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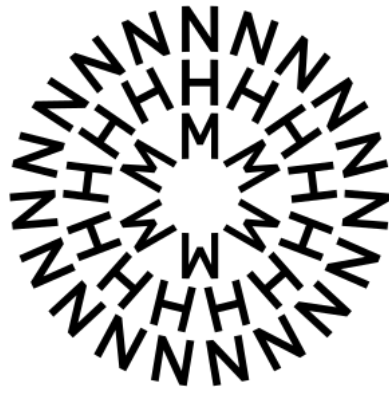
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New insights on the systematics, palaeoecology and palaeobiology of a plesiosaurian with soft tissue preservation from the Toarcian of Holzmaden, Germany

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Abstract

The Posidonien-schiefer Formation (Toarcian) of Holzmaden, Baden-Württemberg in southwestern Germany has yielded several excellently preserved plesiosaurian specimens and received considerable research attention. The plesiosaurians found within these deposits are always significantly outnumbered by ichthyosaurs and close examination of these rare specimens is crucial to a better understanding of the diversity and palaeoecology of Plesiosauria in this very peculiar ecosystem. The plesiosaurian specimen SMNS 51945 found in this area is a juvenile individual consisting of a partial, crushed skull and an exquisitely preserved postcranial skeleton. Its anatomical characters seem to differ from the long-necked

1 plesiosauroids *Microcleidus brachypterygius* and *Seeleyosaurus guilelmiimperatoris* that are
2 the most abundant taxa within the plesiosaurian assemblage. However, the juvenile status of
3
4 this specimen makes comparisons with other taxa problematic and features potentially less
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6 influenced by the ontogenetic status will be discussed in term of taxonomic utility. The post-
7
8 cranial skeleton also contains gastroliths and very likely soft tissues around the vertebral
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10 column and hindlimb of the animal, which could provide new insights into the palaeoecology
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12 and palaeobiology of plesiosaurians.
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16 **Keywords:** Germany, Holzmaden, Lower Jurassic, Plesiosauria, soft tissues
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22 **Introduction**

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24 Among European palaeontological sites that yield Mesozoic marine reptiles, the Posidonien-
25 schiefer Formation of the Holzmaden region (Baden-Württemberg, southwestern Germany) is
26
27 one of the most productive sources of well-preserved plesiosaurian and ichthyosaur fossils
28
29 (Sander 2000; Großmann 2006, 2007). The plesiosaurians found within these deposits are
30
31 always significantly outnumbered by ichthyosaurs and, probably as a consequence,
32
33 plesiosaurians with unusual intrinsic (e.g. anatomical) or extrinsic (taphonomic) characters are
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35 rare, whereas these are often reported for ichthyosaurs (e.g., juvenile individuals, pregnant
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37 females, soft tissues, gastric contents: Böttcher 1990; Martill 1993; Dick et al. 2016). Hence,
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39 juvenile specimens of plesiosaurians are rare in this locality as well as plesiosaurians with soft
40
41 tissue preservation, and plesiosaurians with gastric content are unknown. The purpose of the
42
43 present study is therefore to provide a thorough and detailed anatomical description of
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45 specimen SMNS 51945, compare it with other Jurassic taxa, and comment on its extrinsic
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47 characters.
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55 **Institutional abbreviations:** GPIT, Institut für Geowissenschaften der Universität Tübingen,
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57 Tübingen, Germany; MB, Naturkundemuseum Berlin, Berlin, Germany; NHM, Natural
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1 History Museum, London, UK ; SMF, Senckenberg Museum, Frankfurt, Germany; SMNS,
2 Staatliches Museum für Naturkunde, Stuttgart, Germany.
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7 **Systematic Palaeontology**

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10 Sauropterygia Owen, 1860

11 Plesiosauria de Blainville, 1835

12 Plesiosauroidea Welles, 1943

13 Genus and species indet.
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19 **1. Description**

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22 Specimen SMNS 51945 (Fig. 1) is preserved largely articulated. The skeleton is
23 almost complete but lacks most of the skull, only the posteriormost part of the crushed
24 braincase (mostly hidden by cervical centra) and mandibular rami remaining (Fig. 2a).
25 Among braincase elements, only the exoccipital-opisthotic is recognisable (Fig. 2b). All the
26 skeletal elements are preserved in almost anatomical connexion, with the exception of the
27 neural spines of the vertebrae, girdle elements and elements of the right limbs. The
28 disarticulated nature of the neural spines and girdle elements can be ascribed to the juvenile
29 status of the specimen, in which the girdle elements are probably not fused together and the
30 neural spines not fused with the vertebral centra. The lack of fusion between neural arches,
31 cervical ribs and vertebral centra, and the rounded distal margins of the propodials, epipodials
32 and mesopodials, are consistent with Brown's (1981) definition of a juvenile specimen.
33 However, considering its relatively large size (~3 m in length), it was probably not at an early
34 stage juvenile. The articulated nature of the skeleton suggests that the body was rapidly buried
35 after reaching the sea floor and that it was protected from destructive biological processes, as
36 is usual in the Toarcian strata of the Holzmaden area (Martill 1993). Because the
37 stratigraphically lower sides of vertebrate specimens from Holzmaden are generally better
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preserved than the upper sides, most specimens have been prepared from below (Martill 1993; Lingham-Soliar 2001; Vincent 2011). Assuming a similar treatment for the studied specimen, the left side of the specimen was certainly partly buried in the sediment soon after its death. As suggested for ichthyosaurs from the same site, the bones of the right limbs of SMNS 51945 probably became dislocated by weak sea floor currents or scavengers (Martill 1993).

Axial skeleton. The vertebral column preserves 39–40 cervicals, 4–5 pectorals, 17–19 dorsals, 4–5 sacrals and 40–41 caudals. The total length of the axial skeleton is approximately 3.07 metres: the cervical series is approximately 1.32–1.36 metres in total length, while the combined length of the preserved pectoral and dorsal vertebrae is approximately 0.73 metres.

Although the cervical series is largely articulated, the anterior-most vertebrae do not correspond to the atlas-axis (as noted by Grossmann 2006), and it is possible that a few cervicals may be missing. Thus, the minimum cervical count is 41–42 including the atlas-axis, a number close to those observed in specimen SMNS 51141 (40: Vincent 2010), *Seeleyosaurus* (37: Gossmann 2006), *Plesiopterys* (39: O’Keefe 2001), *Muraenosaurus* (44: Brown 1981), *Eoplesiosaurus* (38: Benson et al. 2012), *Microcleidus tournemirensis* (43: Bardet et al. 1999), *Plesiosaurus* (36–42: Storrs 1997), and *Microcleidus homalospondylus* (38: Brown et al. 2013), but greater than that observed in *Microcleidus brachypterygius* (35–36: Grossmann 2006). The centra do not possess a lateral longitudinal ridge or a ventral ridge. The articular surfaces exhibit bevelled rims. The ventral foramina are closely spaced and remain close to each other throughout the neck. The increase in centrum length only occurs in the anterior two-thirds of the neck, whereas the centra in the posterior third possess a relatively constant absolute length, after which the length shortens over the last 10% of the cervical series. This is a pattern common to long-necked plesiosaurians (O’Keefe and Hiller 2006). The cervical rib facets, located on the ventrolateral surfaces of the centra, are anteroposteriorly elongate in the first half of the neck (C1–C24; the numbering starts with the

1 first centrum preserved, nominally C1; Fig. 2a), whereas they became wider than long in the
2 posterior half. They are double-headed in most of the centra, as is common in early
3 plesiosaurians (Benson et al. 2015), but the rib head is single in the posterior part of the neck
4 (C37–C40; Fig. 2c) and thus differs from that reported for the genus *Microcleidus* which
5 exhibits widely separated posterior cervical rib facets (diagnosis of Benson et al. 2012). The
6 diapophysis and parapophysis are identical in length and shape in the anterior half of the neck
7 (C1–C20), and are closely spaced so that there is no horizontal groove between the two facets.
8 The diapophysis is subtriangular with a dorsally directed apex and is larger than the suboval
9 parapophysis (C20–C27). The rib heads are divided into two facets by a horizontal groove
10 (C30–C36; Fig. 2c). Except for the most anterior cervicals (C1–C11), the cervical neural
11 arches are preserved, having been only slightly disarticulated from the preserved centra. The
12 neurocentral sutures are V-shaped. They possess mediolaterally thin neural spines that
13 gradually increase in height towards the base of the neck. The anterior and middle neural
14 spines are low-aspect rectangles (C11–C31) and have a slight constriction situated near the
15 apex of the spine (C11–C29). Posteriorly, the constriction disappears and there is a slight
16 posterodistal curvature to the spine. The axial length of the neural spine is approximately 65%
17 of the length of the centrum and remains constant along the neck length and neural spines are
18 taller than long. The pre- and postzygapophyses protrude only a very short distance from the
19 posterior margin of the neural spine, having an approximately equal anteroposterior length
20 (the prezygapophyses are slightly longer than the postzygapophyses). Neural spines have a lot
21 of space between them when articulated and direct contact of the spines is limited to the
22 zygapophyseal area. Most of the anterior cervical ribs (C1–C11) are not preserved or have
23 been displaced after burial. Preserved cervical ribs are hatchet-shaped with a sharp anterior
24 process (C14–C39; Fig. 2a, c). Beginning with cervical C30, the posterior projection increases
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its length relative to the anterior process, the anterior projection weakens after cervical C33–C34, and is absent by cervical C39.

Postcervical vertebrae are tentatively divided into 4–5 pectorals, 17–19 dorsals, 4–5 sacral and 40–41 caudals. However, distinguishing between cervicals and pectorals is difficult due to the preservational orientation of the posterior centra of the neck, which are observable lateroventrally, and because some centra are obscured by other bones (mainly ribs). However, thanks to the neural arch morphologies it is possible to determine which vertebrae bear rib facets on both the centrum and the neural arches, a character that usually defines pectoral and sacral vertebrae. Four to five vertebrae are pectorals. Centrum number 40 or 41 thus likely belongs to the first (or two first) pectoral vertebra. The ventral surfaces of the pectoral centra appear to be flattened and the foramina subcentralia remain in ventral position as in the cervical series. There are 17–19 dorsal vertebrae. The dorsal centra are largely obscured by the ribs and their morphologies are therefore difficult to observe. They do not appear to be constricted in their mid-section, as in elasmosaurids. All of the neural arches are preserved; however, eight of them are preserved slightly disarticulated, but still close to their initial positions. In these neural arches, only the canal is observable, the spine being still embedded in the matrix. The dorsal ribs are partially or entirely crushed and none of them are found in near-articulation with their centra. Several gastralia are preserved in disarticulation in the abdominal region, some of which are boomerang-shaped with tapering ends and presumably represent medial elements. It is not possible to discern the number of gastralia in each row. There are 40–41 caudal vertebrae. The caudal centra CA15 to CA28 bear paired chevron facets. The chevron facets are shared between adjacent centra but are primarily positioned on the posterior edge of the centrum. Chevron facets are depressed in the centre and their circular rim projects ventrally. A total of 37 caudal neural spines are observable but they are poorly preserved. The neural spines are rectangular, dorsally oriented, and decrease in height

1 posteriorly. The rib facets of the caudals are circular and are positioned laterally on the centra.
2 The anterior caudal ribs are generally subrectangular, then the caudal ribs have a convex
3 anterior margin and they taper distally to form a blunt end.
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7 *Appendicular skeleton.* Large parts of the pectoral girdles are not preserved or
8 obscured by the matrix and other bones (Fig. 2d). The interclavicle-clavicle complex is
9 strongly developed and is composed of a median thick elongated interclavicle flanked by two
10 lateral and large wing-like extensions corresponding to the clavicles. Its anterior margin is
11 deeply notched anteriorly, the concavity being deep as in *Plesiosaurus*. The interclavicle
12 bears along its full length a thin ventral crest. The clavicles are apparently ventral to the
13 interclavicle, although the exact outline of each element is not clearly determined. The
14 scapula is a triradiate bone. The posterior and dorsal rami are approximately of the same
15 length. The posterior ramus is robust, expanded at its extremity; however, the presence of two
16 facets as usually observed among plesiosaurians cannot be confirmed. The dorsal ramus is
17 thin and broad. Its anterior and posterior borders are parallel, giving a rectangular shape. The
18 ventral ramus is thin, broad, short and rectangular in shape. Little of the coracoids are
19 observable as they are obscured by the matrix and other bones, making an accurate
20 description impossible. The pelvic girdle is entirely preserved but disarticulated and partially
21 hidden by other bone elements (Fig. 3a). The pubis is approximately as long as wide. There is
22 a deep semicircular notch on the posterior border of the pubis, mostly hidden by the femora,
23 forming the anterior margin of the pelvic foramen. The left and right pubes probably shared a
24 long, straight, median contact for most of their length, forming an abrupt, almost orthogonal
25 angle with the anterior, almost straight border. The acetabular surface is posteromedially
26 directed. The ischia are hatchet-shaped, as is typical in plesiosaurians (Andrews 1913). They
27 are relatively long bones, slightly longer than wide, contrary to the usual condition in juvenile
28 specimens in which ischia are short (e.g., Storrs 1997). The elongated ischia of SMNS 51945
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1 are thus possibly not related to its juvenile status. Additionally, SMNS 51945 has ischia
2 shorter than the pubis, a plesiosauromorph feature according to O’Keefe and Carrano (2005:
3 table 7). The pubis and ischium do not touch along the midline and thus do not form a solid
4 pelvic bar, a condition possibly related to the juvenile condition of the specimen. The ilium
5 (Fig. 3b) is a transversely narrow bone with anteroposteriorly expanded proximal and distal
6 ends. Both the anterior and posterior surfaces are proximodistally concave. Despite being
7 crushed during fossilisation, it seems to be somewhat twisted.
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17 The preserved humerus (Fig. 3c) was crushed by compression, resulting in the collapse
18 of internal structures. It is robust and markedly asymmetrical in lateral view, with a
19 posterodistal curved shaft. Its anterior border is almost straight. The humeral head is only
20 slightly convex and was undoubtedly covered in life by a thick cartilage cap. The distal
21 extremity is well rounded and does not exhibit epipodial facets as in juvenile plesiosaurian
22 specimens (e.g., SMNS 51141). The radius and ulna are slightly longer (proximally to
23 distally) than they are broad (preaxially to postaxially). The proximal and distal margins of
24 the radius are slightly convex, and do not show facets for their contacts with the humerus,
25 radiale or intermedium. The preaxial and postaxial margins of the radius are both concave in
26 outline (the preaxial more than the postaxial one), giving a subtle hourglass shape to the
27 radius (contrary to that observed in adult specimens where the hourglass shape is
28 pronounced). Druckenmiller (2006) considers a mid-shaft constriction along the preaxial
29 margin of the radius as a character of early plesiosaurians. The ulna is lunate, with a
30 posteriorly convex margin and a slightly concave anterior one. It has a straight proximal
31 margin for articulation with the humerus and two distinct distal facets for articulation with the
32 intermedium and ulnare along their postaxial margin. The postaxial margin of the radius and
33 the preaxial margin of the ulna are both concave, and together enclose a proximodistally thin
34 spatium interosseum. The proximal carpal row preserves (from the preaxial to postaxial
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margin of the limb): the radiale, the intermedium, and the ulnare. The radiale is smaller than the intermedium and the ulnare. The distal row consists of distal carpal I, fused distal carpals II and III, and distal carpal IV; carpal I being the smaller. All are distinctly smaller than the proximal bones. The bones of each digit are preserved in almost natural positions. The metacarpals and phalanges are hourglass-shaped, but the mid-shaft constriction along the preaxial and postaxial margins is not well marked in the metacarpals. Metacarpal V has shifted proximally, as is usual in plesiosaurians (O'Keefe 2001; Druckenmiller 2002). The phalanges decrease in size distally and their extremities are flat to slightly convex. The phalangeal count (from the preaxial to postaxial margin of the limb) consists of: 1-6-8-8-7, this count represents a minimal number of phalanges as some might have been lost during fossilisation or preparation. Grossmann (2007) noted that the first digits of the two juvenile specimens SMNS 51945 and SMNS 51141 are very incompletely developed and suggested that ossification of the metapodial could have spread from postaxial to preaxial as proposed by Caldwell (1997) for mesopodial elements.

The femur (Fig. 3d) like the humerus was crushed by compression, resulting in the collapse of internal structures. It expands nearly symmetrically, though the postaxial margins are very slightly more expanded than the preaxial. The distal articular surface forms a convex arc, with no development of epipodial facets. The femur is longer than the humerus. The difference between propodial proportions has been considered an important taxonomic character but only when considered in adult forms (Welles 1943; Brown 1981). In general shape and proportions, the tibia and fibula mirror the radius and ulna, respectively. The general outlines of the metatarsals and phalanges are similar to those of the metacarpals and phalanges of the forelimb. The phalangeal count (from the preaxial to postaxial margin of the limb, for the left paddle) consists of: 3?-6-9-9-8.

2. Comparison with other Lower Jurassic taxa

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2 Numerous anatomical characters are useless for systematic purposes when examined
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4 in juvenile specimens. Vertebral centra and neural arch proportions have been reported by
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6 Brown (1981) as varying with ontogeny, as well as some girdle elements proportions (clavicle
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8 size, coracoid cornua) (see also Storrs 1997). Allometric growth has been suggested for the
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10 propodials (Caldwell 1997; Kear 2007), thus making the relative length between humerus and
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12 femur usually uninformative in juvenile specimens (Vincent 2010). The shape of the
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14 neurocentral suture in cervical vertebrae could also be related to ontogenetic status, as the
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16 suture is respectively U-shaped and V-shaped in adult and juvenile specimens of *Plesiosaurus*
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18 (Storrs 1997). Although the juvenile status of SMNS 51945 makes comparisons with other
19
20 taxa potentially problematical, features less influenced by ontogeny remain taxonomically
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22 useful: 1) the centra lack both a lateral longitudinal ridge and a ventral ridge in SMNS 51945.
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24 These absences are probably not related to the juvenile status of the specimen, as some other
25
26 juvenile plesiosaurian specimens possess lateral or ventral ridges (e.g., Knutsen et al. 2012:
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28 holotype of *Spitrasaurus*; O’Gorman 2012: MLP 86-X-28-3; Vincent et al. 2013:
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30 NHMUK2018, a juvenile specimen of *Thalassiodracon*); 2) no important variation in the
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32 interclavicle-clavicle complex morphology has been reported through ontogeny, and clavicles
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34 are comparatively large in juveniles (Brown 1981). This may suggest that this structure
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36 emerged relatively early during ontogeny, in line with the ontogenetic sequence seen in
37
38 scincid lizards in which the clavicle is among the first elements to begin ossification (Hugi et
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40 al. 2012). The morphology of the interclavicle-clavicle could thus provide reliable anatomical
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42 and taxonomic information.
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53 In general outline (gracile skeleton and elongated neck) SMNS 51945 resembles
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55 plesiosauroid taxa. However, SMNS 51945 differs markedly from known plesiosauroid taxa
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57 in that it has:
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1) at least 41 cervical vertebrae (including the atlas-axis), a greater number than that reported for *Seeleyosaurus*, *Eoplesiosaurus*, *Microcleidus brachypterygius* and *M. homalospondylus*, but close to the reported number in *Plesiosaurus*, *M. tournemirensis*, *Plesiopterys* and SMNS 51141 (see description section; Storrs 1997; O’Keefe 2004; Goßmann 2007; Vincent 2010; Benson et al. 2012);

2) no keels or ridges on ventral surfaces of cervical centra, a condition differing from that observed in *Plesiosaurus*, *Eretmosaurus*, and *Eoplesiosaurus* but similar to *Microcleidus*, *Seeleyosaurus*, *Westphaliasaurus* and *Plesiopterys* (Storrs 1997; O’Keefe 2004; Goßmann 2007; Schwermann and Sander 2011; Benson et al. 2012);

3) no lateral longitudinal ridge on the anterior cervical centra, in contrast to *Microcleidus* and *Seeleyosaurus* (Goßmann 2007; Benson et al. 2012);

4) posterior cervical neural spines that curve posterodorsally, a condition that differs from that of *M. brachypterygius*, *M. homalospondylus*, *Seeleyosaurus*, *Plesiosaurus*, *Eoplesiosaurus* and *Plesiopterys* but is close to that observed in *M. tournemirensis*, *Eretmosaurus* and *Westphaliasaurus* (Storrs 1997; Bardet et al. 1999; O’Keefe 2004; Goßmann 2007; Benson et al. 2012);

5) single rib facets on the posteriormost cervical centra, as in *Cryptoclidus* but in contrast to that reported for *Eretmosaurus*, *Seeleyosaurus*, *Microcleidus*, *Eoplesiosaurus* and *Plesiopterys* (Brown 1981; Benson et al. 2012);

6) absence of a strong anteroposterior constriction at the base of the neural spines in dorsal vertebrae, unlike the condition in *Microcleidus* (Benson et al. 2012);

7) anterior margin of the clavicle-interclavicle complex with a tight and deep concavity as in *Plesiosaurus* but differing from the condition in *M. tournemirensis*, *Plesiopterys*, and *Seeleyosaurus* (Storrs 1997; Bardet et al. 1999; Großmann 2006; Benson et al. 2012);

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2 8) ulna lunate without concave posterior margin in contrast to *M. brachypterygius*
3 (Großmann 2006; Vincent et al. submitted).
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7 These various features indicate that specimen SMNS 51945 differs substantially from
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9 all the lower Toarcian plesiosauroids previously described, and importantly, from coeval
10 plesiosauroid specimens known from the same region. If correctly interpreted, these
11 differences suggest that the studied specimen represents an additional plesiosauroid taxon that
12 has not yet been reported in the Holzmaden area, which would increase the diversity of
13 plesiosauroids from 3 to 4 taxa (i.e., the new taxon represented by SMNS 51945,
14 *Microcleidus brachypterygius*, *Seeleyosaurus guilelmioperatoris* and *Plesiopterys wildii*; but
15 see Großmann 2007 for discussion). Taken together with the two pliosauroid taxa known
16 from the same area (*Hauffiosaurus* and *Meyerasaurus*), this would imply that at least 6
17 plesiosaurian taxa would have been present in the SW German Basin during the early
18 Toarcian. However, considering the juvenile status of SMNS 51945 and the poor skull
19 preservation, we refer the specimen to Plesiosauroidea indet. Attributing this specimen to a
20 potentially new adult taxon awaits discovery and documentation of new plesiosaurian
21 specimens from this area.
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43 **Soft tissues**

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45 Buff-coloured and dark-coloured structures are present around the neck, tail and
46 hindlimb of the animal. They are found adjacent to the ventral and dorsal surface of the
47 vertebral column: dorsally to cervicals 32 to 33 (Fig. 4a), dorsally to cervicals 39 to anterior
48 pectorals, dorsal to caudals 13 to 16 (Fig. 4b), ventral to caudals 8 to 14 (Fig. 5a), dorsal to
49 caudals 23 to 25 (Fig. 6) and at the posterior margin of the hindlimb, adjacent to the fibula
50 (Fig. 7a). The buff-coloured areas have four different patterns: 1) areas dorsal to the caudals
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1 (Fig. 4b, c) show a single generation of continuous striae, which are roughly orthogonal to the
2 axis of the vertebral column; 2) areas ventral to the caudal vertebrae show a succession of
3 agglutinated buff-coloured pustules surrounded by sediment (Fig. 5a, c); these ‘bumps’ seem
4 to be roughly aligned along the axis of the vertebral column and there is no discernable sign
5 of a secondary orientation; 3) some areas show alveolar structures, which comprise regularly
6 spaced tiny pits revealing the underlying sediment or black films (Fig. 7b-e); these pits are
7 organized into a larger network of fiber-like alignments showing a main orientation
8 approximately perpendicular to the long axis of the paddle and a possible second orientation
9 approximately parallel to the long axis of the paddle; 4) in one area (Fig. 7), where the buff-
10 coloured material is not strongly pitted, a fine examination of the structure shows clear criss-
11 cross fibers (Fig. 7f), intersecting at an angle between 75 and 85°; in addition, traces of rare
12 fibers intersecting at lower angles (about 40°) to the main fiber orientation are also visible.
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29 The pattern of tubercles at first suggests a modular construction as found in many
30 colonial invertebrates and more particularly in bryozoans. Cyclostome bryozoans attributed to
31 ‘*Berenicea*’ are common in shallow marine deposits throughout the Jurassic (Taylor and Ernst
32 2008), and examples of this form-genus have been described previously from Holzmaden
33 (Seilacher, 1982). Furthermore, bryozoans today are capable of fouling living reptiles,
34 including sea snakes (Key et al. 1995). However, details of the configuration and shape of the
35 tubercles do not closely match the modular zooids found in known bryozoans or other
36 colonial organisms from the Jurassic. There are no clear boundaries between the tubercles
37 unlike bryozoan zooids, and the structures are apparently not calcitic as they would be in
38 cyclostome bryozoans. Therefore, the possibility can be discounted that the structures
39 represent bryozoan epizoans or, alternatively, post-mortem encrusters of the plesiosaurian.
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55 Because the occurrence of potential soft tissue is exceptional in plesiosaurians, it was
56 decided to avoid destructive analysis that may have helped to establish their chemical
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1 composition. Nevertheless, there is a striking resemblance between the dark- and buff-
2 coloured materials surrounding the neck, tail and hindlimb of SMNS 51945 and the soft
3 tissues documented in several ichthyosaur and cephalopod specimens from the same strata
4 (Keller 1992), as well as Sinemurian and Callovian-Oxfordian ichthyosaurs from the UK and
5 Cretaceous fish from Brazil (Martill 1995). In all these fossils, the buff-coloured material was
6 interpreted as phosphatised muscle tissue. In the Holzmaden ichthyosaur specimen SMNS
7 10013, this buff-coloured material was identified as mainly composed of calcium phosphate
8 using energy-dispersive X-ray spectroscopy and also interpreted as phosphatised muscle
9 tissues (Keller 1992).
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21 In the specimen studied here, SMNS 51945, the black-coloured material is only
22 situated very close to the bone elements. Structures showing a similar black coloration in the
23 studied locality are only found in deeply transformed woody material known as ‘jet’ (‘Gagat’
24 in German) (Keller 2000) and as black films surrounding fish and ichthyosaur specimens. The
25 shape and very limited thickness of the films make their attribution to jet very unlikely, and
26 they are more likely to be equivalent to the material forming the dark-coloured body outlines
27 common among Holzmaden ichthyosaurs (Martill 1993; Lingham-Soliar 2001). The tubercle-
28 bearing buff-coloured material is almost always associated with the smooth, black films, and
29 the two materials sometimes interdigitate (Fig. 6, Fig. 7b, c), as can be found in ichthyosaur
30 specimens (Martill 1995). These observations indicate that the dark-coloured and buff-
31 coloured material present around the neck, tail and hindlimb of the animal most likely
32 correspond to soft tissues.
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51 Although a number of ichthyosaur skeletons with soft tissue preservation have been
52 documented from the Posidonien-Schiefer of Holzmaden (Martill 1993), this kind of
53 preservation is exceptionally rare among plesiosaurian specimens. Only two other
54 plesiosaurian specimens are known with potential soft tissue preservation, which in both cases
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1 are represented by dark-coloured films: the type specimen of *Microcleidus brachypterygius*
2 (GPIT/RE/3185) and the type specimen of *Seeleyosaurus guileliimperatoris* (MB.R.1992).
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4 MB.R.1992 shows soft-tissue preservation at the posterior end of the caudal vertebrae (Dames
5 1895), whereas, GPIT/RE/3185 shows soft-tissue preservation on the posterior margin of both
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7 forelimbs, between the level of the ulna and the second row of phalanges, that extends
8
9 posteriorly for about half the width of the limb itself (Huene 1923; Großmann 2006).
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12 However, none of the specimens preserve buff-coloured phosphatic soft-tissues – specimen
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14 SMNS 51945 is the first plesiosaurian from which such preservation has been reported.
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19 Interpretation of the pitted and alveolar structures of some parts of this material (Fig.
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21 7) is, however, complicated by the fact that no comparable soft part preservation has been
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23 reported in ichthyosaurs. In most Jurassic ichthyosaurs with soft-tissue preservation, the buff-
24
25 coloured material is characterized by ripple-like ridges and lacks a network of ‘bumps’ or
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27 hollow ‘pits’ (Keller 1992; Martill 1995; E.E.M. personal observation of SMNS 10013). A
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29 network of hollow ‘pits’ organized into fibers of buff-coloured material was reported in the
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31 caudal fin of *Stenopterygius* SMF 457 from the lower Toarcian of Holzmaden (Lingham-
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33 Soliar and Plodowski 2007), and in the skull region of *Ichthyosaurus* GLAHM V1180 from
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35 the Lower Lias of Gloucestershire, UK (Lingham-Soliar and Wesley-Smith 2008). These
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37 fibers, which show striking resemblance in terms of size, orientation and organisation to the
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39 fibers located posteriorly to the hindlimb of SMNS 51945 (Fig. 7f), were interpreted as
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41 phosphatized collagen fibers that helped to stiffen the dorsal fin in *Stenopterygius* SMF 457
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43 (Lingham-Soliar and Plodowski 2007). It can thus be hypothesized that the network of fibers
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45 located posterior to the left hindlimb in SMNS 51943 also represents phosphatized collagen
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47 fibers.
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56 The alveolar structures located ventral to the caudal vertebrae (Fig. 5) are unusual in
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58 that they have never been reported in ichthyosaurs with soft-tissue preservation. The
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1 plesiosaurian SMNS 51945 was collected from the lower Toarcian strata (Lias EII_1 ,
2 ‘Koblenzer’, *tenuicostatum* Zone, upper *semicelatum* Subzone) that yielded rare ichthyosaurs
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4 with soft-tissue preservation (e.g. Hofmann 1958). However, the more abundant ichthyosaurs
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6 with preserved soft tissues from overlying beds are presumed to have undergone a very
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8 similar diagenetic history, suggesting that differential preservation is unlikely to account for
9
10 such differences. It could be argued that such structures were artificially produced by the
11
12 mechanical preparation of the specimen, which would have created striae along the tail axis
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14 (particularly deep in the ventral portion of this zone), thus leaving small ‘bumps’ of buff-
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16 coloured material. The ‘scaly’ aspect of the buff coloured material is, however, also visible in
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18 areas where such striae are less marked (left-hand side and upper right-hand side of Zone Db),
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20 suggesting that these structures are genuine features that have been enhanced rather than
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22 artificially produced by preparation. Besides, most of the Holzmaden ichthyosaur specimens
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24 have been prepared mechanically in a very comparable fashion, implying that similar
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26 preparation artefacts would logically also occur in ichthyosaurs. The pitted aspect of the
27
28 structures seen in SMNS 51945 may thus suggest that, contrary to ichthyosaurs, some
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30 plesiosaurians possessed small, scale-like epidermal ornamentations on parts of their bodies.
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32 Epidermal scales are also preserved in a crocodylomorph from the Posidonia Shale of Baden-
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34 Württemberg (Böttcher 1998), but do not resemble the structures observed in SMNS 51945.
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46 The scant soft-tissue preservation observed in SMNS 51945 has implications for the
47
48 general body outline and locomotion of plesiosaurians. Assuming that the buff-coloured
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50 material located posterior to the left hindlimb represents phosphatised collagen fibers, it can
51
52 be hypothesized that such structures, as in the collagen fibers of the dorsal fin of the great
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54 white shark (Lingham-Soliar and Plodowski 2007), resulted in considerable stiffening of the
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56 soft parts constituting the paddles. Importantly, this buff-coloured material extends posteriorly
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1 for about the same width as the limb itself. Considering that the bone elements of the skeleton
2 are in close articulation, it can be reasonably assumed that the posterior extension of the soft
3 tissues of the limb underwent limited displacement after burial. Accordingly, this organic
4 structure would have doubled, at least at the level of the epipodial and mesopodial elements,
5 the wing area of the hindlimb, thus implying a much greater soft paddle area than based solely
6 on the extent of the dark film of GPIT/RE/3185. However, considering the juvenile status of
7 the specimen SMNS 51945 we cannot exclude the possibility that the size of the wing area
8 could be ontogenetically influenced. These mineralized soft tissues could thus bring limited
9 but crucial constraints when determining the efficiency and manoeuvrability of the propulsive
10 organs. Indeed, several studies have explored the buoyancy, swimming ability and velocity of
11 plesiosaurians (e.g., Long et al. 2006; Massare 1988; Motani 2002; O’Keefe 2001; Henderson
12 2006; Liu et al. 2015), and the evidence presented here would thus support the idea that wing
13 area in plesiosaurians was much larger than that suggested by skeletal remains alone.
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31 **Gastric content**

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37 The stomach cavity of specimen SMNS 51945 contains numerous medium-to-coarse,
38 sand-sized grains mainly composed of quartz (Fig. 8). They are located in an area under the
39 dorsal ribs, between the pectoral and pelvic girdles at the level of the midpoint of the trunk.
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41 The majority of the grains remain almost fully enclosed within the matrix. Their position in
42 the skeleton and the low-energy depositional environment of the surrounding shale indicate
43 that they were most likely ingested during the animal’s life. Following the definition of Wings
44 (2007), they can be referred to as gastroliths: “ a hard object of no caloric value [...] which is,
45 or was, retained in the digestive tract of an animal “ (Wings 2007, p.2). This implies that
46 distinguishing between gastroliths with a real biological function and accidentally swallowed
47 objects is not feasible (Wings 2007). Although gastroliths are commonly found associated
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with plesiosaurians, they have been mainly documented in elasmosaurids (e.g., Welles and Bump 1949; Everhart 2000; Schmeisser and Gilette 2009; McHenry 2005; Sato et al. 2006; Kubo et al. 2012). Only two occurrences have been reported for Lower Jurassic taxa (Taylor 1993; O’Keefe et al. 2009). Evidence is available suggesting that juvenile plesiosaurians also ingested gastroliths of a size smaller than gastroliths in adult elasmosaurids (e.g., Martin et al. 2007; O’Gorman et al. 2012). The function of these gastroliths in plesiosaurians is still largely unknown. They may have been used for food trituration (Everhart 2000, McHenry 2005), or for buoyancy control analogous to crocodiles (Darby and Ojakangas 1980, Taylor 1981, 1993, 2000; Henderson 2006).

The gastroliths present within specimen SMNS 51945 have a grain size of <0.5 mm to 3 mm, and are thus markedly smaller than those previously reported in most Jurassic and Cretaceous plesiosaurians. Even juvenile plesiosaurians with gastroliths show a larger grain size (0.4–10 mm in diameter: Martin et al. 2007; O’gorman et al. 2012). However, sand grains have been reported as part of the stomach contents of *Brancaesaurus*, and a sandstone mass is reported in the abdominal cavity of the Triassic sauropterygian *Augustasaurus* (Wegner 1914; Sander et al. 1997). These sand grains may have two different sources: 1) a larger sandstone clast(s) that disintegrated in the stomach; 2) relatively coarse sediment ingested intentionally, or accidentally (e.g., during feeding on benthic prey). Accidental ingestion is consistent with evidence suggesting that long-necked plesiosaurians may have been specialised predators of invertebrates dwelling on or in seabed sediments (McHenry et al. 2005; Geister 1998).

Whatever the cause of the ingestion, the sand gastroliths clearly have an exotic provenance, as the sediments surrounding the skeleton are fine-grained black mudrocks. The benthic environment of the Posidonia Shale sea was relatively quiet (Röhl et al. 2001), characterized by prolonged phases of anoxia, sporadically interrupted by short-lived events of improved oxygenation that allowed the transient colonization of a low-diversity epibenthic

1 fauna (Röhl et al. 2001). The succession itself does not contain detrital grains larger than silt-
2 grade, and these are confined to rare tempestite/turbidite horizons occurring in epsilon II₄
3 (Röhl et al. 2001). To our knowledge, sandy turbidites have never been reported from the SW
4 German Basin, thus excluding a local source. Instead, the individual may have acquired the
5 sand-sized grains, or the prey containing or surrounding them, many kilometres away from
6 the burial site. The dominance of quartz grains and their relatively good sorting point to a
7 relatively mature detrital sediment source, indicative of a nearshore or estuarine environment.
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17 The nearest regions where such environments may have existed during the early
18 Toarcian were the Black Forest, Vosges and the Jura Massif, which were presumably
19 emergent at this time (Röhl and Schmid-Röhl 2005). It is unclear whether the Jura massif was
20 truly emergent, as contemporaneous strata of the top *tenuicostatum* zone in the Franconian
21 Jura are composed of black shale unconformably resting on upper Pliensbachian limestone
22 beds (Röhl and Schmid-Röhl 2005), without any indication of relatively coarse, quartz-rich
23 detrital input. Riegraf (1985) reported strata containing fine sand in the *tenuicostatum* Zone
24 ('Glaukonit und viel Feinsand') at Obereggenen im Breisgau (western side of the Black Forest
25 between Freiburg & Basel), about 200 km from Holzmaden, suggesting that a sand source and
26 hence emerged land existed at that time near the Black Forest. Calcareous sandstone beds
27 with abundant detrital quartz are also known in the *tenuicostatum* ammonite Zone from the
28 EST433 borehole located near Bure (France) (Lézin et al. 2013), about 300 km from
29 Holzmaden, which may point to the Vosges Massif as an alternative source. Fine to medium
30 sandstone beds also occur near the top of the *tenuicostatum* ammonite Zone in Grimmen,
31 Northern Germany (Prauss 1991) where a diverse marine reptile fauna (including
32 plesiosaurians) has been reported (Stumpf 2016), in Bornholm (Denmark) (Hesselbo et al.
33 2000), and over large areas in the Polish Basin (Hesselbo and Pienkowski 2011), more than
34 700 km away from the Holzmaden locality. The latter localities suggest that an extensive sand
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1 belt, possibly linked to detrital input from the Scandinavian shield, existed towards the north
2 of the Tethyan European seaway.
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4 Regardless of their exact source, the medium- to coarse-grained sands found within
5 specimen SMSN 51945 indicate that the animal spent at least some of its time in shallow
6 coastal waters, tens or hundreds of kilometres from the final place of burial. Given the
7 excellent state of preservation and articulation of the specimen, it appears unlikely that the
8 carcass was transported such considerable distances. Consequently, the petrological nature of
9 the gastroliths of SMSN 51945 suggests that the animal was able to migrate, at least
10 occasionally, for distances exceeding tens of kilometres. Interestingly, quartz grains occurring
11 as gastric contents have been rarely reported among the hundreds to thousands of ichthyosaur
12 specimens discovered in the Posidonien-schiefer Formation. However, they may be more
13 common than reported in the literature (E.E.M. pers. obs.) and are probably not restricted to
14 the gut contents (Bronn 1844). Ichthyosaur specimens, however, commonly contain gastric
15 contents, which are chiefly composed of fish remains and cephalopod hooklets in
16 *Stenopterygius* (Dick et al. 2016), and fish remains, cephalopod hooklets and bones of smaller
17 ichthyosaurs in *Temnodontosaurus* (Böttcher 1989). These differences in gastric contents
18 suggest that ichthyosaurs and plesiosaurs had only limited overlap in their geographical
19 ranges, possibly correlated with different feeding habits. Although further work is needed to
20 understand where plesiosaurians spent most of their time, such a niche and geographical
21 partitioning may explain why only a dozen of plesiosaurs specimens have been discovered in
22 the relatively distal Posidonien-schiefer compared to hundreds of ichthyosaurs.
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10 **Figure captions**

11 **Fig. 1** SMNS 51945 from the Posidonien-schiefer Formation (Toarcian) of Holzmaden,
12
13 Baden-Württemberg. Skeleton in lateral view. Scale bar = 10 cm
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16 **Fig. 2** SMNS 51945, from the Posidonien-schiefer Formation (Toarcian) of Holzmaden,
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18 Baden-Württemberg. a, skull and anterior cervical vertebrae in ventral view; b, exoccipital-
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20 opisthotic; c, posterior cervical vertebrae in lateral view; d, pectoral girdle. Abbreviations: C,
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22 cervical vertebra with number; co, coracoid; icl, interclavicle-clavicle complex; h, humerus;
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24 gl, glenoid; sc, scapula; Scale bars = 5 cm (a, c and d) and 1 cm (b)
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29 **Fig. 3** SMNS 51945, from the Posidonien-schiefer Formation (Toarcian) of Holzmaden,
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31 Baden-Württemberg. a, pelvic girdle; b, ilium; c, forelimb; d, hindlimb. Abbreviations: f,
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33 femur; fi, fibula; h, humerus; il, ilium; is, ischium; pu, pubis; r, radius; ti, tibia; u, ulna; sc,
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35 scapula. Scale bars = 5 cm (a, b) and 10 cm (c, d)
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39 **Fig. 4** SMNS 51945, from the Posidonien-schiefer Formation (Toarcian) of Holzmaden,
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41 Baden-Württemberg. a, region showing area of organic materials dorsal to the neck region; b
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43 and c, region showing area of phosphatic material dorsal to the caudal region. Scale bars = 5
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45 cm (a), 1 cm (b), and 50 mm (c)
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48 **Fig. 5** SMNS 51945, from the Posidonien-schiefer Formation (Toarcian) of Holzmaden,
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50 Baden-Württemberg. a, b, c, d, regions showing area of phosphatic material ventral to the
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52 caudal region. Scale bars = 1 cm (a), 50 mm (b, c, d)
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Fig. 6 SMNS 51945, from the Posidonien-schiefer Formation (Toarcian) of Holzmaden,
Baden-Württemberg. a, b, c, d, regions showing area of phosphatic material dorsal to the
caudal region. Scale bars = 1 cm (a), 50 mm (b, c, d)

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Fig. 7 SMNS 51945, from the Posidonien-schiefer Formation (Toarcian) of Holzmaden,
Baden-Württemberg. a, b, c, d, e, f, region showing area of phosphatic material dorsal to the
caudal region; f, regions showing area of crossing fibers, line drawing show main fiber
directions Scale bars = 2 cm (a), 50 mm (b, c, d, e), 20 mm (f)

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Fig. 8 SMNS 51945, from the Posidonien-schiefer Formation (Toarcian) of Holzmaden,
Baden-Württemberg. Gastroliths. Scale bar equals = 1 cm



