history of this genus is given by Hoffstetter (1964) and of its present status by Estes (1981).

Owing to the exceptional nature of the preservation of the Uppsala specimen, the morphology of *A. brevipes* can be clarified and its relationships with contemporary gekkotans considered in more detail. These lizards are of some importance since they represent amongst the earliest 'modern' lizards with a fully developed kinetic skull.

The following acronyms are used: BMNH, British Museum (Natural History); CM, Carnegie Museum, Pittsburgh; PMU, Paleontological Museum, Uppsala.

SYSTEMATIC DESCRIPTION

Infra-order GEKKOTA Cuvier, 1817
Superfamily GEKKONOIDEA Underwood, 1954
Family ARDEOSAURIDAE Camp, 1923
Genus ARDEOSAURUS Meyer, 1860
Ardeosaurus brevipes Meyer, 1860

Plate 48

1855 *Homeosaurus brevipes* Meyer, p. 335.
1860 *Ardeosaurus brevipes* Meyer, p. 106, pl. 7.
1908 *Ardeosaurus brevipes* Nopcsa, p. 37.
1923 *Ardeosaurus brevipes* Camp, p. 306, fig. *c*.
1925 '*Homeosaurus* (*Ardeosaurus*) *brevipes* Meyer' Broili, p. 108.
1938 ?*Ardeosaurus brevipes* Broili, p. 105.
1953 *Ardeosaurus brevipes* Hoffstetter, p. 346, fig. 1*b*.

[Palaeontology, Vol. 25, Part 3, pp. 461–469, pls. 48–49.]

1955 *Ardeosaurus brevipes* Hoffstetter, p. 612, fig. 3*b*.
1963 *Ardeosaurus brevipes* Cocude-Michel, p. 145.
1964 *Ardeosaurus brevipes* Cocude-Michel, p. 704.
1964 *Ardeosaurus brevipes* Hoffstetter, p. 282.
1966 *Ardeosaurus brevipes* Hoffstetter, p. 592, fig. 1.

Holotype. The original described by Meyer (1855) is apparently lost, but a cast remains of the near complete, but poorly preserved specimen, BMNH no. 38006.

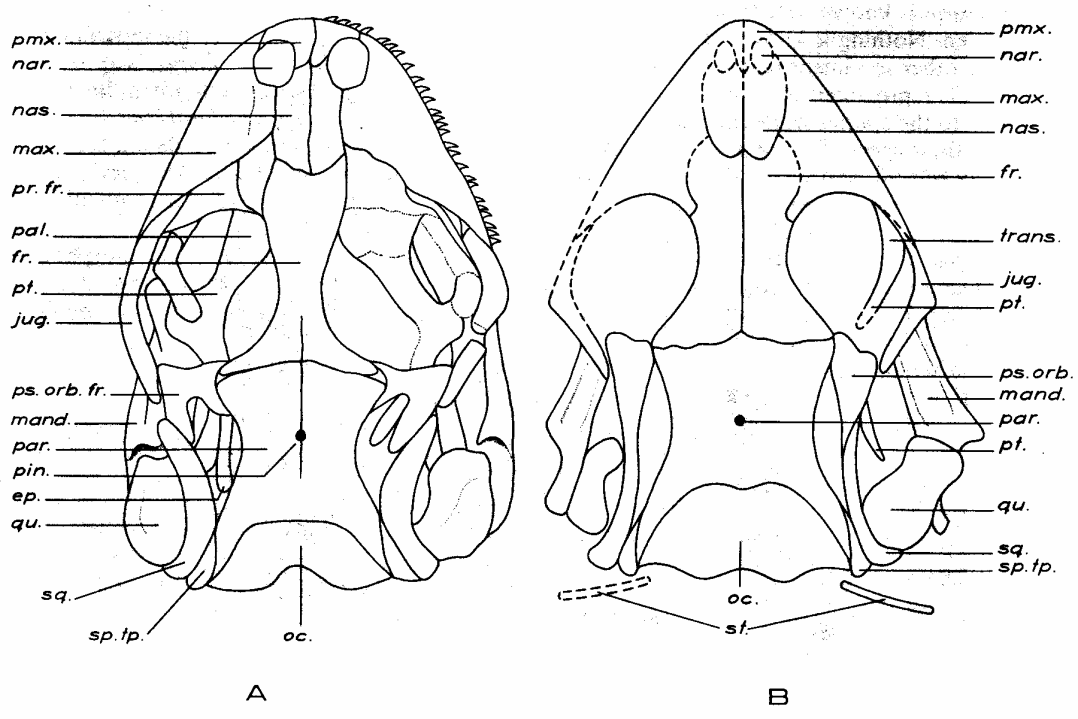
Horizon. Upper Kimmeridgian (Solnhofen Plattenkalk), Upper Jurassic.

Locality. The holotype and the present specimen (PMU.R58) are from the Eichstätt quarries, Bavaria, Federal Republic of Germany.

DESCRIPTION

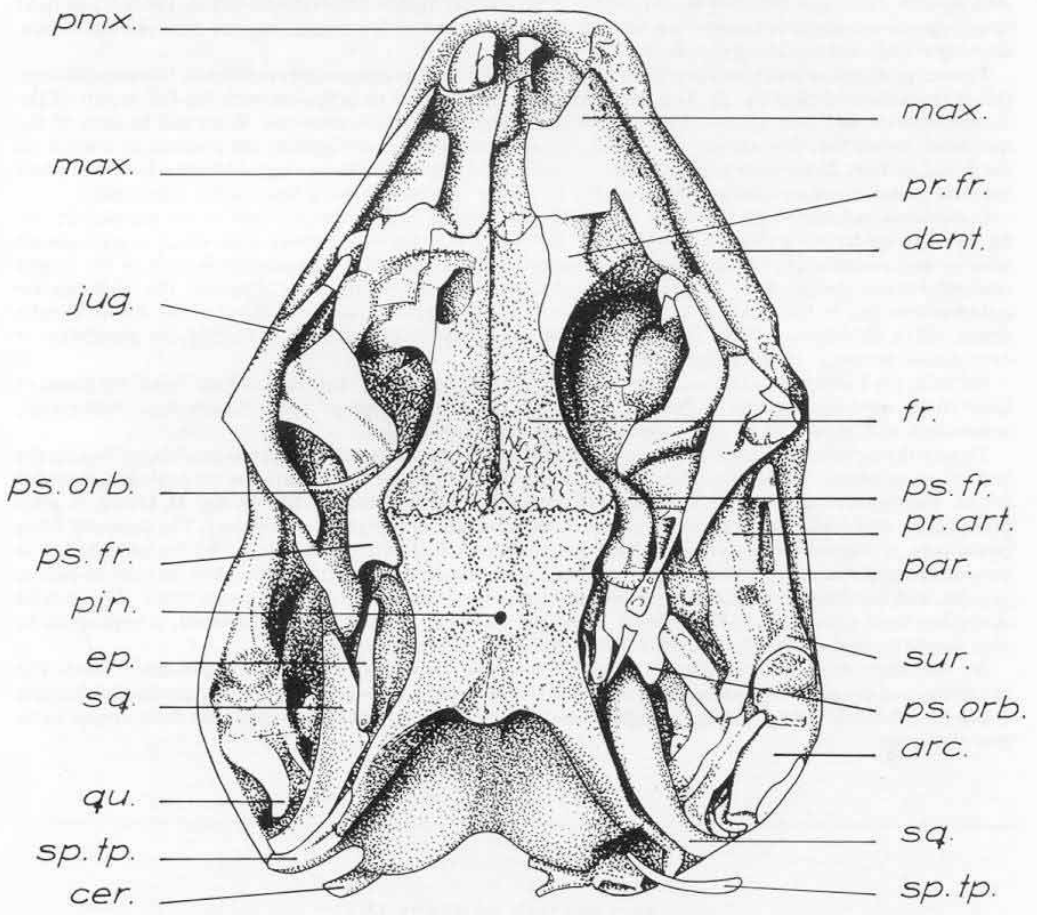
The new specimen is complete except for the distal part of the tail (Pl. 48). The preservation is mostly excellent, although it is dorso-ventrally compressed; relative to other specimens from the Upper Jurassic, it is exceptional. Since the other specimens are so poor and scarce, descriptions, photographs, and diagrams by Hoffstetter (1964, 1966) have been relied upon heavily in the comparisons made below.

Nearly all the bones from the dorsal surface of the skull are clearly defined (text-figs. 1*b*, 2; Pl. 49, figs. 1, 2, 3). The overall shape is triangular anterior to the parietals, but with a slightly squared margin. The narial



TEXT-FIG. 1. Comparative outlines of (*a*) *Eichstaettisaurus schroederi* (Munich 1937-I-1) ×2·5, (*b*) *Ardeosaurus brevipes* (BMNH. 38006) ×3·5. ep, epipterygoid; fr, frontal; jug, jugal; mand, mandibular; max, maxillae; nar, narial; nas, nasal; oc, occipital; pal, palatine; par, parietal; pin, pineal; pmx, premaxillae; pr.fr, prefrontal; ps.orb, postorbital; ps.orb.fr, postorbito-frontal; pt, pterygoid; qu, quadrate; sp.tp, supratemporal; sq, squamosal; st, stapes; trans, transpalatine.

openings are relatively large and oval, set almost parallel to the midline. The premaxillae are not clearly seen but appear, nevertheless, to be paired. The nasals are quite short and straight-sided; the outer border of these bones, however, are somewhat obscured by the dorsal processes of the maxillae concealing their true shape. The maxillae meet the jugals at a short concave suture. The prefrontals are large and extend anteriorly to halfway between the anterior border of the orbit and the premaxilla border. They comprise almost the entire anterior arc of the orbit. The anterior border of the prefrontals is not clearly seen along its full extent, but it would appear to be rather broad, extending antero-laterally further than in *Eichstaettisaurus*. The lachrymals are absent. The frontals are paired along their full length and are straight-sided after the initial constriction anterior to the parietal contact, which finishes at the mid-orbital level. The sinuous nature of the naso-frontal contact suggests that this was not a kinetic joint. The jugals are moderately robust and have a boomerang-shape. The posterior end of the jugal articulates with the postorbital tapering on the inner side. The components of the postorbito-frontal complex (Hoffstetter 1964) are here clearly separate entities, but nevertheless do complete the postorbital arc. Anteriorly, the postfrontal flutes narrowly into the orbital border of the frontal;



TEXT-FIG. 2. Skull of *Ardeosaurus brevipes* (Meyer) (PMU.R58). ×6·4. arc, articular; cer, ceratohyal; dent, dentary; pr.art, prearticular; ps.fr, postfrontal; sur, surangular (other abbreviations, see text-fig. 1).

it expands posteriorly to form the anterior margin of the supratemporal foramen. It is triangular and connects the jugal and postfrontal to the squamosal. The postorbital of the type of *A. brevipes* is poorly known, but a clear similarity is apparent with the Uppsala specimen; the postorbital and postfrontal in *Eichstaettisaurus* has a quite different form (text-fig. 1*a* is based upon a reconstruction by Hoffstetter (1967); Estes (1981) holds that the postorbital and postfrontal are separate bones, not fused as Hoffstetter showed). The supratemporal foramen is typically elongate, bordered by the constricted parietal on the inner side, and by the postorbitofrontal and squamosal on the outer side.

The squamosal is substantial and evenly curved resembling a 'hockey stick' (Robinson 1967), although this shape may vary with the preserved aspect. The nature of the contact to the quadrate is not clear, although the peg for insertion into the quadrate notch can be distinguished. This latter notch is not seen. The supratemporal separates the posterior part of the squamosal from the paroccipital.

The parietal is square with moderately robust paroccipitals; these latter have a very slight tendency to incline inwardly, otherwise being quite straight. The parietals are co-ossified and the pineal opening lies centrally and is quite small. The substantial suture between the parietal and the frontals is straight transversely and the marked fracture along this contact suggests a certain weakness, or previous mobility, indicating that mesokinesis (a hinging of the snout relative to the posterior part of the skull) was fully developed in *Ardeosaurus*. Thus, this specimen would appear to be a rather typical amphikinetic lizard. The left and right epipterygoids are preserved appearing through the supratemporal foramena; they are slim rod-like bones, showing a kink midway along the shaft.

The occipital region is not well preserved and the definition of the components is difficult. Notwithstanding, this is reconstructed (text-fig. 3). The paroccipitals extend around to articulate with the full length of the supratemporals and meet the quadrates which are obscured by the squamosals. What can be seen of the quadrates, shows that they are not broad and a longitudinal groove may indicate the presence of a notch on the dorsal surface. There is no quadratojugal connecting the jugal with the quadrate to form a lower temporal bar; this indicates a streptostylic condition. The left hyoid is preserved lying near the left paroccipital.

Osteoderms and epidermal scutes are present on the frontals and the anterior half of the parietal (Pl. 49, fig. 1). Four epidermal scutes are recognizable; most notable is the interparietal scute which is split into an anterior and posterior part, in contrast to the normal single interparietal. The anterior borders of the frontal epidermal scutes are not seen. The frontoparietal and parietal scutes are more apparent. The markings are not characteristic of the Gekkota and Iguania, rather they show similarity to those of the Scincomorpha (Estes 1981). Hoffstetter (1964) mentioned minor rugosities or granulations indicating the possibility of osteodermal sculpture in *A.* cf. *digitatellus*.

No teeth are sufficiently well preserved to state the type of dentition *Ardeosaurus* had. There are traces of teeth on the right dentary (not visible in Pl. 49, fig. 2) which would appear not to be acrodont; presumably, in common with most lizards, *Ardeosaurus* had a pleurodont dentition.

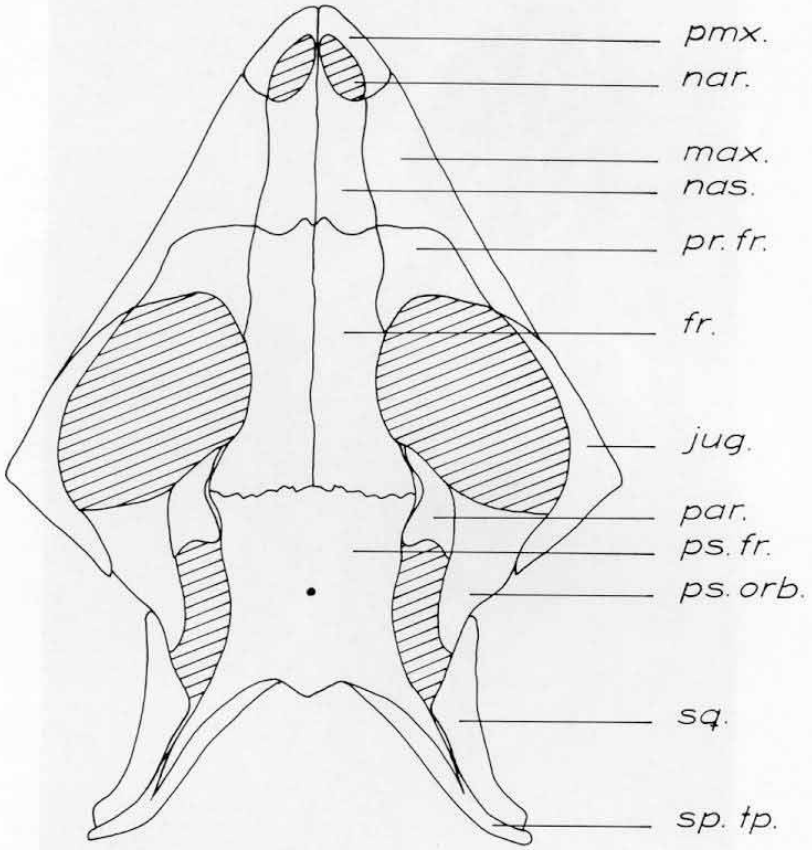
Twenty-three presacral vertebrae are present and only some ten poorly preserved caudals, excluding the two sacral vertebrae. The dorsal series do not vary much in size and their centra are procoelous and rather broad. Twenty-two pairs of ribs are seen. The pectoral is badly dislocated (Pl. 49, fig. 4). Owing to poor preservation and a lack of comparative material, the structure of the girdle is not clear. The coracoid, lying posteriorly, is relatively slim compared with recent forms (Hoffstetter 1964, fig. 4). A coracoid window is present, although the exact form is not certain. The scapula appears only a little thinner than the postero-palinal process, and has become detached from the anterior part of the coracoid during preservation. The glenoid cavity has been extensively re-mineralized. Although the pelvic girdle is poorly preserved, it appears to be very similar to that figured by Cocude-Michel (1963, fig. 39*a*) for *A. digitatellus*.

All four limbs are largely complete, though the tarsi and carpi have been extensively re-mineralized. The astragulus and calcaneium have not co-ossified and this indicates a juvenile condition. The phalangeal formula is 2-3-4-5-3/2-3-4-5-3; the first digit is slightly obscured by the overlying second digit, but there appear to be two phalanges.

EXPLANATION OF PLATE 48

Dorsal view of *Ardeosaurus brevipes* (Meyer) (PMU.R58) from the Upper Jurassic of southern Germany. × 1·4.

MATEER, Jurassic lizard



TEXT-FIG. 3. A cranial reconstruction of *Ardeosaurus brevipes* dorsal view, based on *A. brevipes* (Meyer) (PMU.R58) in Uppsala. See text-fig. 1 for explanation of abbreviations. ×6·4.

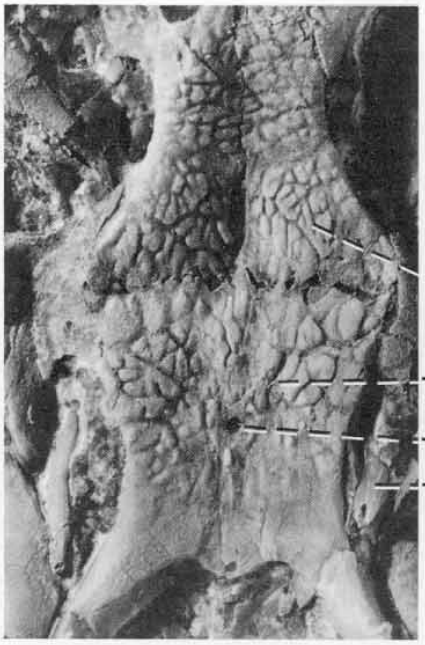
EXPLANATION OF PLATE 49

Fig. 1. Dorsal view of the parietal and posterior frontals of *Ardeosaurus brevipes* (Meyer) (PMU.R58) showing the position of the pineal opening and the nature of the osteoderms. See text-fig. 1 for explanation of abbreviations. ×6·70.

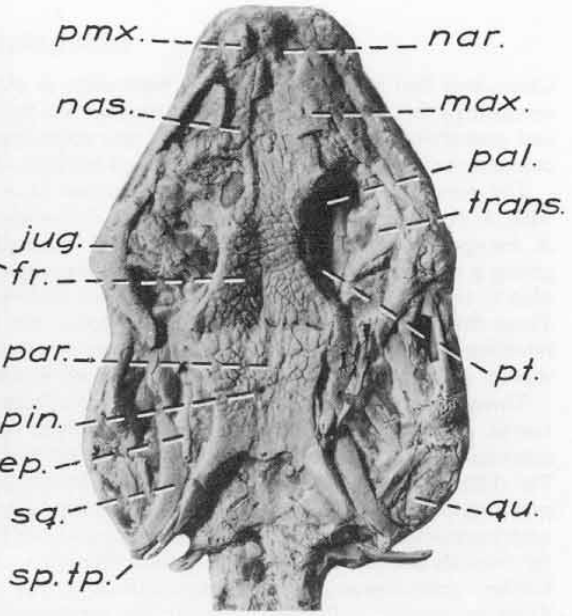
Fig. 2. A detailed dorsal view of *Ardeosaurus brevipes* (Meyer) (PMU.R58). See text-fig. 1 for explanation of abbreviations. ×3·25.

Fig. 3. A detailed view of the left quadrate suspensorium of *Ardeosaurus brevipes* (Meyer) (PMU.R58). See text-fig. 1 for an explanation of abbreviations. ×6·70.

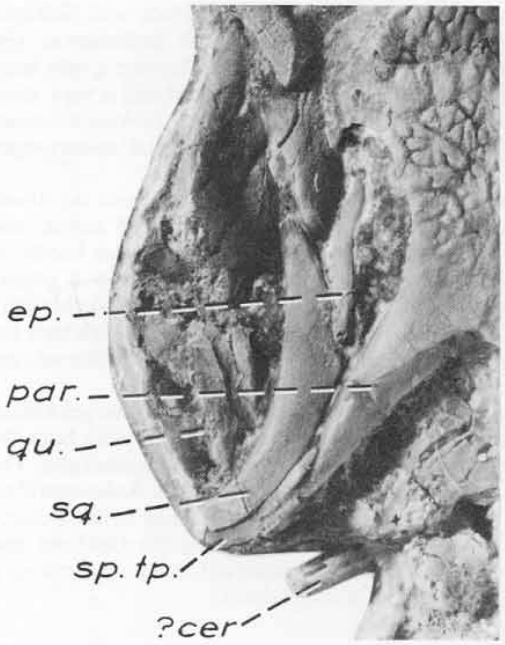
Fig. 4. A dorsal view of the left pectoral girdle of *Ardeosaurus brevipes* (Meyer) (PMU.R58). cor, coracoid; hum, humerus; sca, scapula. ×6·70.



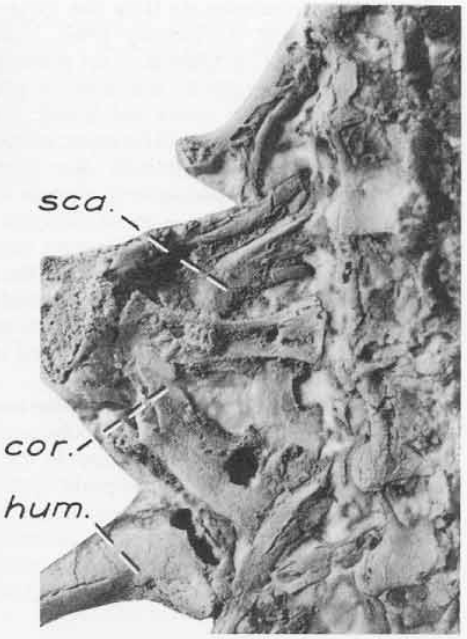
1


pmx.
nar.
nas.
max.
pal.
trans.
jug.
fr.
par.
pt.
pin.
ep.
sq.
qu.
sp.tp.

2


ep.
par.
qu.
sq.
sp.tp.
?cer

3


sca.
cor.
hum.

4

DISCUSSION

Characters that have not previously been seen, or clearly seen, in this species and genus that are revealed in this specimen include: osteoderms on the frontals and parietal; separated postfrontal and postorbital; a complete postorbital arc; epipterygoids; paired nasals and the nasal-premaxilla contact; the narial openings; straight-sided frontals and large prefrontals.

The poor preservation of the two specimens of *A. digitalellus* makes an accurate comparison with *A. brevipes* difficult. Nevertheless, the following minor differences are noted with respect to *A. brevipes*: a less pointed snout; the width to length ratio of the parietal is somewhat higher, giving a more squared shape; the jugals are less robust but more curved; the ratios humerus plus ulna to manus/femur plus tibia, to pes, differ: 1·0/1·4 in *A. digitalellus*, and 1·3/1·2 in *A. brevipes*. These differences are minor and would appear not to carry much taxonomic weight, thus the retention of these two species of *Ardeosaurus* is seriously questioned. Hoffstetter (1964) suggested that *A.* cf. *digitalellus* may be an adult form of *A. brevipes*, but this is difficult to justify.

Three further genera of lizard are also known from the Upper Jurassic of Germany: *Eichstaettisaurus*, *Bavarisaurus*, and *Palaeolacerta*, of which only *Eichstaettisaurus* is known from a good specimen. These various specimens are reviewed in detail by Hoffstetter (1964) and Estes (1981). The differences between *Ardeosaurus* and *Eichstaettisaurus* are clear despite some confusion in the previous literature. *Eichstaettisaurus* has a much larger and more rounded snout with a depressed anterior margin; the orbits are much larger and are placed more posteriorly than in *Ardeosaurus*; the frontals are fused and very narrow giving rise to a pronounced expansion toward the parietal border; *Ardeosaurus* has only twenty-three to twenty-five presacral vertebrae versus thirty in *Eichstaettisaurus*; a different shape to the supratemporal foramen is caused by the much shorter postorbital and postfrontal; longer nasals than in *Ardeosaurus*; and a partially sutured parietal (text-fig. 1*a*). This emphasizes Hoffstetter's defence of keeping *Ardeosaurus* and *Eichstaettisaurus* separate, *contra* Cocude-Michel's (1965) suggestion that they are synonomous. (See also Estes 1981.)

The genus *Yabeinosaurus* from the Upper Jurassic of Manchuria, China (Endo and Shikama 1942; Young 1958; Hoffstetter 1964), shows a very close association with *Ardeosaurus* and *Eichstaettisaurus*. The differences are primarily proportional, except for the following: a very large orbit in which the jugals do not meet the postorbital to complete the postorbital arc; a very small pineal opening; a very short and broad postorbito-frontal, not unlike that of *Eichstaettisaurus*, giving a broad supratemporal foramen; a smaller and more posteriorly placed parietal; twenty-eight presacral vertebrae, and relatively short limbs.

Bavarisaurus and *Palaeolacerta*, though in general similar, are distinguishable from the above genera. *Palaeolacerta* has a more elongate skull, larger and less anteriorly placed orbits, and amphicoelous vertebrae. The supposed large pineal opening near the fronto-parietal border is thought to be an artifact (Estes 1981). *Bavarisaurus* also has amphicoelous vertebrae, a greatly enlarged supratemporal foramen, an apparent absence of a pineal opening, and remarkably long limbs. The type, and only specimen, is not well preserved, thus the absence of a pineal (which lies in an area of breakage) should be treated tentatively; the amphicoelous vertebrae, however, are significant.

The relationships of the Ardeosauridae and Bavarisauridae to the early history of the gekkotans are not clear. Estes (1981) discusses characters that these families share in common with both the Gekkota (generally recognized as one of the most primitive of lizards) and the Scincomorpha. The epidermal scutes seen in the Uppsala specimen of *Ardeosaurus* suggest that the Ardeosauridae, comprising *Ardeosaurus*, *Eichstaettisaurus*, and *Yabeinosaurus*, should be assigned to the Scincomorpha (see Robinson 1967) thus indicating possible relationships between the Gekkota and Scincomorpha (Estes 1981). In the absence of sufficiently well-preserved early specimens, a conservative course is taken here, placing these families within the Gekkota.

Acknowledgements. I should like to thank Drs. Richard Estes, Robert Hoffstetter, and Pamela Robinson for their helpful comments and suggestions on various drafts of this paper. Dr. Richard Estes kindly allowed me to see part of his forthcoming review of fossil lizards.

REFERENCES

BROILI, F. 1925. Beobachtungen an der Gattung *Homeosaurus* H. von Meyer. *S.-B. bayer. Akad. Wiss. München, math.-naturw. Abt.* 81–121.

—— 1938. Ein neuer Fund von ?*Ardeosaurus* H. von Meyer. Ibid. 97–114.

CAMP, C. L. 1923. Classification of the lizards. *Bull. Am. Mus. nat. Hist.* **48,** 289–481.

COCUDE-MICHEL, M. 1963. Rhynchocéphales et les Sauriens des calcaires lithographiques (Jurassique supérieur) d'Europe occidentale. *Nouv. Arch. Mus. Hist. Nat. Lyon.* fasc. VII, 187 pp.

—— 1964. Étude d'*Eichstaettisaurus digitatellus* (= *Homeosaurus digitatellus* Grier 1914). Saurien du Portlandien inférieur de Solenhofen. *Bull. Soc. géol. France,* **6,** 704–706.

ENDO, R. and SHIKAMA, T. 1942. Mesozoic reptilian fauna in the Johol mountainland. *Bull. cent. nation. Mus. Manchoukuo.* **3,** 1–19.

ESTES, R. 1981. The Squamata. *In*: P. WELLNHOFER (ed.). *Encyclopedia of Paleoherpetology.* Gustav Fischer Verlag (in press).

GRIER, N. M. 1914. A new rhynchocephalian from the Jura of Solnhofen. *Ann. Carnegie Mus.* **9,** 86–91.

HOFFSTETTER, R. 1953. Les sauriens anté-cretacés. *Bull. Mus. nat. Hist. Nat.* **25,** 345–352.

—— 1955. Squamates de type moderne. *Traité de Paleontologie,* **5,** 606–662.

—— 1964. Les sauria du Jurassique supérieur et spécialement les Gekkota de Bavière et de Mandchourie. *Senck. biol.* **45,** 281–324.

—— 1966. A propos des genres *Ardeosaurus* et *Eichstaettisaurus* (Reptilia, Sauria, Gekkonoidea) du Jurassique supérieur de Franconie. *Bull. Soc. géol. France,* **7,** 592–595.

MEYER, H. von. 1855. Briefliche Mitteilung an Prof. Brown. *Neues Jb. Min. geol. Petrefaktenk.* **1855,** 326–327.

—— 1860. *Zur Fauna der Vorwelt. Reptilien aus dem lithographischen Schiefer des Jura in Deutschland mit Franchreich.* Frankfurt-am-Main.

NOPCSA, F. von. 1908. Zur Kenntnis der Fossilen Eidechs. *Beitr. Paläont. geol. Österreich-Ungarns.* **23,** 33–62.

ROBINSON, P. 1967. The evolution of the Lacertilia. *Coll. int. Cent. nat. Rech. Scient.* **163,** 395–408.

UNDERWOOD, G. 1954. On the classification and evolution of geckos. *Proc. zool. Soc. Lond.* **124,** 469–492.

YOUNG, C. C. 1958. On a new locality of *Yabeinosaurus tenuis* Endo and Shikama. *Vert. Palasiatica.* **2,** 151–156.

NIALL J. MATEER
Department of Geology
McMurry College
Abilene
Texas 79697
USA

Typescript received 9 December 1980
Revised typescript received 6 April 1981