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SHORT COMMUNICATION

# A relict basal tetrapod from Germany: first evidence of a Triassic chroniosuchian outside Russia

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**Abstract** Chroniosuchians are basal tetrapods nesting within the paraphyletic anthracosaurs and were so far only well known from the Permian and Triassic of Russia. In this study, we present evidence for their existence in the upper Middle Triassic of Germany, based on diagnostic osteoderms and vertebrae from the Kupferzell and Vellberg localities in southern Germany. The finds are most similar to *Synesuchus*, a Middle Triassic bystrowianid chroniosuchian from the Northern Ural Pechora region. They demonstrate that by Middle Triassic time, chroniosuchians were much more widespread than previously thought.

**Keywords** Bystrowianidae · Chroniosuchia · Germany · Keuper · Triassic

## Introduction

The Lower Keuper deposits of southern Germany rank among the richest Triassic Fossillagerstätten in the world and since the discovery of the vast Kupferzell assemblage in 1977 have yielded numerous new species of bony fishes, temnospondyl amphibians, and reptiles of diverse clades (Gower 1999; Schoch 1999, 2002, 2006). In this paper, we report the most unexpected and erratic element of that fauna, which represents a relict from deep time: a chroniosuchian basal tetrapod.

Chroniosuchians form typical components of Upper Permian faunas in European Russia and were aquatic, piscivorous non-amniotic tetrapods that superficially resemble extant varanids in proportions (Ivakhnenko and Tverdokhlebova 1980; Novikov et al. 2000). Probably, chroniosuchians are closely related to the Embolomeri within the paraphyletic anthracosaurs (Laurin 2000; Novikov et al. 2000). Whereas recent analyses suggest that anthracosaurs lie on the amniote stem (Ruta et al. 2003; Ruta and Coates 2007), it is also possible that they fall outside the tetrapod crown-group (Laurin 2000). V'yushkov (1957a, b) distinguished two main lineages of chroniosuchians, the chroniosuchids and the bystrowianids. Whereas chroniosuchids are restricted to the Late Permian of Russia, bystrowianids have been found in Late Permian to Middle Triassic deposits of Russia (Golubev 1998) and have also been reported from the Late Permian of China (Young 1979). Chroniosuchian monophyly is well supported by a number of apomorphies (Novikov and Shishkin 2000). The most important are the sculptured, 'butterfly-shaped' osteoderms that were kinetically connected by an elaborate articulation mechanism and the typical intercentra that possess a unique ball-shaped morphology.

In this study, we describe postcranial remains of a new bystrowianid chroniosuchian from the late Middle Triassic (Lower Keuper, Erfurt Formation) of Kupferzell and the Schumann quarry at Vellberg in southern Germany. The new chroniosuchian taxon resembles most closely the bystrowianid *Synesuchus* and forms the first record of the clade outside Russia and China. At the same time, it

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represents one of the geologically youngest examples of a member of this group.

Institutional abbreviation

Institutional abbreviation includes SMNS for Staatliches Museum für Naturkunde Stuttgart.

Materials

The materials used in this study were SMNS 91034, complete osteoderm fused with tip of neural spine (type); partial osteoderms (SMNS 91036, 91037); and vertebrae (SMNS 81698, 81871–81874, 81876, 81877, 81879).

## Localities

Bystrowianid bones were found at two localities in the Lower Keuper: Kupferzell (Bauersbach) and Vellberg (Eschenau), both in Hohenlohe region, northern Baden-Württemberg, Germany.

## Results

Systematic palaeontology

1. Chroniosuchia Tatarinov 1972
2. Bystrowianidae V'yushkov 1957a
3. *Bystrowiella* n. g. (honoring eminent Russian palaeontologist A. P. Bystrow for his contributions to vertebrate palaeontology)
4. *Bystrowiella schumanni* n. sp. (named after the Schumann family for their engagement in securing fossils from Lower Keuper)
5. *Type specimen* SMNS 91034 (Figs. 1 and 2)
6. *Type horizon* Untere Graue Mergel, Upper Lower Keuper (Ladinian, upper Middle Triassic) *Type locality* Schumann quarry at Vellberg (Eschenau), Baden-Württemberg, Germany

## Diagnosis

Autapomorphies for genus and species: (1) osteoderms laterally more expanded (width to length equals 1, in contrast to 0.7 in *Synesuchus*); (2) in dorsal view, the anterior median incisure is approximately as long as wide and thus proportionally distinctly narrower than in *Synesuchus* with a ratio length to width of 2:3, and articular plate proportionally more slender (osteoderm width to articular plate width: 5.7 in *Bystrowiella* and 3.2 in *Synesuchus*); (3) the lateral edges of the wings are nearly straight in *Bystrowiella*, whereas they are distinctly convex in *Synesuchus*; (5) longitudinal grooves on the articular plate hardly concave and extend anteriorly up to small recess in the lateral side of the ventral process, in contrast to concave grooves in *Synesuchus* terminating at the posterior border of the dorsal plate in two horizontal pits.

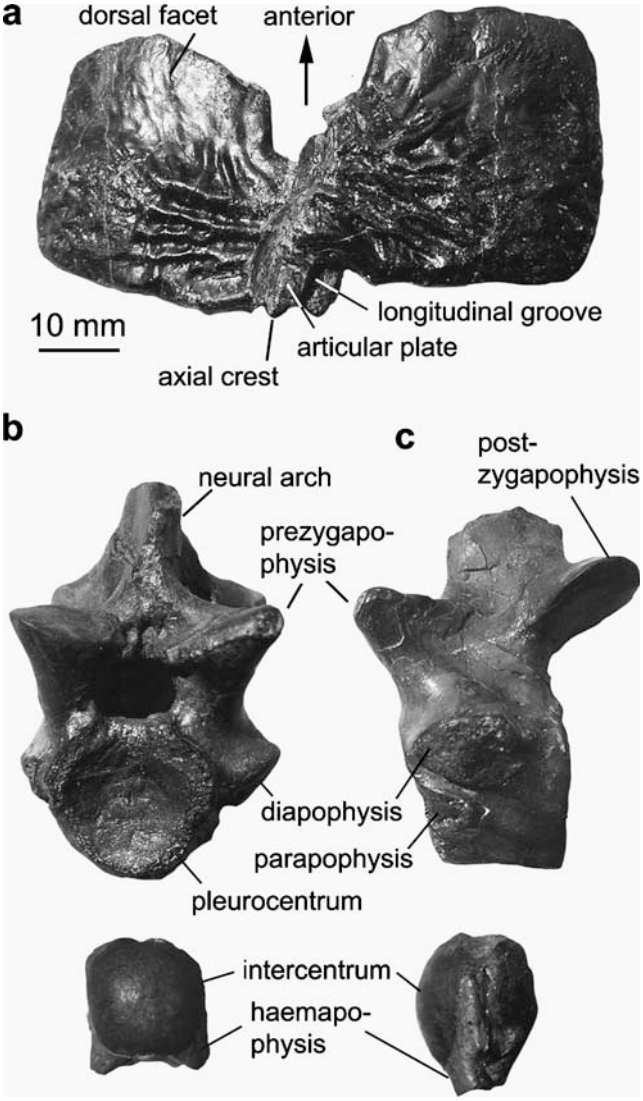


**Fig. 1** Photographs of osteoderm and vertebra of *Bystrowiella schumanni* n. g. n. sp. **a** Osteoderm (SMNS 91034) in dorsal view; **b**, **c** vertebra (SMNS 81698). **b** Anterior view; **c** left lateral view

*Bystrowiella* also shares derived characters with *Synesuchus*: (a) accessory processes are absent; (b) the three posterior processes of the articular plate are not fused, with the medial process being located well above the lateral processes; (c) smooth oblique crests on the ventral surface that terminate anteriorly in the triangular elevation, and (d) ventral depression is comparatively short but deep and has distinct lateral margins.

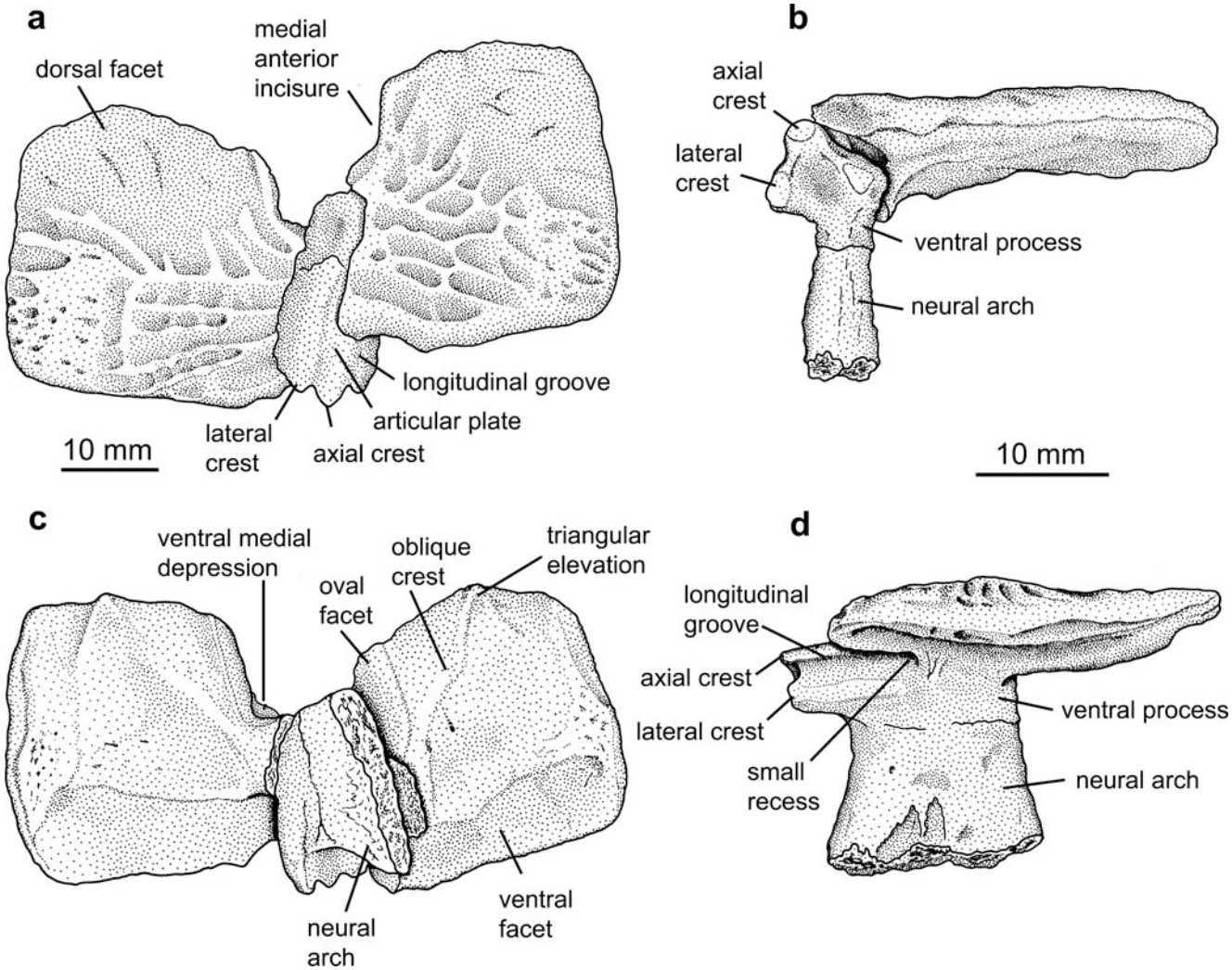


**Fig. 2** Osteoderm of *Bystrowiella schumanni* n. g. n. sp. (SMNS 91034). **a** Dorsal view (left wing displaced); **b** posterior view (left wing omitted); **c** ventral view; **d** right lateral view

Description

*Osteoderms* In this paper, we adopt the terminology of Novikov and Shishkin (2000). The osteoderm (SMNS 91034) consists of a dorsal plate of broad rectangular outline with convex rounded edges, a median articular plate (lamina articularis), and a ventral process (processus ventralis) that was fused to the neural spine (Figs. 1a and 2). The presence of two wings gives the osteoderm the typical butterfly-shaped outline. In contrast to all other bystrowianids except for *Synesuchus* (Novikov and Shishkin 2000), *Bystrowiella* osteoderms have no accessory processes in the median anterior incisure between the wings.

Posterior to the level of the anterior incisure, the dorsal surface is heavily ornamented with sharp ridges that enclose grooves and pits (Figs. 1a and 2a). The median articular plate ends posteriorly in three tapering processes. The median process bears the flat axial crest (crista media) and is located dorsomedially to the lateral processes that bear the lateral crests (cristae laterales) (Fig. 2b). In other bystrowianids, these crests frame two well developed and dorsally conspicuously concave longitudinal grooves (sulci articulares) that terminate at the posterior border of the dorsal, ornamented plate in two horizontal pits (Novikov and Shishkin 2000). These grooves and the pits received the accessory processes of the posteriorly neighboring osteoderm. In contrast, the 'longitudinal grooves' are hardly concave in *Bystrowiella* and reach further anteriorly: they extend beneath the dorsal, sculptured plate and on the lateral face of the ventral process up to a lateral broadening of the latter, where they terminate in a small recess (Fig. 2d). In *Bystrowiella*, the longitudinal grooves receive the oval facets of the anterior incisure (see below) because the accessory processes are absent.

On the ventral surface of the dorsal plate, a well-defined and oval ventromedial facet frames the anterior incisure on either side (Fig. 2c). Posteriorly, it merges into the short

ventral median depression. Immediately posterior to that depression lies the ventral process, which is fused with the tip of the neural spine. The oblique crest runs from the lateral margin of the ventral process towards a triangular elevation at the anterior margin of each wing. From the above-mentioned small recess next to the ventral process, the anterior margin of a shallow, broad ventral facet extends laterally.

*Articulation of osteoderms* In bystrowianids, the dorsal facets of the anterior portion of each wing underplate the ventral facets of the preceding osteoderm (Novikov and Shishkin 2000). The anterior incisure clasped the median articular plate of the preceding osteoderm. In this arrangement, the prominent oval facets of the posterior osteoderm fit exactly the 'longitudinal grooves' of the next anterior osteoderm. The small recess at the anterior end of the 'longitudinal grooves' received the tip of the oval facets. The median posterior process with the axial crest of the median articular plate was accommodated by the ventral median depression of the posteriorly neighboring osteoderm.

*Vertebrae* SMNS 81698 from Kupferzell is the best preserved vertebra, consisting of a ball-shaped intercentrum and a massive pleurocentrum fused to the neural arch. The transverse process is short and terminates in an elongate diapophysis (Figs. 1b,c and 3a–c). The prezygapophyses are oriented dorsomedially and slightly anteriorly, whereas the postzygapophyses are oriented ventrolaterally and posteriorly. A round foramen is present ventral to the left prezygapophysis, at the lateral margin of the large neural canal. A corresponding foramen is also present ventral to the right postzygapophysis. Both between the pre- and the postzygapophyses, directly above the neural canal, are located three foramina. Comparison with other bystrowianids (Novikov and Shishkin 2000; Tatarinov 1972) shows that the described foramina represent the openings of the paraneural canals. Only the base of the neural spine is preserved that is slightly shorter than the pleurocentrum.

The cylindrical, deeply amphicoelous pleurocentrum forms the main part of the vertebral centrum and possesses a small notochordal opening. On the anterior portion of the

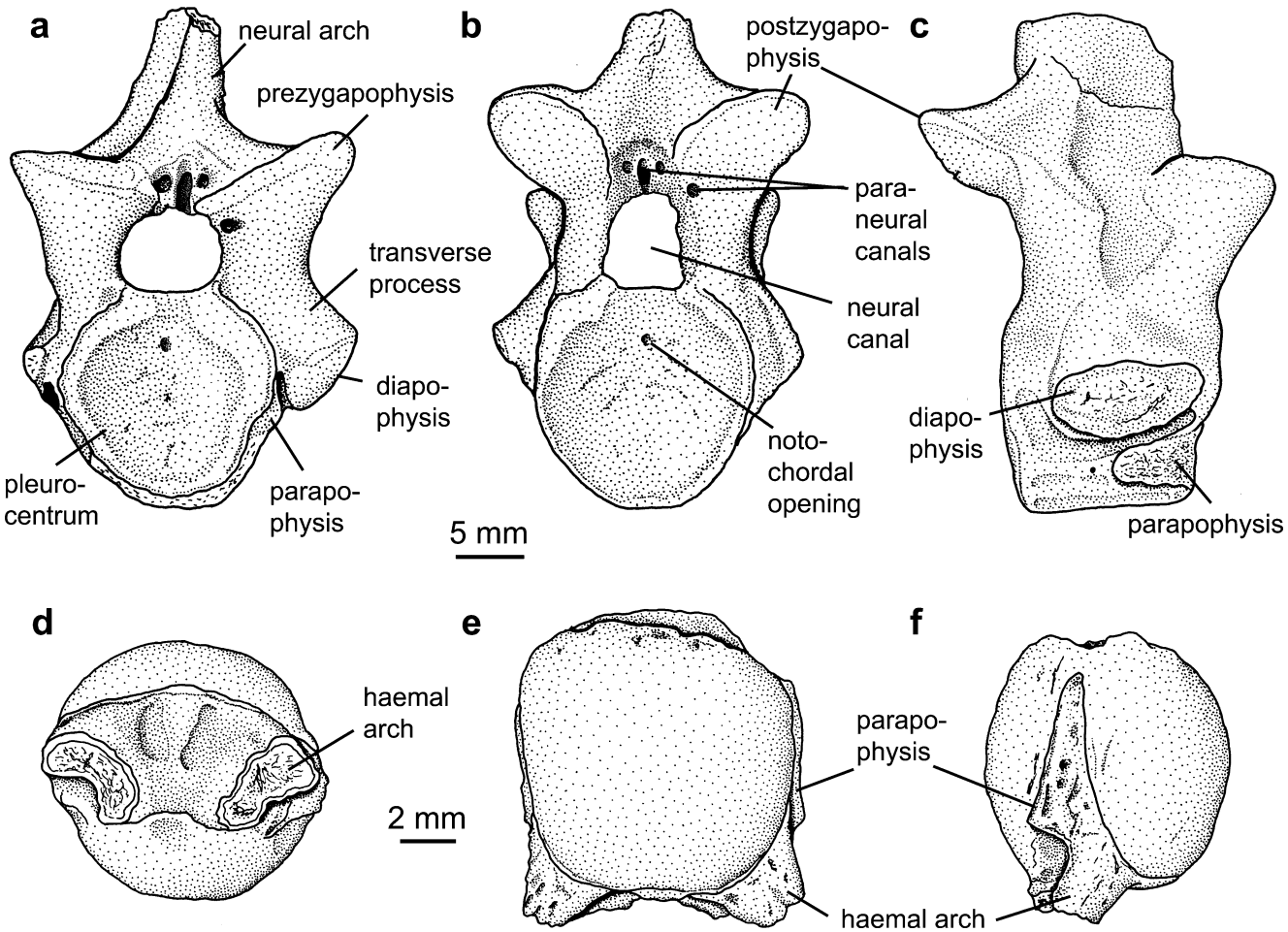


**Fig. 3** Vertebra of *Bystrowiella schumanni* n. g. n. sp. (SMNS 81698). **a**–**c** Pleurocentrum with fused neural arch. **a** Anterior view; **b** posterior view; **c** right lateral view. **d**–**f** Intercentrum. **d** Ventral view; **e** anterior view; **f** right lateral view

ventrolateral surface, the parapophysis is visible that is separated from the posterodorsally located diapophysis by an anterodorsally directed, deep incisure (Fig. 3c). The abrupt anterior termination of the parapophysis suggests its continuation on the intercentrum (see below). Two anteroposteriorly directed, broad but low ridges delimit the faintly concave ventral margin of the pleurocentrum, a feature that is also present in other bystrowianids (Novikov and Shishkin 2000).

Associated with SMNS 81698 was a single intercentrum of square-shaped outline in transverse view (Figs. 1b,c and 3d–f). Its anterior and posterior faces are strongly convex, giving it an overall ball-shaped appearance. The ventral surface consists of smooth periosteal bone, is slightly concave, and bears the ventrolateral bases of the hemapophyses (Fig. 3d). In contrast, most parts of the intercentrum are largely coarse and continued by cartilage. The parapophyses are indicated as small swellings. The dorsal surface of the intercentrum is concave and roughened and did not articulate with the neural arch. Therefore, the intercentrum had a free dorsal margin covered by cartilage, which is also reported in the articulated vertebral column of *Chroniosuchus* sp. (V'yushkov 1957b).

SMNS 81698 stems from the anterior tail region, as indicated by the short transverse processes of the neural arch. Trunk vertebrae in bystrowianids have distinctly longer transverse processes (Novikov and Shishkin 2000). Further support for this assumption is given by the hemapophyses on the ventral side of the intercentrum.

## Discussion

The discovery of chroniosuchians in Germany greatly extends our knowledge of their geographical range and distribution by Middle Triassic time. It adds to the similarities between the vertebrate faunas of the Eastern European Platform and Central Europe, indicated by the occurrence of the temnospondyl *Mastodonsaurus* in the roughly coeval Lower Keuper and Bukobay Horizon (Shishkin et al. 1995). Only recently reported from Middle Triassic strata at all (Novikov and Shishkin 2000), chroniosuchians were conceived erratic relics of that time. Instead, our findings underline how widespread the group still was in the late Middle Triassic. As chroniosuchians have never been found in the well-collected Buntsandstein or Muschelkalk, the Lower Keuper could reflect the earliest occurrence of this group in Central Europe, and the close resemblance between *Bystrowiella* and *Synesuchus* suggests immigration from the Ural Forelands. However, the absence of chroniosuchians in the Permian and Lower Triassic of Central Europe could alternatively mean a taphonomic overprinting in the way that their habitats are simply not preserved.

In both Russia and Germany, chroniosuchians occupied aquatic environments normally dominated by temnospondyls of broad size range and diverse morphologies (Schoch 2002; Shishkin et al. 1995). It is not clear how they managed to co-exist with the much more numerous temnospondyl taxa, but at least the Kupferzell deposit suggests that while temnospondyls were autochthonous, bones of *Bystrowiella* were washed in from more distant habitats. This indicates that chroniosuchians might have lived in different habitats within the same general area. As the Lower Keuper is known to have formed in diverse swamps and deltas (Schoch 2002), an according differentiation of habitats is likely.

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