

# THE DIAPSID REPTILE, *PACHYSTROPHEUS RHAETICUS*, A PROBABLE CHORISTODERE FROM THE RHAETIAN OF EUROPE

by G. W. STORRS, D. J. GOWER and N. F. LARGE

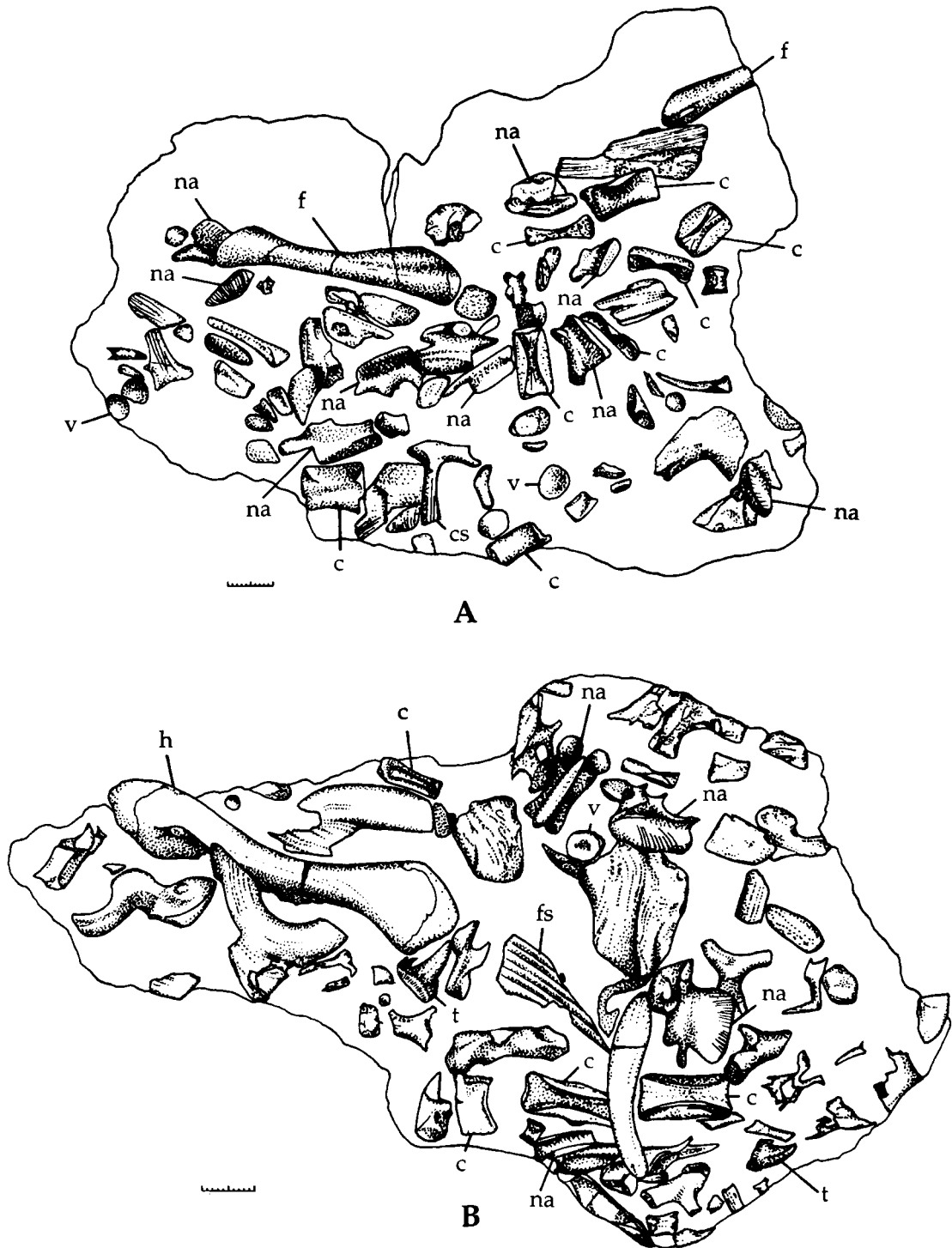
**ABSTRACT.** The enigmatic Upper Triassic reptile, *Pachystropheus rhaeticus*, displays characters suggestive of choristoderan affinity and, as such, is potentially the oldest known choristoderan reptile. Examination of the known skeletal elements indicates that the choristoderan lineage remained morphologically conservative throughout its recorded history. The occurrence of *Pachystropheus* fossils in marginal marine bone beds, however, may reflect a previously unrecognized shift of habitat for the Choristodera, from the paralic environments occupied by early representatives, to the more typical freshwater, often fluvial, deposits containing later forms.

THE fossil reptile *Pachystropheus rhaeticus* was described by E. von Huene (1935) from generally isolated elements in the bone beds of the Rhaetian (uppermost Triassic) Westbury Formation, Penarth Group, of south-west England; in genetically and perhaps stratigraphically equivalent rocks of Baden-Württemberg (Gaisbrunnen near Bebenhausen and Olgahain), Germany; and in the famous Rhaetian fissure fill deposits of Holwell, Somerset, England (F. von Huene 1902; E. von Huene 1933, 1935).

Storrs and Gower (1993) have suggested that *Pachystropheus rhaeticus* may represent the earliest known member of the Choristodera. As such, it would predate the next occurrence of choristoderes in the Middle Jurassic (Bathonian) (Evans 1989, 1990, 1991; Metcalf *et al.* 1992) by approximately 45 million years. In fact, both E. von Huene (1935) and her father (F. von Huene 1956) had assigned *Pachystropheus* to the choristoderan Champsosauridae, at that time considered to be rynchcephalians and known only from Cretaceous and Palaeogene representatives. This identification has been noted briefly in studies and listings of the Choristodera (e.g. Hoffstetter 1955; Kuhn 1961, 1969, 1971; Romer 1966; Appleby *et al.* 1967; Efimov 1975, 1988; Russell-Sigogneau and Russell 1978; Carroll 1988; Evans 1989, 1990; Benton 1993; Evans and Hecht 1993), but has not received general acceptance. Presumably, this was due in part to the brief description and relatively poor quality of the type material which contrast with those for late Mesozoic and early Palaeogene champsosaurs. It may also reflect an unwritten prejudice that such an early occurrence and resultant large gap in the fossil record precluded a true relationship with champsosaurs.

It is now known, however, that stratigraphical position is often a poor indicator of phylogenetic relationship and that substantial gaps occur in the records of many fossil vertebrates. This is in spite of recent studies showing that some clades actually exhibit a significant correlation between time of occurrence of member taxa and phylogenetic branching sequence (Norell and Novacek 1992a, 1992b; Benton and Storrs 1994, 1996). Furthermore, work subsequent to E. von Huene's (1935) description has documented the occurrence of choristoderes in deposits of Jurassic (Evans 1989, 1990, 1991; Metcalf *et al.* 1992) and Oligocene (Hecht 1992) age. In fact, the existence of Triassic, and indeed Permian, choristoderes has been predicted from cladistic analyses of relationships between early diapsid reptiles (Evans 1988, 1990; Gauthier *et al.* 1988; Storrs and Gower 1993).

Material of *Pachystropheus* is very common in the Westbury Formation but its morphology and relationships have remained obscure because of its general preservation as isolated or disassociated elements. The exposures from which came E. von Huene's (1935) fossils include two Somerset localities: Vallis Vale, near Frome [ST 755 490] and Blue Anchor Point [ST 034 435], and two well known Gloucestershire localities: Garden Cliff, Westbury-on-Severn [SO 717 130], and Sedbury ('Slime Road') Cliff [ST 555 930] (it should be noted that although E. von Huene (1933) listed Vallis



TEXT-FIG. 1. For caption see opposite.

Vale as the site of origin of several of her specimens, the matrix on some of these matches that of undoubted Holwell [ST 727 452] material). Numerous *Pachystropheus* bones have come also from the classic Rhaetian exposure at Aust Cliff, Avon [ST 566 898] (Storrs 1994).

Most of the present material is from Aust and Garden cliffs, although useful examples have also been collected from 'bone beds' (once known collectively as the 'Rhaetic Bone Bed') at numerous localities in the south-west and midlands of England, and south Wales (Owen 1842; Browne 1894; F. von Huene 1902; E. von Huene 1933, 1935; Macfadyen 1970; Sykes *et al.* 1970; Duffin 1978, 1980; Antia 1979; Martill and Dawn 1986; Storrs 1994). A collection recently made by M. T. and S. A. Curtis from the Hampstead Farm (Curtis and Curtis 1987) and Southfields quarries, Chipping Sodbury, Avon [ST 726 839], has been particularly valuable, as have the 102 collecting visits made to Garden Cliff between 1987 and 1992 as part of this study (N.F.L.).

The few German specimens of this taxon are relatively poor (F. von Huene 1902; E. von Huene 1933, 1935), and E. von Huene's (1933) figured material from Gaisbrunnen (GPIT 19552) includes only half a sacral centrum, a small phalanx, a fragmentary 'metatarsal', and two elements from a selection of isolated neural spines. Six recently collected dorsal centra (SMNS 58791), one retaining most of the neural arch, from the 'Rhätbonebed' of Ochtersum, near Hildesheim, Lower Saxony, are identical to the English material in morphology and preservation. Numerous abraded dorsal centra (MNHN SNP101) are known from the Late Triassic sands of Saint-Nicolas-de-Port, near Nancy, north-eastern France. This occurrence is of interest because of its potential, although controversial, Norian age (Buffetaut and Wouters 1986; Cuny and Ramboer 1991; Duffin 1993). Another notable example (BRSMG Cd2678) was collected *in situ* from the lowermost Jurassic (Hettangian) Lower Lias, *Psiloceras planorbis* Zone, at Lilstock [ST 16 44], Somerset.

#### GEOLOGICAL SETTING

The Westbury Formation, the basal unit of the Penarth Group (Rhaetian) of south-west Britain (Warrington *et al.* 1980), is a widespread, 1–15 m thick unit of black, pyritic shale, thin siltstone bands and a few limestone beds and shelly horizons. It is particularly well known for its bone beds which, together with the base of the formation in general, represent the end of regional Triassic continental deposition and the onset of an extensive, disconformable, marine transgression. Westbury Formation rocks are cyclical in nature and suggestive of fluctuating depositional conditions and water depth in marginal marine environments (Ivimey-Cook 1974; Hamilton 1977; Storrs 1994). The water was never deep, but conditions within the sediment were often anoxic, as evidenced by abundant pyrite, especially at Garden Cliff. A plentiful supply of terrestrially derived iron (here the limiting factor for pyrite deposition) attests to nearshore conditions. Anoxia probably resulted from high organic input and possible salinity stratification (Storrs 1994).

Garden Cliff provides the most spectacular accumulations of *Pachystropheus* remains, including rare, potentially associated individuals (Text-fig. 1). Bones are most commonly, however, mixed with those of other vertebrate taxa. Most new specimens used in this study have come from Garden Cliff, an approximately 1 km long section beside the Severn Estuary, on the upstream side of the Arlingham meander loop. The exposed rocks range from the uppermost Triassic (Norian and Rhaetian) to the lowermost Jurassic (Hettangian). The section achieves its greatest height of 21 m near the downstream end, where the cliff face is entirely Triassic Mercia Mudstone. Upstream, the Westbury Formation appears in the cliff top; its entire thickness is present. Tidal erosion is active in the downstream half of the section, where Norian marls dominate; resistant rocks in the overlying Rhaetian become undercut, and cliff falls occur periodically. These falls provide the best

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TEXT-FIG. 1. Garden Cliff bone bed specimens with associated remains of *Pachystropheus rhaeticus* E. von Huene, showing style of preservation and distribution of elements. A, STGCM 60.62/1, potentially a single individual; B, BRSMG Cb9065. Scale bars represent 10 mm. Abbreviations: c, centrum; cs, caudal spine; f, femur; fs, fin spine of *Hybodus* sp.; h, humerus; na, neural arch; t, tooth of *Hybodus minor*; v, neoselachian vertebra.

supply of fossils, and conspicuous amongst these are disarticulated but extremely well preserved bones of *Pachystropeus*.

The 'bone bed' occurs as a seam of pyritic siltstone, between 20 and 30 mm thick, between soft black shales. Vertebrate remains and pyrite crystals are locally common on the surface of 'bone bed' slabs. The 'bone bed' lies approximately 2 m above the base of the Westbury Formation, 430 mm above a 300 mm thick sandstone band locally known as the 'Pullastra Bed', and 600 mm below a band of highly fissile black shale that develops a rust-coloured coating of limonite on weathering.

The abundance of *Pachystropeus* is a unique characteristic of Garden Cliff. Local conditions were extremely favourable for the preservation of *Pachystropeus*, in contrast with other known Rhaetian sites. The density of material is quite variable, however, and the presence in some places of faint oscillation ripples and small runnel features on the surface of the 'bone bed' suggests a sorting mechanism by which winnowed bones were concentrated (Storrs 1994). The 'bone bed' may preserve a shoal or strand line deposit. Certainly, a degree of sorting is evident in the distribution and preferred orientations of incorporated elements; most *Pachystropeus* bones (largely vertebrae and propodials) fall within the same relatively small size range. Bones from larger animals, or rare elements, are typically found at Aust and elsewhere.

Repository abbreviations. BATGM, Bath Royal Literary and Scientific Institution ('Bath Geological Museum'); BGS, British Geological Survey (including material from the former Geological Survey Museum), Keyworth; BMNH, The Natural History Museum, London; BRSMG, Bristol City Museum and Art Gallery; BRSUG, The University of Bristol Geology Museum; CMNHS, Geier Collections and Research Center, Museum of Natural History and Science, Cincinnati Museum Center, Cincinnati, Ohio; GPIT, Geologische und Paläontologische Institut, Tübingen; LEIUG, The University of Leicester Department of Geology; MM, Manchester Museum; MNHN, Muséum National d'Histoire Naturelle, Paris; PIN, Palaeontological Institute, Russian Academy of Science, Moscow; RSM, Royal Scottish Museum, National Museums of Scotland, Edinburgh; SMNS, Staatliches Museum für Naturkunde, Stuttgart; STGCM, Stroud Gloucestershire County Museum.

#### SYSTEMATIC PALAEOLOGY

DIAPSIDA Osborn, 1903

ARCHOSAURMORPHA F. von Huene, 1946

CHORISTODERA Cope, 1876

Family PACHYSTROPHEIDAE Kuhn, 1961

Genus PACHYSTROPHEUS E. von Huene, 1935

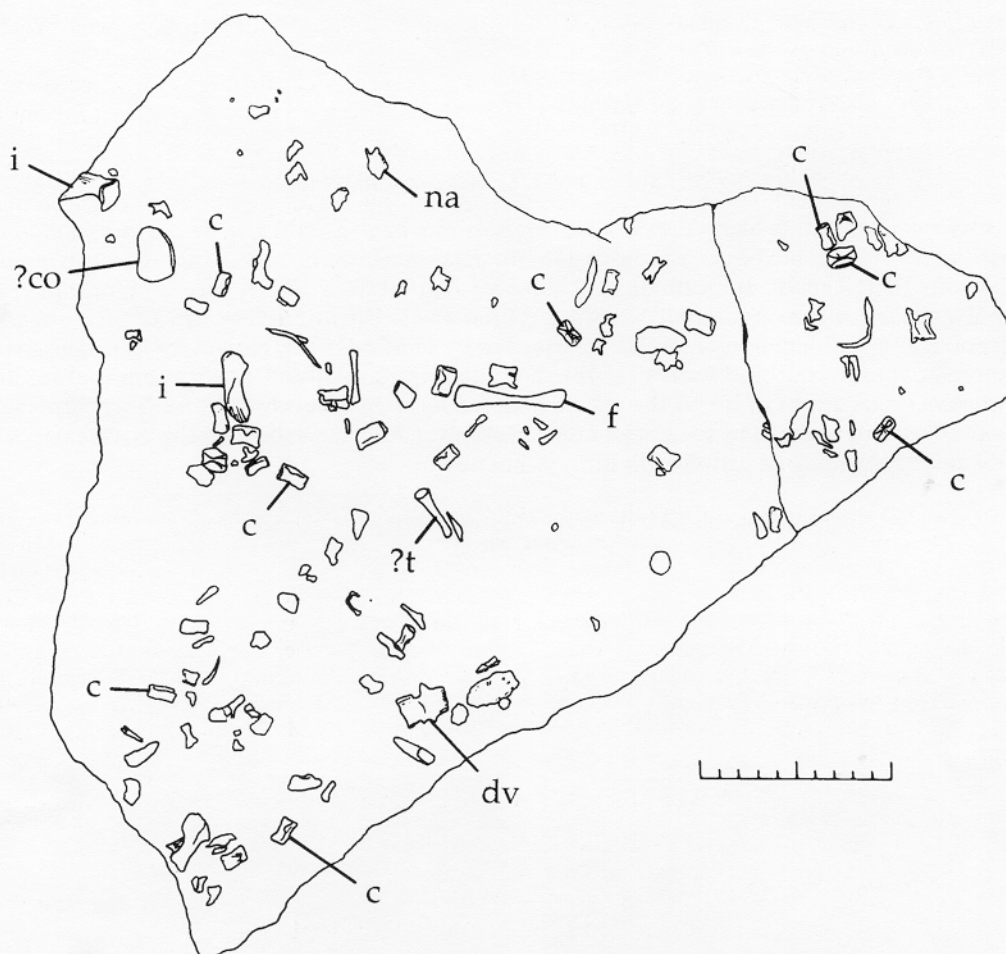
*Type species. Pachystropeus rhaeticus* E. von Huene, 1935.

*Diagnosis.* As for the type and only species.

*Pachystropeus rhaeticus* E. von Huene, 1935

Plates 1–2; Text-figures 1–13

- ?1842 *Rysosteus* Owen, p. 159.
- ?1854 *Rysosteus*; Morris, p. 353.
- ?1890 *Rysosteus oweni* Woodward and Sherborn, p. 282.
- 1935 *Pachystropeus rhaeticus* E. von Huene, pp. 441, 446–447.
- 1945 *Pachystropeus*; Romer, p. 595.
- 1946 *Rysosteus*; Reynolds, pp. 30, 35.
- 1955 *Pachystropeus*; Hoffstetter, p. 571.
- 1956 *Pachystropeus*; F. von Huene, pp. 637, 639, 683, 693.
- 1961 *Pachystropeus rhaeticus*; Kuhn, p. 38.
- 1964 *Pachystropeus*; Maleev, p. 455.
- 1966 *Pachystropeus*; Kuhn, p. 36.
- 1968 *Pachystropeus*; Müller, p. 225.



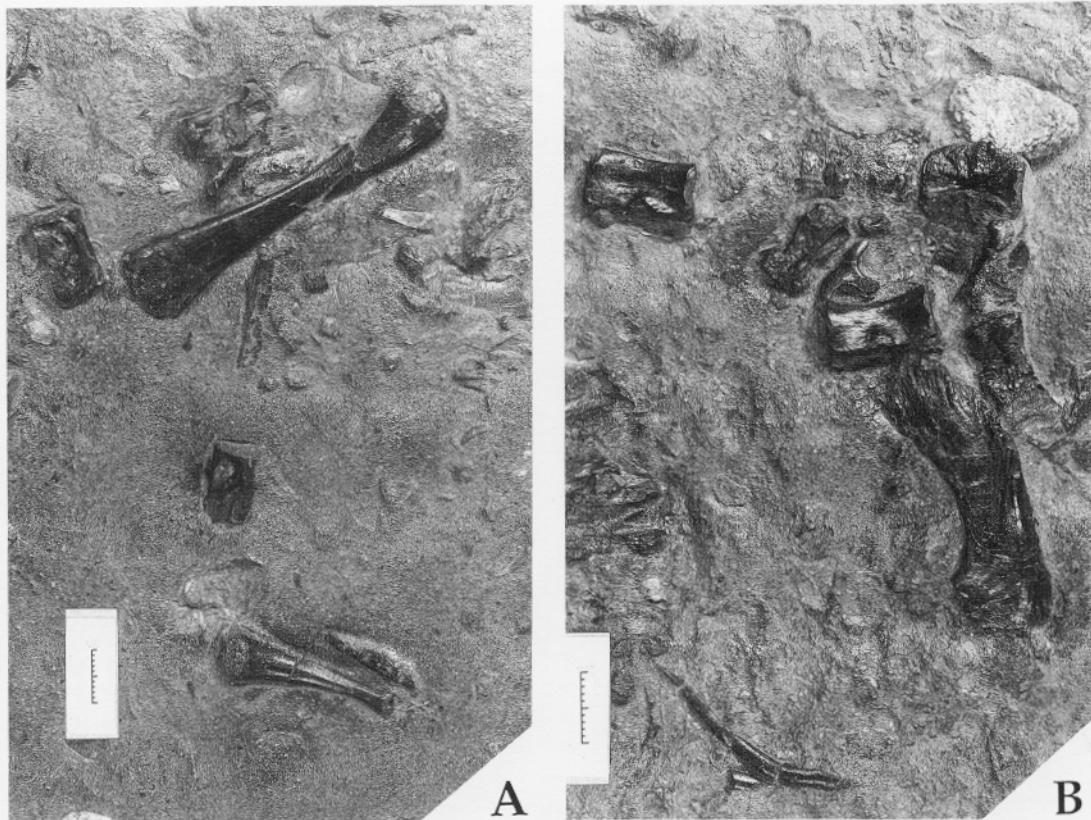
TEXT-FIG. 2. Holotype of *Pachystropeus rhaeticus* E. von Huene, BMNH R747; Blue Anchor Point, Somerset. Scale bar represents 100 mm. Abbreviations: c, centrum; ?co, ?coracoid; dv, dorsal vertebra; f, femur; i, ilium; na, neural arch; ?t, ?tibia.

- 1969 *Pachystropeus rhaeticus*; Kuhn, pp. 58, 64.  
 1970 *Rysosteus oweni*; MacFadyen, p. 202.  
 1970 *Rhsosteus oweni*; Sykes *et al.*, p. 260.  
 1971 *Pachystropeus rhaeticus*; Kuhn, pp. 6, 10, 55.  
 1975 *Pachystropeus rhaeticus*; Efimov, pp. 84, 93.  
 1978 *Rysosteus*; Duffin, p. 62.  
 1978 *Pachystropeus*; Russell-Sigogneau and Russell, p. 82.  
 1979 *Rysosteus*; Antia, p. 134.  
 1980 *Rysosteus oweni*; Duffin, pp. 258, 260.  
 1982 *Rysosteus oweni*; Duffin, p. 2.  
 1983 *Rysosteus*; Duffin *et al.*, p. 312.  
 1985 *Rysosteus*; Duffin, p. 143.  
 1986 *Rysosteus oweni*; Martill and Dawn, p. 130.  
 1987 *Rysosteus oweni*; Curtis and Curtis, p. 12.  
 1988 *Pachystropeus*; Carroll, p. 616.  
 1988 *Pachystropeus rhaeticus*; Efimov, p. 40.  
 1989 *Pachystropeus*; Evans, p. 586.

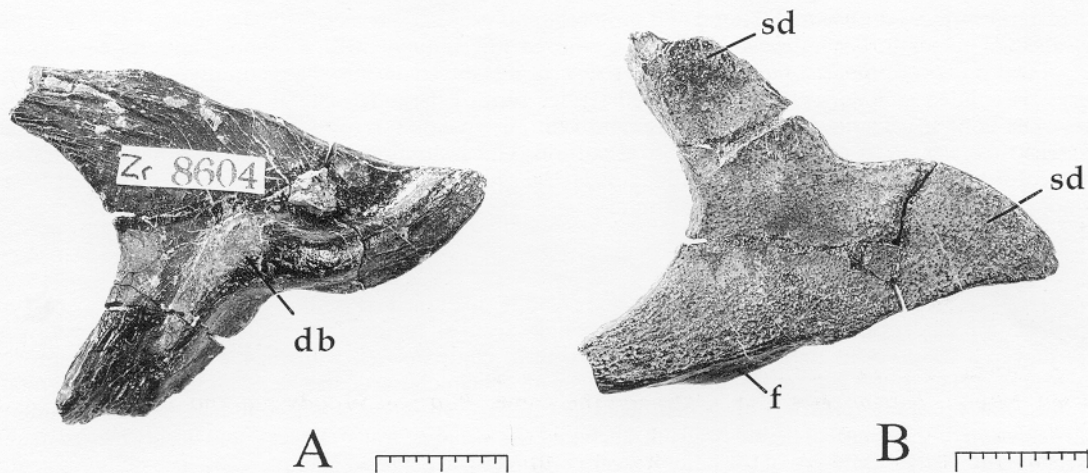
- 1990 *Pachystropeus*; Evans, p. 206.  
 1992 *Pachystropeus rhaeticus*; Storrs, p. 53A.  
 1993 *Pachystropeus rhaeticus*; Benton, p. 693.  
 1993 *Pachystropeus*; Evans and Hecht, p. 329.  
 1993 *Pachystropeus rhaeticus*; Storrs, p. 448.  
 1993 *Pachystropeus rhaeticus*; Storrs and Gower, p. 1103.  
 1994 *Pachystropeus rhaeticus*; Storrs, pp. 238, 241–242, 244, 251–253.

*Remarks on synonymy.* It is likely that *Pachystropeus rhaeticus* E. von Huene is synonymous with *Rysosteus oweni* Woodward and Sherborn (1890). *Rysosteus*, described on the basis of a single vertebra from the 'Rhaetic Bone Bed' exposures of Aust (Owen 1842), was supplemented with additional specimens from Aust and Westbury (Owen 1842; Browne 1894). Indeed, *Rysosteus* has been accepted as a senior synonym of *Pachystropeus* by Duffin (1978). However, *Rysosteus* cannot be diagnosed accurately from Owen's (1842) short description without illustration, and is thus a *nomen dubium*. This applies also to the specific name, *R. oweni* Woodward and Sherborn (1890), which was never diagnosed. The location of the holotype of *Rysosteus*, once in the private collection of a Mr James Johnson of Hotwells, Bristol, is unknown.

*Holotype.* Associated partial skeleton BMNH R747 (Text-figs 2–3).



TEXT-FIG. 3. Detail of *Pachystropeus rhaeticus* E. von Huene, holotype, BMNH R747; Blue Anchor Point, Somerset. A, vertebral centra, left femur and presumed epipodial (?tibia); B, centra, left ilium, gastralium and associated shark cephalic spine (left centre next to vertebrae). Scale bars represent 10 mm.



TEXT-FIG. 4. Ectopterygoid of *Pachystropheus rhaeticus* E. von Huene, BGS Zr 8604, in A, medial, and B, palatal aspects. Anterior to the right. Scale bars represent 10 mm. Abbreviations: db, dorsal boss; f, facet; sd, shagreen denticles.

*Referred material.* See appendix.

*Type locality and horizon.* Blue Anchor Point, Somerset, England (National Grid Reference ST 034 435; Westbury Formation, Penarth Group, latest Triassic (Rhaetian)).

*Diagnosis.* Lacertiform reptile, approximately 1 to 2.5 m long, presumably a choristodere of relatively plesiomorphic proportions and morphology; triradiate ectopterygoid with vestigial tuberculate dentition; elongate amphi- to platycoelous vertebral centra; dorsal neural spines squarish in lateral aspect with transversely expanded, corrugated tips; tall, narrow, vertically oriented caudal neural spines; interclavicle with short posterior ramus; humerus with little relative torsion of articular ends; extremely sharp and prominent supinator ridge; pubic fenestration in at least juvenile condition; iliac blade narrow and heavily corrugated.

*Description.* The disarticulated fossils do not allow a full reconstruction, and examples of only one cranial element (the ectopterygoid) have been identified. However, many postcranial bones can be assigned to *Pachystropheus* on the basis of partial associations, the similarity of the bones to those of well known choristoderes, and the seeming lack of other semi-aquatic reptiles in the Westbury deposits. Each vertebral type (excepting atlas/axis), dorsal ribs, gastralia, several interclavicles, clavicles, humeri, pubes, ilia, femora, a probable tibia, and a few possible phalanges are known. The holotype contains at least 35 vertebrae (mostly mid-series dorsal centra, but also a probable anterior caudal centrum, possible cervical neural arches and the arches of two caudals), perhaps representing two or more individuals, two or more gastralia, a possible clavicle and coracoid, right and left ilia, a left femur, an epipodial (probably the tibia) and numerous unidentifiable fragments; a tooth of '*Hybodus*' minor, a selachian cephalic spine, and a few other shark remains are also present on the slab (Text-figs 2-3).

Whilst some enigmatic jaw fragments (e.g. Storrs 1992) are present in Westbury collections, these commonly belong to the giant palaeonisciform, *Severnichthys* Storrs, 1994. Other putative cranial elements are equivocal; the potential for some to belong to *Pachystropheus* remains to be investigated.

#### Skull

*Ectopterygoid.* This bone (Text-fig. 4) is known from several examples in a wide range of sizes; the largest (BRSUG 25332) is 51 mm long  $\times$  26 mm across; the smallest (CMNHS VP4128) is only 17 mm  $\times$  13 mm. It is generally shaped as in *Simoedosaurus* (Sigogneau-Russell 1981), but its anteromedial process is much longer, as in *Champsosaurus* (Erickson 1972). This process formed the posteromedial margin of the suborbital fossa; its medial edge is faceted for reception of the pterygoid. Conspicuous maxillary and jugal facets lie on the

dorsolateral surfaces of the anterolateral and posterolateral processes, respectively. These latter two processes are subequal in length. The anterolateral process is broad and spatulate, with a rounded anterior edge, unlike the pointed process of *Simoedosaurus*; in *Pachystropheus* it is directed somewhat ventrally. The posterolateral process is pointed and slopes dorsally; its medial edge formed the anterolateral corner of the subtemporal fossa. The bone has a smooth dorsal surface, and ventrally (palatally), bears very fine, almost microscopic, shagreen tubercles on its gently concave central portion. This is an unusual, presumably primitive character. A large dorsal boss occurs above the middle of its lateral side, as in *Simoedosaurus* (Sigogneau-Russell 1981), for apparent contact with the 'postorbitofrontal'.

#### *Axial skeleton*

*Vertebrae.* The vertebrae are characteristic and readily identified (Pls 1–2, Text-figs 1, 3, 5–6), but disarticulation renders series counts impossible. Examples from all regions of the column are known; only the atlas and axis have yet to be identified. In general, these compare well with their counterparts in proven choristoderes. The centra are amphi- to platycoelous with subcircular articular faces, and are longer than tall. All presacral vertebrae retain an open neurocentral suture, even in the adult condition, often resulting in disarticulation of the neural arch and centrum, such that the broad neural arch facets and deeply incised neural canal floor are visible. Only five of the holotype vertebrae retain articulated neural arches. The holotype centra are 14–17 mm long.

The neural arch facets extend the entire length of the centrum and are lozenge-shaped in plan (Text-fig. 5H, J). The midpoint of the neural canal is conspicuously constricted. There is no median keel on the neural canal floor as in *Cteniogenys* (Evans 1991) and *Simoedosaurus* (Sigogneau-Russell 1981), save for slight indications of a remnant keel at the anterior and posterior ends, like the 'fine central ridge' of *Champsosaurus* (Parks 1956); the keel in *Simoedosaurus* may also be interrupted. The floor of the canal is deepest at its centre.

The centra of the cervical vertebrae are like those of *Cteniogenys* (Evans 1991) and *Lazarussuchus* (Hecht 1992) in being significantly longer than they are tall (at least 2.5 times so in most examples) (Text-fig. 5A). This central elongation is presumed to represent the plesiomorphic choristoderan condition (Evans 1991; Hecht 1992; Storrs and Gower 1993). Between the terminal articular surfaces, the centrum is strongly constricted and the ventral margin is arched. There is a marked, longitudinal ventral keel as in *Cteniogenys* (Evans 1991), *Champsosaurus* (Erickson 1972), *Ikechosaurus* (Brinkman and Dong 1993) and others (Sigogneau-Russell and Efimov 1984). In *Pachystropheus*, however, the keel does not protrude below the level of the articular face of the centrum as in other taxa.

The anterior edge of each anterior cervical bears a diapophysis just below the neurocentral suture; there is no sign of a parapophysis, a common condition amongst choristoderes (Brown 1905; Russell 1956; Erickson 1972; Evans 1991). The neural spine is very long and low, whereas advanced choristoderes (e.g. *Champsosaurus*, *Simoedosaurus*) have spines taller than long (Russell 1956; Erickson 1972; Sigogneau-Russell 1981). The *Pachystropheus* spine increases in transverse width distally; the flat, or slightly convex, tip is broader than the base. The lateral surfaces of the anterior cervical spines may be only slightly rugose, or else are smooth and featureless. The zygapophyses are broad, spatulate and nearly horizontally oriented. The posterior cervical vertebrae are generally similar, but have taller neural spines.

The anterior dorsal vertebrae are distinguished from the posterior cervicals by their bilobed rib facets, positioned at approximately one-third of the length of the centrum across the neurocentral suture (Plate 1, figs 1–6). A parapophysis lies anterior and ventral to the diapophysis, together forming an hourglass-shaped surface. The centra are again long (at least twice as long as high) and low, with a sharp longitudinal keel, but with a straight ventral margin. The neural spines remain low and essentially smooth.

A number of morphological changes occurs through the dorsal series (Pls 1–2; Text-fig. 5). For example, the centra become shorter relative to their height (approximately 1.5 times longer than tall), and the rib facets migrate to the middle of the centrum. The parapophysis becomes vertically aligned with the diapophysis and

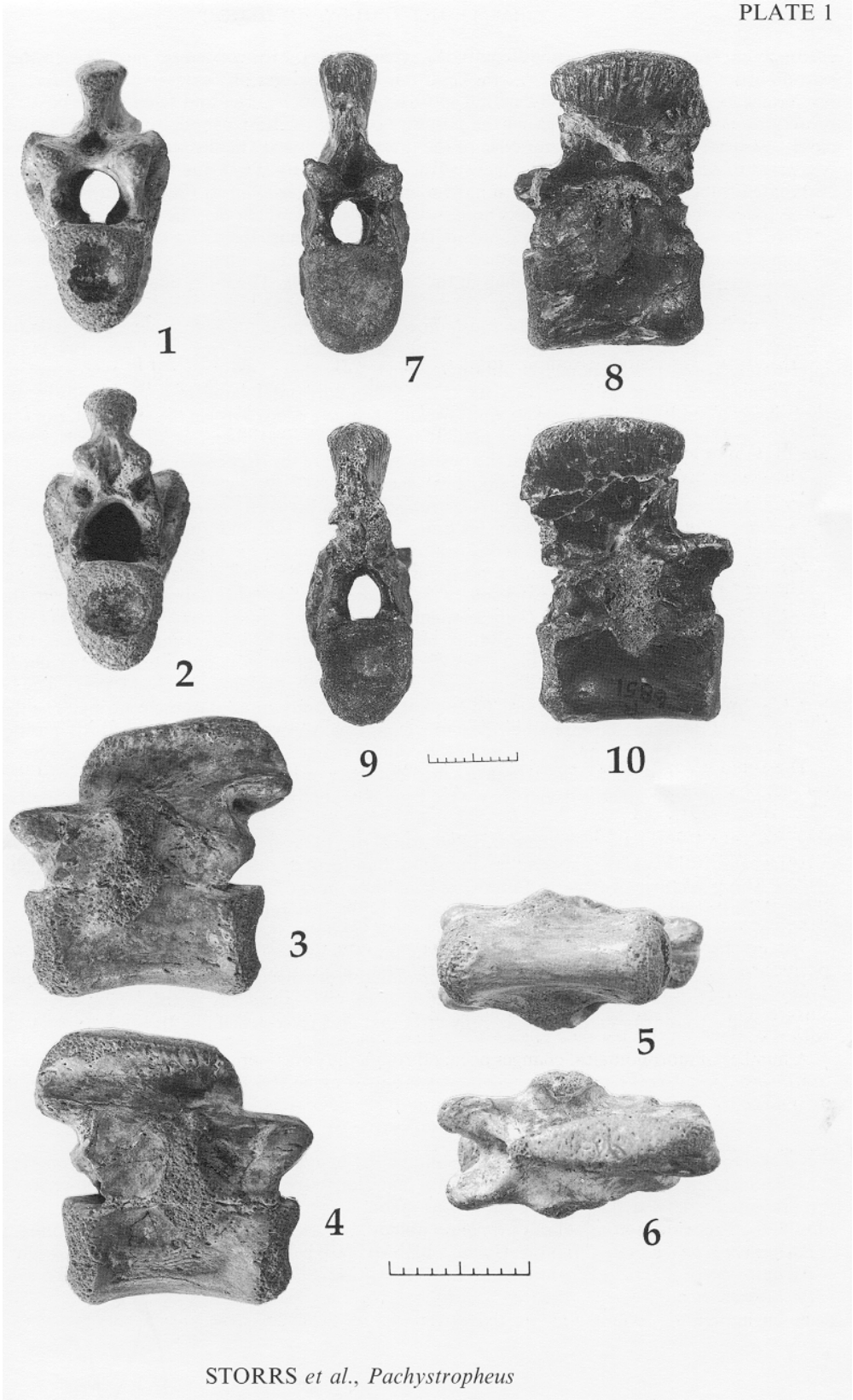
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#### EXPLANATION OF PLATE 1

Figs 1–6. Anterior dorsal vertebra of *Pachystropheus rhaeticus* E. von Huene, BATGM C28, in 1, anterior, 2, posterior, 3, left lateral, 4, right lateral, 5, ventral (anterior to left) and 6, dorsal, views. Scale bar represents 10 mm.

Figs 7–10. Mid-series dorsal vertebra of *Pachystropheus rhaeticus* E. von Huene, BMNH R6851, in 7, anterior, 8, left lateral, 9, posterior and 10, right lateral views. Scale bar represents 10 mm.





STORRS *et al.*, *Pachystropeus*

gradually merges with it as an undifferentiated synapophysis. Most of the rib facet lies on the arch; a small portion arises from the dorsal edge of the centrum. The transverse process is extremely short; its dorsal edge may overhang its ventral edge. The neural spine becomes much larger and taller in the posterior dorsals. Its posterior margin lies above or behind the posterior edge of the postzygapophyses, whereas the anterior rises almost vertically from the posterior edge of the prezygapophyses. The distal tip is transversely expanded and rugose, as in *Khurendukhosaurus* (Sigogneau-Russell and Efimov 1984), and the dorsolateral surfaces strongly corrugated, much as are the dorsal to caudal spines of *Simoesosaurus* (Sigogneau-Russell 1981; Erickson 1987). Indeed, save for relative proportions and spine length, which may be partly dependent upon column position, *Pachystropheus* dorsal vertebrae are largely indistinguishable from examples of *Khurendukhosaurus*, as evidenced by BRSUG 25334 and others (e.g. PIN 3386/6-1-1). In lateral aspect, the posterior dorsal spine of *Pachystropheus* is more squarish than in the anterior dorsals. The longitudinal keel of the centrum is lost, although its lateral constriction may persist.

Many of the dorsal vertebrae possess a shallow, pit-like depression or foramen in the lateral surface of the centrum, representing the lateral fossa typical of many choristoderes (see e.g. Evans 1991). This usually lies immediately below the synapophysis, although there is some slight variation in its presence and position; it may itself lie in a broad depression. In BRSUG 25325, a thin horizontal flange of bone extends from the top of the diapophysis to ventral to the postzygapophysis, and shelters a deep cavity in the arch posterior to the transverse process. Similar struts and fossae are present both anterior and posterior to the transverse process in an example from SMNS 58791, although the posterior fossae are the deeper. There are no accessory articulations such as are found in *Simoesosaurus* (Sigogneau-Russell 1981).

In the sacral vertebrae there is, of course, stronger fusion between centrum and arch than in the presacrals. The sacral centra are never more than 1.5 times longer than tall, and approximate the posterior dorsals in shape. The synapophysis covers much of the lateral surface across the neurocentral suture (Text-fig. 6A, C-D). The neural spine is similar to that of a posterior dorsal vertebra, but is clearly taller than long.

As in other choristoderes (e.g. Erickson 1972), the anterior caudal vertebrae are similar to the sacrals. The centrum of a more typical caudal is subrectangular and it is at least twice as long as high (Text-fig. 6E-G). The articular ends are also subquadrate, and are tall and narrow. The ventral surface bears a deep longitudinal furrow bordered by a pair of carinae; this distinctive morphology is common to other choristoderes (e.g. *Champsosaurus*, Erickson 1972; *Simoesosaurus*, Erickson 1987; *Ctenioenys*, Evans 1991). The lateral surfaces of the centrum are weakly constricted. The neural arch is firmly sutured to the centrum. The neural spines of mid-series and distal caudals are anteroposteriorly narrow, vertically aligned, posteriorly positioned and very tall (Text-fig. 6E). Whereas in other parts of the column the articular faces of the zygapophyses are essentially horizontal, those of the caudal vertebrae are oriented more or less vertically. Nowhere has an articular surface for a caudal rib been identified, but they were probably confined to the anteriormost caudal vertebrae.

*Ribs.* No cervical ribs have been identified, but dorsal ribs (Text-fig. 5i) are known from several specimens. As in typical choristoderes, the tuberculum and capitulum form distinct areas of a single, confluent articular surface whose relative sizes vary. Following champsosaurs (*Champsosaurus*, Russell 1956; Erickson 1972; *Simoesosaurus*, Sigogneau-Russell 1981; Erickson 1987), it is probable that the capitulum was increasingly dominant caudally. The shaft is tapered, first curving ventrally at a sharp angle, then straightening to a blunt tip. Proximally, the anterior surface bears a shallow but distinct depression, also as in champsosaurs; the posterior surface has a wide and distinctive groove that fades distally. This posterior groove may be the 'deep sulcus' of *Lazarussuchus* (Hecht 1992), also seen in *Champsosaurus* (Parks 1927; Erickson 1972). The anterodorsal edge of the shaft bears a gentle crest that also recedes distally. In some *Pachystropheus* ribs, the

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#### EXPLANATION OF PLATE 2

Figs 1-4. Dorsal vertebra of unusually large individual of *Pachystropheus rhaeticus* E. von Huene, BATGM M205, in 1, left lateral, 2, posterior, 3, ventral (anterior to the top) and 4, right lateral views. This specimen represents the largest known vertebra of this taxon.

Figs 5-6. Size variation in *Pachystropheus* humeri. 5, complete left humerus of young individual of *Pachystropheus rhaeticus* E. von Huene, BRSMG Cb4907. 6, proximal head of right humerus of *Pachystropheus rhaeticus* E. von Huene, BRSMG Cd2422. Fig. 6 represents the largest known individual of *Pachystropheus*.

Scale bar represents 10 mm.



1



2



3



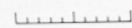
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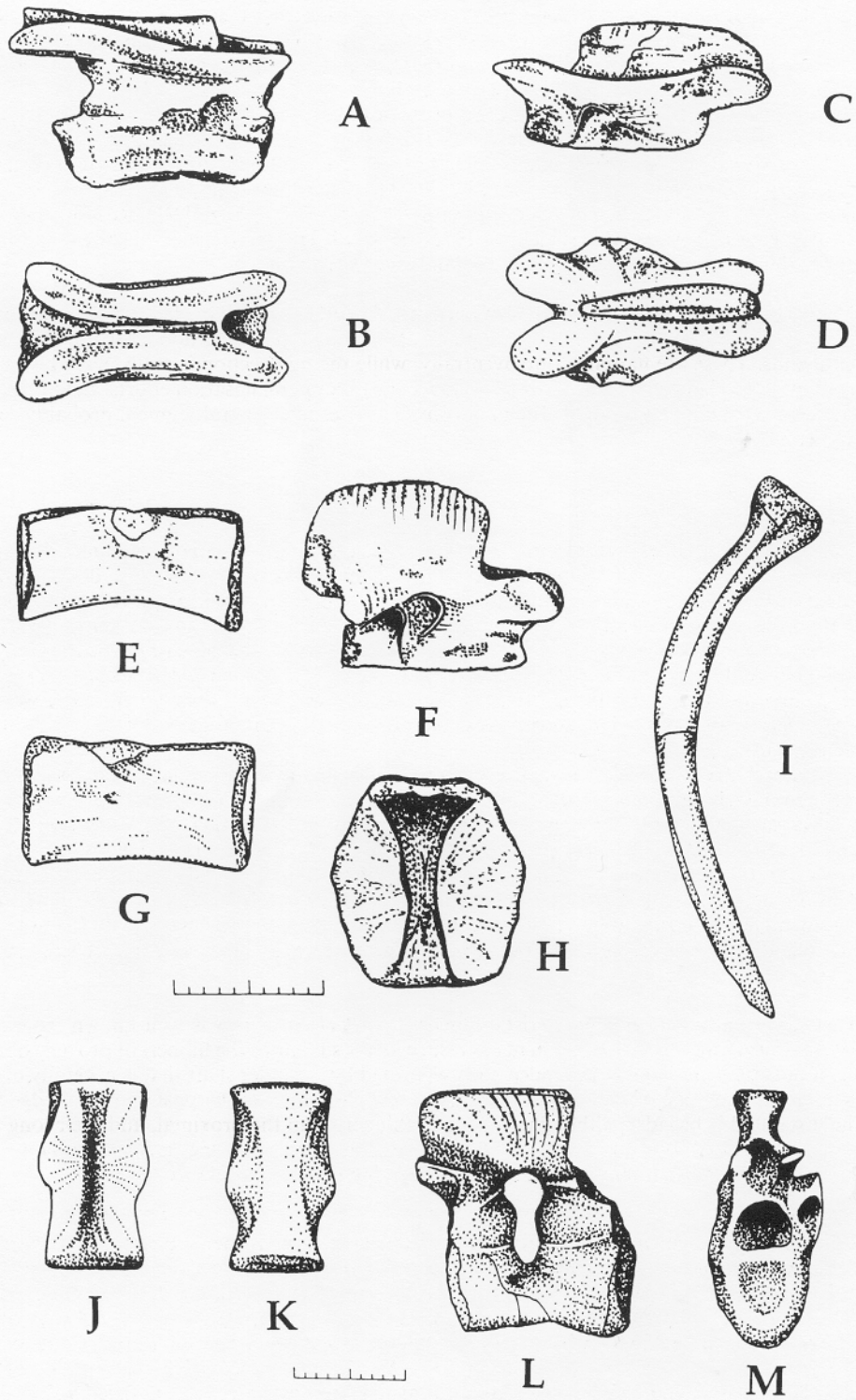


5



6





TEXT-FIG. 5. For caption see opposite.

ventral edge of the shaft forms a thin flange ventral to the posterior sulcus, again as in other taxa. There is as yet no evidence for true histological pachyostosis as may have existed in, for instance, *Champsosaurus* (Erickson 1972), but the ribs are generally dense and thickened as an apparent aquatic adaptation. There are no 'uncinate processes' as are found in *Champsosaurus* (Parks 1927; Erickson 1972).

The stout sacral ribs are fused to the transverse processes (Text-fig. 6A), are long (40 mm for a vertebra 32 mm high), and broadly downturned so that the distal end is directed at an angle of approximately 10° below horizontal. The proximal end is robust and circular in transverse section; distally the rib is dorsoventrally flattened with a broad extremity and lateroventrally directed iliac articulation.

The known caudal ribs are extremely flat and rather short (27 mm in BMNH R6245), and are broad anteroposteriorly as in *Champsosaurus* (Erickson 1972; Parks 1927). The flattened distal end is rounded and blunt and approximately twice as wide as the proximal end (Text-fig. 6B).

*Gastralia.* The best preserved gastral rib (BRSMG acc. no. 45/1991), a median element, is unexceptional (see Storrs and Gower 1993). It is 'V'-shaped at an angle of approximately 120°, is about 80 mm long, and tapers to blunt lateral ends. These are flattened dorsoventrally, while the mid-section is stout. Such heavy gastralia, like the dense ribs, potentially aided *Pachystropeus* in its buoyancy compensation efforts. Lateral elements are similarly dense, but are relatively straight. Judging from their size, each gastral segment probably consisted of only three elements.

#### *Appendicular skeleton*

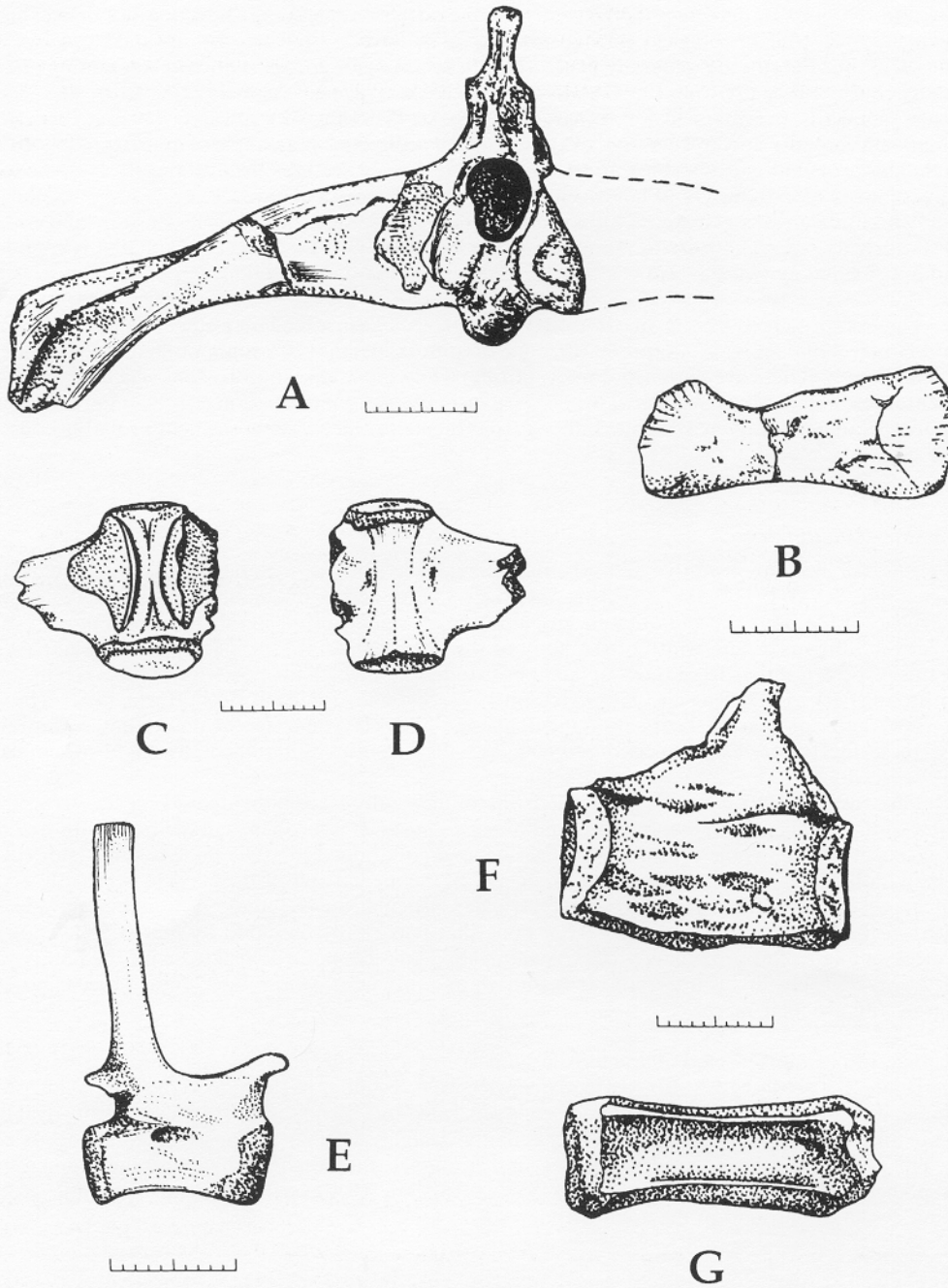
*Pectoral girdle.* As in many primitive diapsids, the interclavicle is a flat, triradiate to diamond-shaped bone; the best example, RSM 1911.5.5887 (Text-fig. 7A–B), is 35 mm across by 28 mm long. Both the dorsal and ventral surfaces of the bone are smooth and unsculptured. A significant posterior process is present, but this is no longer than the maximum width of the body of the interclavicle; it tapers smoothly to a narrow, blunt point. In this respect, it differs from those of later choristoderes, in which the posterior process is long and may be rather broad (Parks 1927; Russell 1956; Erickson 1972; Sigogneau-Russell 1981; Hecht 1992). The convex (in plan view) anterior margin bears prominent, trough-like, clavicular facets on its anteroventral edge. Laterally, these facets are deeply incised grooves, but they shallow anteromedially to form simple, non-confluent depressions.

BRSMG acc. no. 45/1991 contains a clavicle from an unusually large individual (Text-fig. 7D–E) which is very similar to the clavicles of *Champsosaurus* and *Simoedosaurus*. It is a robust, curved bone with well defined articular facets at each end; the tapered ends form an angle of about 125°. The bone is subcylindrical and is stout at its middle. As in *Champsosaurus* (Erickson 1972), the medial end of the clavicle is broadly expanded in dorsal aspect at the point where the interclavicular articulation is found. A possible clavicle is also represented in the holotype by a slender curved bone that is partially obscured by matrix. The ends of this element meet at an angle of approximately 100°. A subovate, plate-like bone associated with the holotype could represent a coracoid, but this is uncertain. It is smooth and measures 34 mm by 22 mm. There is no obvious indication of any articular facets.

*Forelimb.* The rather unusual and characteristic humerus of *Pachystropeus* is well known from a range of specimens (Plate 2; Text-figs 1B, 8–10), yet in many respects, it is similar to the humeri of proven choristoderes. For example, it possesses moderately expanded ends separated by a slender shaft that is generally oval in cross section; the anterolateral edge of the shaft is essentially straight, whereas the posteromedial edge is broadly concave. The distal end is broader, although very much thinner, than the proximal, and their long axes lie in different planes, separated by approximately 55° of torsion. However, the greater amount of torsion (approximately 85–90°) found in most choristoderes is lacking in *Pachystropeus*.

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TEXT-FIG. 5. Selected axial elements of *Pachystropeus rhaeticus* E. von Huene. A–B, anterior cervical vertebra, BRSMG Ce17166, in right lateral and dorsal views (anterior to right), respectively; C–D, mid-series cervical neural arch, BRSUG 17037, in left lateral and dorsal views (anterior to left), respectively; E, dorsal centrum, BMNH R747 (holotype), in right lateral aspect; F, dorsal neural arch, BRSMG Ce17146, in right lateral aspect; G, dorsal centrum, BRSMG Cb4887, in left lateral aspect; H, posterior dorsal or sacral centrum, BMNH R747 (holotype), in dorsal aspect (? anterior to top); I, dorsal rib, BMNH R3711; J–K, dorsal centrum, BRSMG Cb4887, in dorsal and ventral views (anterior at top), respectively; L–M, mid-series dorsal vertebra, BRSMG Ce17165, in right lateral and anterior views, respectively. Scale bars represent 10 mm.



TEXT-FIG. 6. Axial elements of *Pachystropeus rhaeticus* E. von Huene. A, young adult sacral vertebra and rib, BRSUG 25331, in ?posterior aspect; B, ?left caudal rib, BRSMG Ce17775, in dorsal aspect; C-D, anterior caudal or posterior sacral, BATGM C25a, in dorsal and ventral views (anterior at top), respectively; E, mid-series caudal, BMNH R12478, in right lateral aspect; F-G, mid-series caudal, BRSUG 25302.1, in left lateral and ventral views (anterior to left), respectively. Scale bars represent 10 mm.

The articular surfaces of the humerus were cartilage-capped. The distal end possesses a broadly expanded posterior corner with only a moderately sized entepicondyle; this covers a small area of the medial as well as the ventral edge of the bone. There is a somewhat more expanded, bulbous ectepicondyle extending well on to the ventral side of the humerus; the anterodistal corner is sharp. Also distally, an inconspicuous supinator process is present ventrolaterally. On the anterodorsal surface, a well defined ectepicondylar groove or sulcus lies between this and the ectepicondyle. There is, however, neither an ectepicondylar nor entepicondylar foramen. The anterolateral (radial) edge of the humerus is drawn into a characteristic, narrow, blade-like supinator ridge that extends from the supinator process to the base of the humeral head. This ridge, typical of choristoderes is, nevertheless, far sharper and more pronounced than in later examples, perhaps as a more fully aquatic adaptation. The posteromedial edge of the humerus is well rounded.

The proximal end of the humerus is weakly ossified and the humeral head indistinct. Posteroventrally, but separated from the head, is a short, well defined crest, generally referred to as the ectotuberosity (Parks 1927; Russell 1956; Sigogneau-Russell 1981; Evans 1991; Storrs and Gower 1993). This is homologous with the 'deltopectoral' crest of primitive tetrapods (Romer 1956). Another crest ('deltoid crest' of Storrs and Gower 1993) is also evident on the proximal anterodorsal face of the bone. The two crests are separated by the dorsal extension of the supinator ridge. A shallow fossa is present medially for the insertion of the *M. coracobrachialis*. A concavity proximal and dorsal to the supinator ridge was probably for the insertion of the *M. scapulohumeralis*; the distal portion of the ridge may have served as part of the *M. triceps* origin.

The largest complete *Pachystropeus* humerus known, BRSMG Cd2678, is some 90 mm in maximum length and differs from smaller examples in the exaggeration of its major features (Text-fig. 9). Most notably, this includes a more expanded distal end, a deeper ectepicondylar groove, a larger supinator process, a small radius of curvature to the concave posteromedial edge and a deltopectoral crest that lies more distally on the humeral shaft. Unlike smaller specimens, it is also characterized by the greater downward (subaxial) curvature of its distal end. Small examples, such as BRSMG Ce17778, typically lack condyles and crests; the reduced ectepicondyle noted by Storrs and Gower (1993) is now known to represent the immature condition.

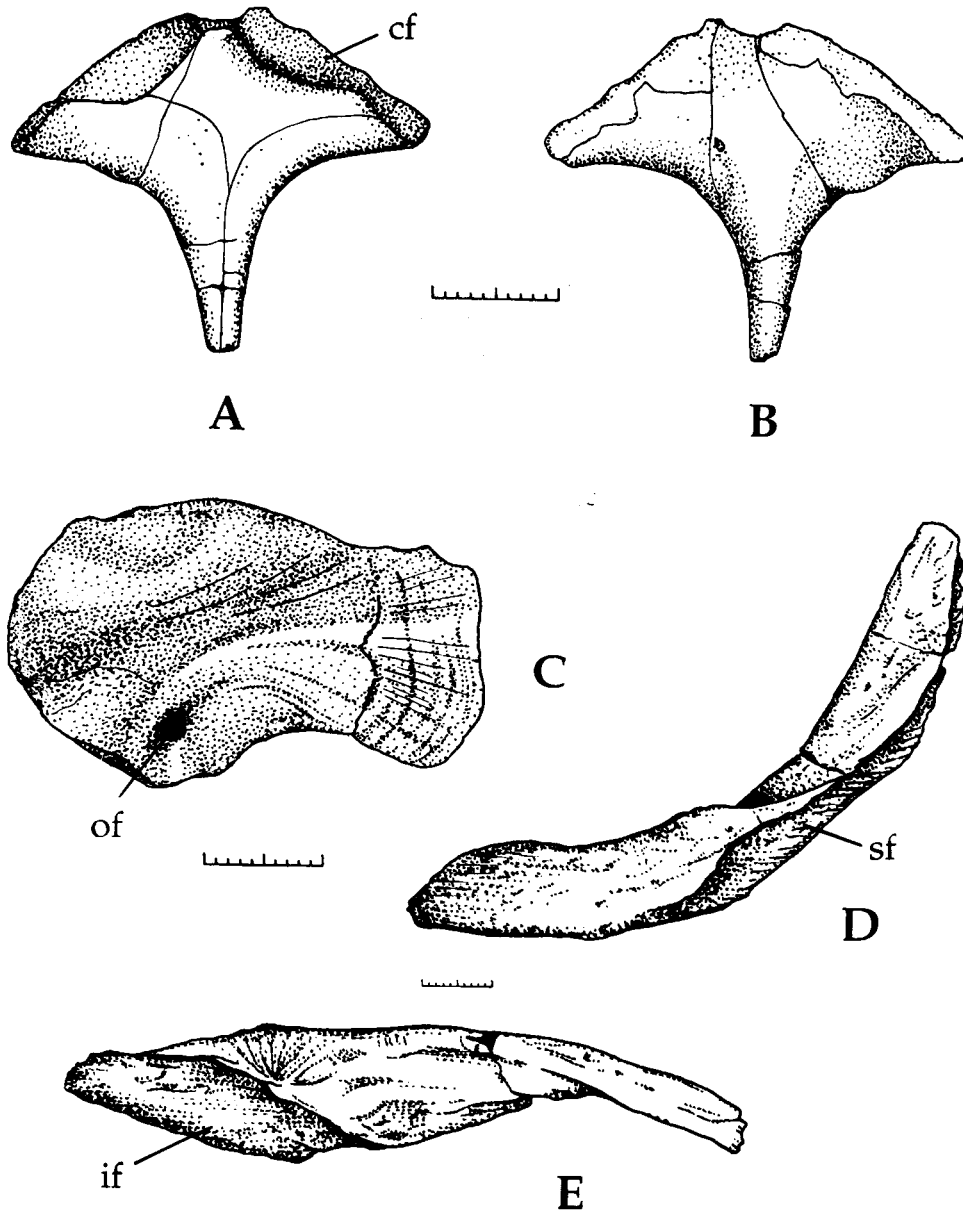
The most notable differences of *Pachystropeus* humeri from those of undoubted choristoderes, such as a lesser degree of torsion, flatter distal end and extremely sharp and prominent supinator ridge, may be related to a more aquatic existence for the Rhaetian form, in keeping with its marginal marine provenance. The sharp supinator ridge, in particular, is an apparent autapomorphy that distinguishes *Pachystropeus* within Choristodera.

*Pelvic girdle.* The pubis (Text-fig. 7c) is best known from a complete example exposed in dorsal view only. It is a broad, smooth, plate-like bone of subrectangular plan. The long (medio-lateral) axis of the bone (40 mm) is approximately twice the length of the longitudinal axis (21 mm maximum); the symphyseal edge is 15 mm long. A clear series of growth lines parallel the symphysis. The posterior edge of the pubis is concave, suggesting the presence of a small pelvic fenestra in this individual, perhaps the result of immaturity. The slightly worn anterior edge is similar to that of *Champsosaurus* (Erickson 1972) in being laterally convex but concave medially. The anterior edge in *Simoedosaurus* is much straighter and the medial symphysis longer (Sigogneau-Russell 1981). The anterolateral corner is thickened in *Pachystropeus* and bears a 'pectineal tuber' which, by inference (Erickson 1972), perhaps served as an attachment site for the *M. pubotibialis*.

The posterolateral corner of the pubis is the most robust portion of the bone and forms the anterior limit of the acetabulum. The acetabular surface forms an angle of approximately 140° with the posterior border. A low, curving ridge, for intracorporeal transmission of hindlimb-generated forces, extends from the posterolateral corner to the centre of the symphysis. The obturator foramen is completely enclosed and lies between the acetabulum and this transverse ridge.

Most of the acetabulum is formed by the ilium (45 mm in total length in the holotype) and is a shallow, subcircular depression, ventral to a pronounced supraacetabular crest (Text-fig. 11). The acetabular ramus is rhomboidal in lateral aspect with an angle between the pubic and ischial facets of approximately 100°; their crescentic articular surfaces are similar in area. The ilium is constricted at the supraacetabular crest before expanding into an iliac blade that projects almost entirely caudally, with little or no anterior ramus. At this constriction, there is a small but pronounced anterior prominence as in *Champsosaurus* and *Simoedosaurus* (Erickson 1972; Sigogneau-Russell 1981). The tip of the iliac blade is blunt and transversely thickened; the blade's ventral edge is oriented more or less horizontally.

There are no obvious facets for sacral rib articulation, but the middle of the blade's medial surface bears a thickened brow-like ridge potentially associated with the sacrum. The posterodorsal portion of the blade is strongly striated; the striae run more or less longitudinally and are heavier and longer medially than laterally. Except for the greater breadth of their dorsal blades, the ilia of *Simoedosaurus* (Sigogneau-Russell 1981;



TEXT-FIG. 7. Appendicular arch elements of *Pachystropeus rhaeticus* E. von Huene. A–B, interclavicle, RSM 1911.5.5887, in medial and ventral views, respectively; C, young adult left pubis, BRSUG 25330, in dorsal (internal) aspect; D–E, adult right clavicle, BRSMG lot acc. no. 45/1991, in dorsal and posterior views, respectively. Scale bars represent 10 mm. Abbreviations: cf, clavicular facet; if, interclavicular facet; of, obturator foramen; sf, scapular facet.



Erickson 1987), *Ikechosaurus* (Brinkman and Dong 1993) and *Champsosaurus* (Parks 1927; Erickson 1972) are comparable with similar striations.

BMNH R4837 (Text-fig. 11A) represents the largest known *Pachystropeus* ilium, although incomplete (the next largest, BMNH R12535, is complete and approximately 80 mm long), and has a broader blade and heavier ribbing than other examples, perhaps a consequence of its greater size. Sykes *et al.* (1970, pl. 17, fig. 13) reproduced a photograph of a smaller ribbed ilium ('?pelvic bone' of an 'indeterminate archosaur') with a far narrower dorsal blade. It is presumed that the blade grew in relative dorsoventral height with increased ontogenetic age and absolute size.

*Hind limb.* The femur is long (63 mm in the holotype) and slender with expanded ends (Text-figs 3A, 12–13), and is very similar to known choristoderan femora, although these conform to a rather primitive reptilian morphology. The shaft is essentially straight with an inconspicuous adductor ridge on its postaxial surface. The distal end is broader than the proximal head, yet is thinner dorso-ventrally while slightly 'downturned' towards the postaxial surface. The distal condyles are very weakly defined with a shallow popliteal space between them, but no intercondylar fossa on the superaxial surface of the femur. The head occupies the whole of the proximal and proxomedial faces of the bone; its unfinished surface lies at nearly 90° to the longitudinal axis of the shaft. In anterodorsal and posteroventral views, the preaxial edge of the proximal part of the shaft is concave and the postaxial edge convex.

The posteroventral surface of the proximal edge of the femur bears a substantial internal trochanter which, in large specimens, is positioned a significant distance from the proximal end. The head and trochanter are therefore not confluent. In smaller, i.e. younger, individuals, the gap between the internal trochanter and the femoral head is less conspicuous, and occasionally is nonexistent. However, the intertrochanteric fossa, adjacent to the internal trochanter, is more clearly defined. Variation in these relationships has attracted attention in other studies of choristodere morphology (e.g. Erickson 1972, 1987; Brinkman and Dong 1993). On the posterodorsal edge of the femur's proximal end, near the end of the internal trochanter, is a low, rugose prominence or 'external trochanter'.

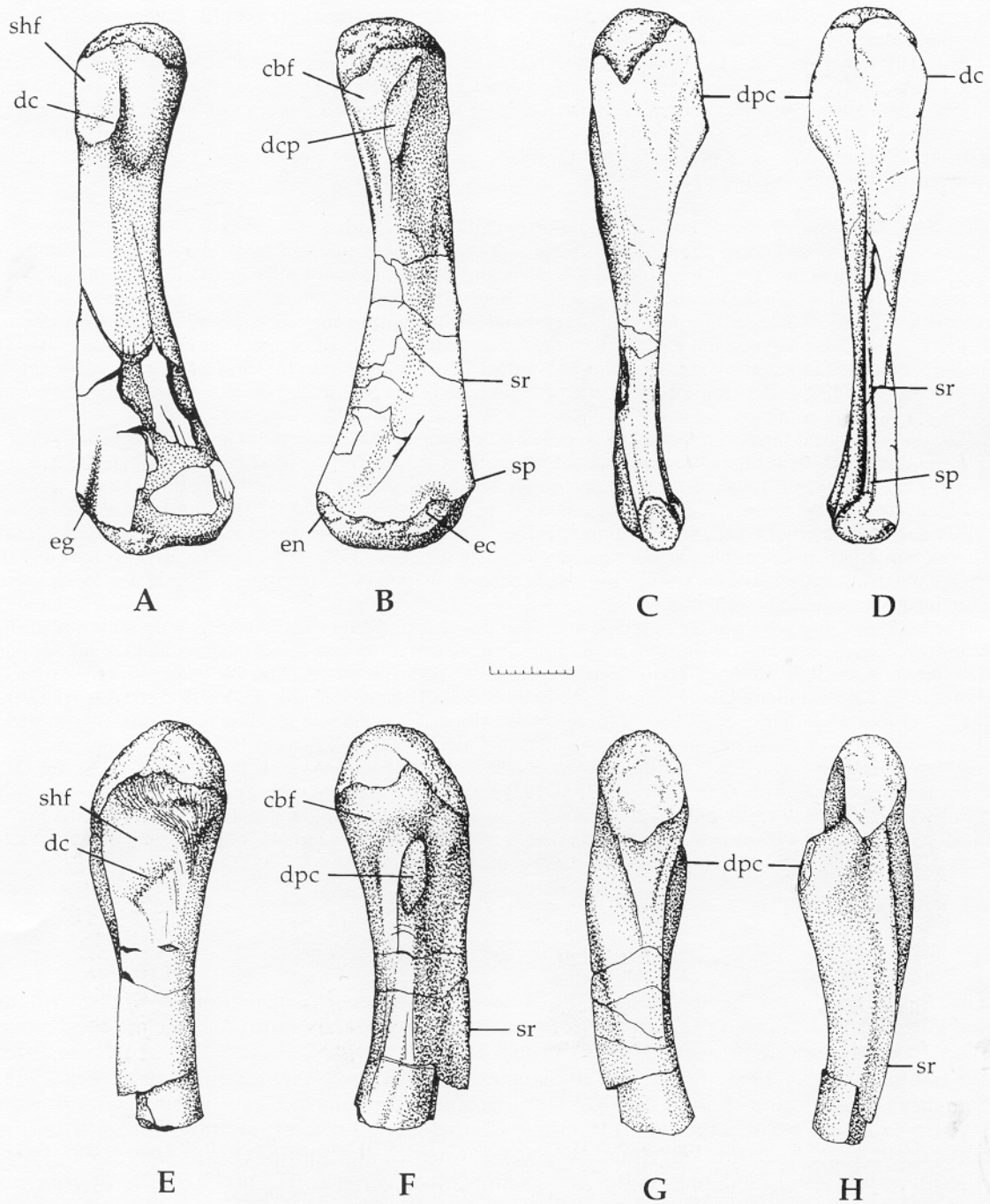
The best epipodial is part of the holotype and, from the associated remains, probably represents a tibia. In primitive reptilian fashion, it is short in comparison with the femur (34 mm versus 63 mm), and the subcircular (in transverse section) proximal end is markedly broader than the ovate distal end. The smooth, exposed (posterior?) edge is longitudinally concave. A similar bone (BRSMG acc. no. 45/1991) exhibits a relatively sharp and straight ?anterior edge. Except for its smaller size and lesser development of muscle attachment sites, the putative tibia of *Pachystropeus* resembles that of *Champsosaurus* (Erickson 1972).

A few phalanges from Rhaetian deposits may belong to *Pachystropeus*. E. von Huene (1933, fig. 28) illustrated a specimen from Gaisbrunnen (GPIT 19552) that she ascribed to this animal. It is 5 mm long with a constricted shaft and expanded articular ends, the proximal larger than the distal. The distal articulation is divided by a trochlear groove. At least two specimens in lot BRSMG acc. no. 45/1991 are similar. The 'distal end of a metatarsal' (E. von Huene 1933, fig. 29) is problematical.

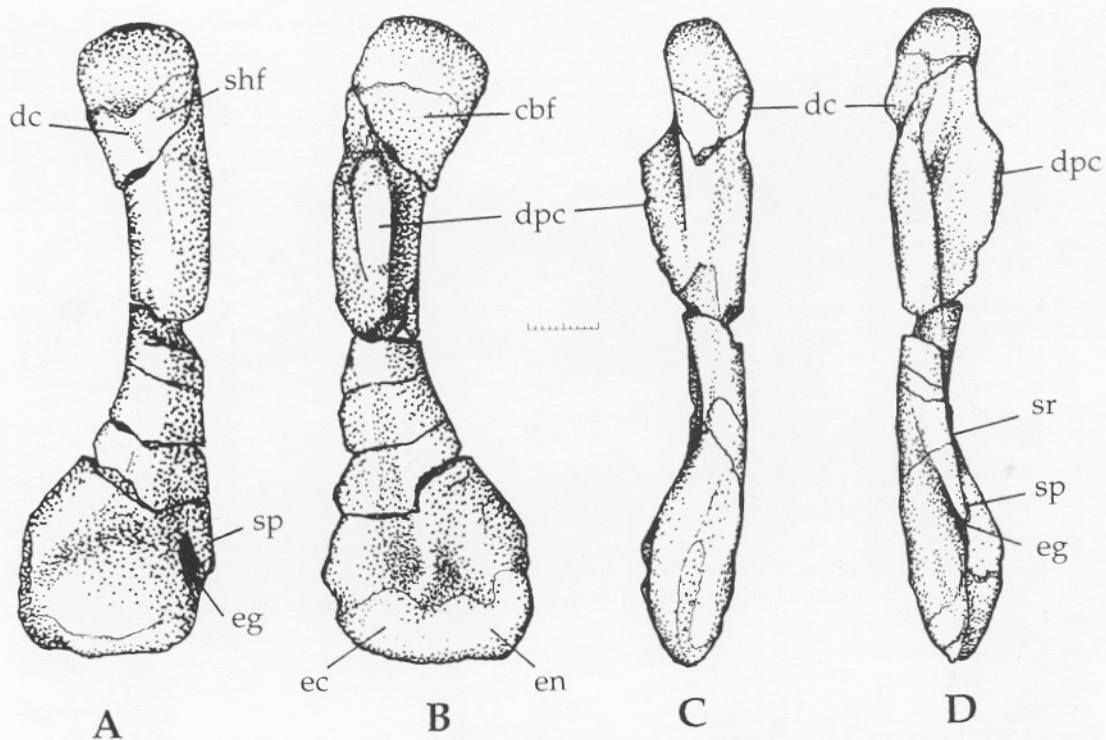
## RELATIONSHIPS

The relatively common champsosaurs of the Cretaceous (Aptian–Albian, Santonian–Maastrichtian) and Palaeogene (Danian–Ypresian) of North America, Europe and central Asia are the best known choristoderes (Cope 1876; Gervais 1877; Brown 1905; Parks 1927; Russell 1956; Erickson 1972, 1987; Efimov 1975, 1983, 1988; Russell-Sigogneau and Russell 1978; Sigogneau-Russell 1981; Sigogneau-Russell and Efimov 1984). Until recently they formed an isolated group with problematical links with other taxa. Primitive Choristodera, however, are now known from the Jurassic (Bathonian, Oxfordian/Kimmeridgian) of America and Europe (Evans 1989, 1990, 1991; Metcalf *et al.* 1992), and the Oligocene (?Stampian) of France (Hecht 1992). *Pachystropeus* seemingly represents the Choristodera in the European Rhaetian (E. von Huene 1935; Hoffstetter 1955; F. von Huene 1956; Kuhn 1961; Storrs 1992, 1993, 1994; Storrs and Gower 1993).

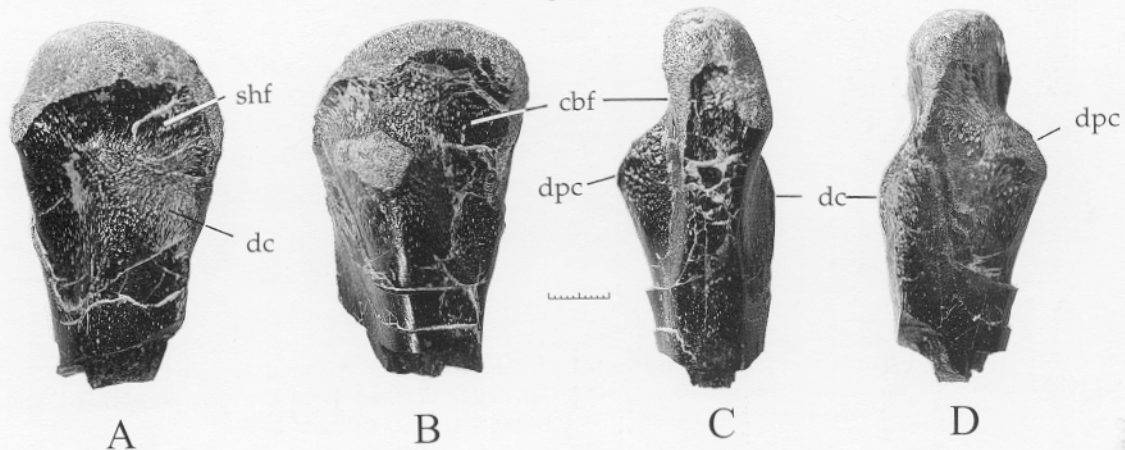
*Pachystropeus* (sometimes '*Rysosteus*') has been identified as an archosaur of unknown affinity (Halstead and Nicoll 1971; Duffin 1978, 1980; Antia 1979; Duffin *et al.* 1983), dinosaur (Reynolds 1946; Macfadyen 1970), crocodylian (E. von Huene 1933; Duffin 1982, 1985), or indeterminate reptile (Sykes *et al.* 1970; Martill and Dawn 1986) as well as a champsosaur/choristodere. The material



TEXT-FIG. 8. Humeri of *Pachystropeus rhaeticus* E. von Huene. A-D, left humerus of young individual, BRSMG Cb4907, in A, superaxial, B, subaxial, C, postaxial, and D, preaxial views; E-H, proximal end of left humerus of mature individual, RSM 1911.5.5918, in E, superaxial, F, subaxial, G, oblique postaxial, and H, preaxial views. Scale bar represents 10 mm. Abbreviations: cbf, coracobrachialis fossa; dc, deltoid crest; dcp, deltopectoral crest; ec, ectepicondyle; eg, ectepicondylar groove; en, entepicondyle; shf, scapulohumeralis fossa; sp, supinator process; sr, supinator ridge.

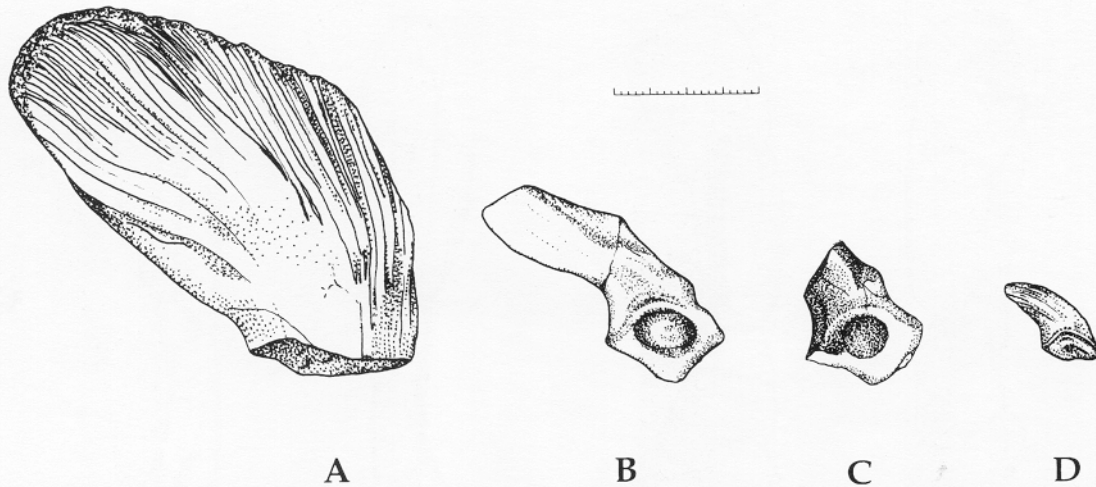


TEXT-FIG. 9. Right humerus of large individual of *Pachystropeus rhaeticus* E. von Huene, BRSMG Cd2678, in A, superaxial, B, subaxial, C, postaxial, and D, preaxial views. Scale bar represents 10 mm. Abbreviations as in Text-figure 8.

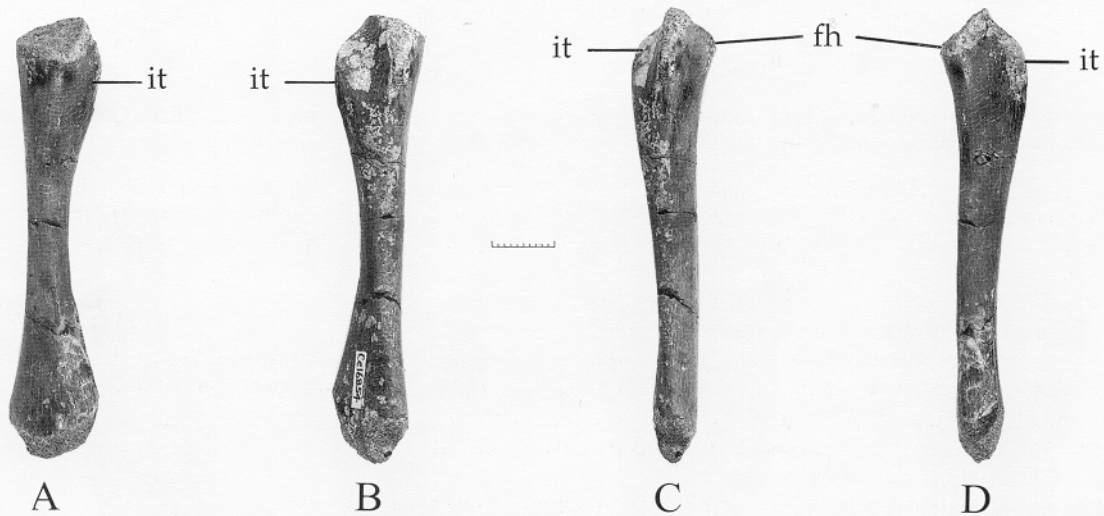


TEXT-FIG. 10. Proximal head of right humerus of extremely large individual of *Pachystropeus rhaeticus* E. von Huene, BRSMG Cd2422, in A, superaxial, B, subaxial, C, postaxial, and D, preaxial views. Scale bar represents 10 mm. This specimen represents the largest known humerus of this taxon. Abbreviations as in Text-figure 8.

described here confirms that *Pachystropeus rhaeticus* may be an early choristodere, or at least belongs to the lineage that gave rise to that group. It possesses several group synapomorphies and E. von Huene's (1935) original hypothesis of choristoderan ('rhynchocephalian') affinity (by comparison with champsosaurs) cannot be rejected.



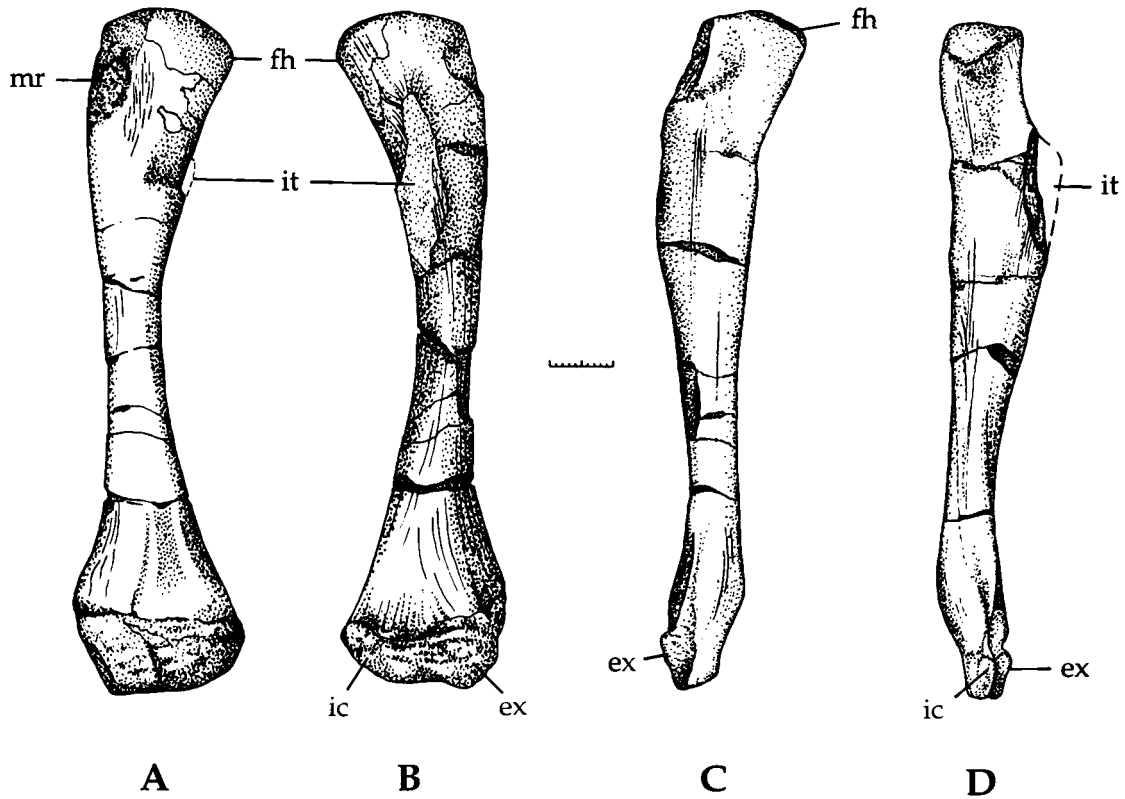
TEXT-FIG. 11. Ontogenetic series of *Pachystropheus rhaeticus* E. von Huene ilia. A, large adult left iliac blade, in medial aspect, BMNH R4837; B, typical left ilium in lateral aspect (image reversed), BRSUG 25329; C, acetabular region of right ilium of young adult individual, BMNH R2727, in lateral aspect; D, complete right ilium of juvenile, in lateral aspect, BRSMG lot acc. no. 45/1991. Scale bar represents 20 mm.



TEXT-FIG. 12. Right femur of immature individual of *Pachystropheus rhaeticus* E. von Huene, BRSMG Ce16854, in A, superaxial, B, oblique subaxial, C, postaxial, and D, preaxial views. Ends slightly abraded. Scale bar represents 10 mm. Abbreviations as in Text-figure 13.

*Pachystropheus* is linked with typical choristoderes by:

1. constricted, amphicoelous to nearly platycoelous, non-notochordal adult vertebrae (only rarely retaining a notochordal pit in juveniles);
2. unfused neurocentral sutures in the presacral portion of the column in all but the oldest individuals;
3. broad neural arch facets;
4. deeply incised, yet constricted neural canal;



TEXT-FIG. 13. Right femur of fully adult individual of *Pachystropeus rhaeticus* E. von Huene, BRSUG 7010.4, in A, superaxial, B, subaxial, C, postaxial, and D, preaxial views. Scale bar represents 10 mm. Abbreviations: ex, external condyle; fh, femoral head; ic, internal condyle; it, internal trochanter; mr, muscle rugosity.

5. small fossa in the lateral surface of the centrum;
6. strongly corrugated, subrectangular neural spines in the middle and posterior dorsal vertebrae;
7. caudal vertebrae with deep, midventral, longitudinal furrows and strong border keels;
8. vertical articular faces to the caudal zygapophyses;
9. dorsal ribs with flange-like ridge and posterior sulcus;
10. broad, flat sacral ribs;
11. elongate iliac blade, heavily ribbed with longitudinal striae; and
12. humerus bearing very sharp, long and prominent supinator ridge.

Plesiomorphic characters that are not definitive, but nevertheless suggestive, of choristoderan relationships are:

1. simple, thickened ribs and gastralia;
2. confluent capitulum and tuberculum;
3. cervical parapophyses absent;
4. dorsal transverse processes lying across the neurocentral suture;
5. triradiate interclavicle with strong posterior process;
6. robust, L-shaped clavicle;
7. simple humerus with broad, flat distal end;
8. deep ectepicondylar sulcus;

9. no entepicondylar foramen;
10. plate-like, subrectangular pubis with fully closed obturator foramen; and
11. largely straight femur with robust internal trochanter and poorly ossified articular ends.

The complete character suite strongly suggests that *Pachystropheus* either lies within, or very close to, Choristodera. No obvious characters are incongruent with this interpretation, and therefore, we believe *Pachystropheus rhaeticus* to be the earliest known representative of this enigmatic group of semi-aquatic reptiles. Currently, if somewhat tenuously, choristoderes are envisaged as primitive members of the Archosauromorpha (Evans 1988, 1990; Gauthier *et al.* 1988; Storrs and Gower 1993). Additional material of *Pachystropheus*, particularly cranial elements, could conceivably elucidate the relationship of the Choristodera with other diapsid reptiles.

### DISCUSSION

The identification of *Pachystropheus* as a potential choristodere pushes back their known fossil history by nearly 45 million years (Storrs and Gower 1993). It seems, at least on the basis of postcranial morphology, and excepting the few autapomorphies of the *Pachystropheus* humerus, that choristoderes have been a remarkably conservative lineage since at least the latest Triassic (Rhaetian). A relative shortening of the vertebral centrum over time is one of the few obvious morphological trends within the clade, although *Lazarussuchus*, as the latest known representative, nevertheless retained the primitive condition (Hecht 1992).

The known *Pachystropheus* material comes from individuals of a wide size range. The majority of specimens are from animals of approximately 1 m or less in size, and seemingly immature. However, occasional examples indicate animals in the range of 2–2.5 m (Plate 2; Text-figs 10, 11A), as typically were *Champsosaurus* and *Simoedosaurus*, although champsosaurs also grew unexpectedly large (Langston 1958). To date, *Cteniogenys* and *Lazarussuchus* are known only from much smaller individuals (Gilmore 1928; Seiffert 1973; Evans 1989, 1990, 1991; Hecht 1992; Metcalf *et al.* 1992), while most Asian forms (*Tchoiria*, *Ikechosaurus*, *Khurenduhkosaurus*) were apparently intermediate in size (Efimov 1975, 1988; Sigogneau-Russell and Efimov 1984; Brinkman and Dong 1993). There is thus no demonstrable size trend for choristoderes. The only obvious anatomical variation within Choristodera, other than size and centrum length, may be rostrum length/breadth ratio, a metric unknown for *Pachystropheus*.

A notable feature of *Pachystropheus* accumulations is their environment of deposition. All other accepted choristoderes are known from freshwater, usually fluvial, palaeoenvironments, although *Lazarussuchus* was preserved in a freshwater limestone, presumably a fossil pond or marsh (Hecht 1992). *Pachystropheus* is uniquely preserved in marginal marine sediments. While marine elements, such as selachians, plesiosaurs and ichthyosaurs, dominate the Westbury Formation fauna, occasional terrestrial components, such as dinosaurs (cf. *Camelotia*, *Megalosaurus?*) and lungfish (*Ceratodus*), are also found; their presence suggests a fluvial contribution to the deposit (Storrs 1993, 1994). Interestingly, the lungfish teeth and *Pachystropheus* bones are generally unabraded with little evidence of transportation; their source must have been close. Similarly mixed elements occur in the French and German 'Rhaetic' localities containing *Pachystropheus*, but the French fossils in particular, are abraded and clearly allochthonous.

Discovery of an articulated specimen of *Pachystropheus rhaeticus* from Rhaetian 'bone beds' is unlikely. However, intervening shales, although rarely suitable for bedding plane prospecting, may offer the hope of better material from which a clearer picture of *Pachystropheus* may emerge. Significantly, the occurrence of a single humerus (BRSMG Cd2678) in the lower Lias of Lillstock, Somerset, is the only example of *Pachystropheus* above the Rhaetian. Although lying only a few metres above the Westbury Formation, this range extension gives a tantalizing reminder that rare semi-terrestrial to terrestrial fossils can be found in Lias Group shales.

The age of the vertebrate-bearing sands of Saint-Nicolas-de-Port is a matter of some dispute. Although generally considered Rhaetian (Russell *et al.* 1976; Clemens *et al.* 1979; Clemens 1980),

Buffetaut (1985), Buffetaut and Wouters (1986), and Cuny and Ramboer (1991) have suggested that this French locality is Norian, although equating the late Norian with the Rhaetian. Duffin (1993) tentatively supported a Norian age, but left open the possibility of a Rhaetian assignment. All of these chronostratigraphical determinations have been based solely on the vertebrate assemblage, and therefore are not wholly reliable. If, however, the Saint-Nicolas-de-Port material is older than that of the Westbury Formation, a further range extension is provided for *Pachystropheus* and, presumably, Choristodera. As Storrs and Gower (1993) have discussed, this is not an unexpected development.

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## APPENDIX

### List of referred material:

- BATGM C18, C25, C25a (anterior caudal? vertebra; Text-fig. 6C–D; E. von Huene 1933, pl. 3), C28 (anterior dorsal vertebra; Plate 1, figs 1–6; E. von Huene 1933, pl. 3; Duffin 1978, pl. 2, fig. 6), M205 (large, matrix-free, dorsal vertebra, Plate 2, figs 1–4; F. von Huene 1956, fig. 649) and others, uncatalogued.
- BGS GSM 610, GSM 53508 (large femur), GSM 53594–53598, GSM 112033, GSM 112036, GSM 112039, Zr 8601–8604 (isolated, matrix-free ectopterygoid; Text-fig. 4).
- BMNH R395, R2728 (right iliac acetabulum; Text-fig. 11C; Storrs and Gower 1993, fig. 2), R3711 (dorsal rib; Text-fig. 5; Storrs and Gower 1993, fig. 1), R4837 (large left iliac blade; Text-fig. 11A; Storrs and Gower 1993, fig. 2), R6242 (dorsal rib), R6243 (dorsal centrum), R6245 (caudal rib), R6259, R6851 (mid-series dorsal vertebra; Plate 1, figs 7–10), R12466–12478 (mid-series caudal vertebra; Text-fig. 6E); R12479–12488 (slab with large femur, 100 mm long), R12489–12494, R12496–12498, R12500, R12505, R12507–12508, R12510–12512, R12514, R12516–12517, R12520–12521, R12523–12525, R12527–12528 (slab bearing an ectopterygoid), R12529, R12531–12535 (includes a large partial pubis and ilium), R12536–12537

- (indeterminate epipodial), R12539–12543, R12546–12548, R12550–12554 (miscellaneous postcranial remains on Garden Cliff slabs), 44835 (block containing anterior dorsal vertebra, dorsal rib).
- BRSMG** Cb4887 (isolated dorsal centrum; Text-fig. 5G; Storrs and Gower 1993, fig. 1), Cb4907 (matrix-free left humerus; Text-fig. 8A–D; Plate 2, fig. 5; Storrs and Gower 1993, fig. 2; Storrs, 1994, fig. 7), Cb9065 (slab of associated remains; Text-fig. 1B), Cd2422 (proximal end of large right humerus; Text-fig. 10; Plate 2, fig. 6), Cd2678 (large, matrix-free, right humerus; Text-fig. 9), Cd3174, Cd3365, Ce16854 (matrix-free, immature, right femur; Text-fig. 12), Ce17081 (interclavicle; Storrs and Gower 1993, fig. 2), Ce17082, Ce17093–17094, Ce17102, Ce17112, Ce17146 (dorsal neural arch; Text-fig. 5F), Ce17151, Ce17165 (mid-series dorsal vertebra; Text-fig. 5L–M; Storrs and Gower 1993, fig. 1), Ce17166 (anterior cervical vertebra; Text-fig. 5A–B), Ce17173, Ce17191–17192, Ce17200 (interclavicle; Storrs and Gower 1993, fig. 2), Ce17322–17323, Ce17330 (small femur), Ce17656 (distal caudal vertebra), Ce17770 (slab with associated postcrania; Storrs 1994, fig. 8), Ce17775 (?left caudal rib; Text-fig. 6B), Ce17777–17778 (juvenile humerus), Ce17801 and numerous specimens in lot acc. no. 45/1991 (including a large, matrix-free, right clavicle; Text-fig. 7D–E; a juvenile right ilium; Text-fig. 11D; a ?tibia and phalanges; also a matrix-free gastralium; Storrs and Gower 1993, fig. 1).
- BRSUG** 7010.4 (matrix-free, right femur, 100 mm long; Text-fig. 13; Storrs and Gower 1993, fig. 2), 17037 (mid-series cervical neural arch; Text-fig. 7), 19415.3, 19969 (interclavicle), 25301 (dorsal centrum), 25302.1 (mid-series caudal vertebra; Text-fig. 6F–G; Storrs and Gower 1993, fig. 1), 25302.2, 25304, 25305.1 (anterior caudal? vertebra), 25306, 25308–25314 (dorsal rib), 25315–25320 (dorsal vertebra), 25321–25323 (dorsal rib), 25324–25325 (anterior dorsal vertebra), 25326–25329 (left ilium; Text-fig. 11B), 25330 (isolated left pubis; Text-fig. 7C), 25331 (sacral vertebra and rib; Text-fig. 6A), 25332–25333 (ectopterygoids), 26161.
- CMNHS** VP4112 (humerus), VP4113, VP4114 (ectopterygoid), VP4115–4116, VP4117 (humerus), VP4118, VP4119–4120 (right humeri), VP4121–4124, VP4125 (partial pubis), VP4126–4127, VP4128 (small ectopterygoid), VP4129–4131, VP4132 (propodials), VP4133 (vertebrae), VP4134, VP4135 (dorsal vertebra), VP4136–4138, VP4139 (vertebrae and partial femur), VP4140, VP4642 (femur), VP4644.
- GPIT** 19552 (one half a sacral centrum, phalanx, isolated neural arches; E. von Huene 1935, pl. 3; Kuhn 1971, fig. 20).
- LEIUG** 88988 (proximal end of humerus, Martill and Dawn 1986, pl. 8, fig. B), 88989 (juvenile humerus, Martill and Dawn 1986, pl. 8, fig. C), 88990 (?sacral vertebral centrum, Martill and Dawn 1986, pl. 8, fig. G).
- MM LL.8018** and others (associated postcrania from 'Slime Road' Cliff, E. von Huene, 1933, pl. 3 and various in E. von Huene 1935, currently unlocated).
- MNHN** SNP101 (abraded dorsal centra).
- RSM** 1888.87.1, 1911.5.5887 (matrix-free interclavicle; Text-fig. 7A–B), 1911.5.5918 (proximal end of matrix-free, left humerus; Text-fig. 8E–H), 1911.5.6023.
- SMNS** 58791 (six isolated dorsal centra).
- STGCM** 60.62/1 (slab of associated remains, including vertebrae and limbs, potentially a single individual; Text-fig. 1A), 1986.145/1-8 (W9).