

## On the Emsian (Lower Devonian) arthropods of the Rhenish Slate Mountains: 2. The synziphosurine *Willwerathia*

LYALL I. ANDERSON, Aberdeen, MARKUS POSCHMANN, Koblenz  
& CARSTEN BRAUCKMANN, Clausthal-Zellerfeld

With 9 figures

**Kurzfassung:** Die ursprünglich als Eurypteride beschriebene *Willwerathia laticeps* (STØRMER 1936) wird nunmehr als Angehörige der Synziphosurina erkannt und der Familie Weinberginidae RICHTER & RICHTER 1929 zugeordnet. Unter Berücksichtigung aller erhältlichen Daten läßt sich an neu aufgesammeltem, zumeist disartikuliertem Material von der Lokalität, aus der der verschollene Holotypus stammt, darauf schließen, daß das Opisthosoma von *Willwerathia* zehn Tergite umfaßte. Mit einer Carapax-Breite von etwa 90 mm war *Willwerathia laticeps* die größte bisher bekannte Synziphosurinen-Art. Das gemeinsame Vorkommen von Synziphosurinen und Eurypteriden bestätigt die Erkenntnisse über bereits früher beschriebene Taphozöosen.

**Abstract:** *Willwerathia laticeps* (STØRMER 1936) originally described as a eurypterid is reinterpreted as a synziphosurine belonging to Family Weinberginidae RICHTER & RICHTER 1929. Recently collected material from the locality, from which the destroyed holotype comes, suggests that *Willwerathia* possessed ten opisthosomal tergites, deduced from all available arrays of disarticulates. *Willwerathia* is the largest synziphosurine yet discovered with a carapace approximately 90 mm across. The occurrence of synziphosurines with eurypterids mirrors previously described preservational associations.

### Introduction

Synziphosurines are a loose grouping of chelicerate arthropods with a fossil record spanning the Lower Silurian to the Upper Devonian (ANDERSON 1996), reaching a peak of diversity during Upper Silurian times. The Upper Devonian synziphosurine *Kasibelinurus* PICKETT 1993 appeared in a recent classification of the Xiphosura as a sister taxon to the xiphosurids sensu ANDERSON & SELDEN (1997). Xiphosurids are represented by extant forms such as *Limulus*, *Tachypleus* and *Carcinoscorpius*. Although xiphosurids appear to be a relatively well-defined group united by the possession of a thoracetrone of fused opisthosomal segments, synziphosurines are more difficult to classify due to a lack of synapomorphies between taxa. In this paper, we describe fossil material from

Willwerath in Germany as being of synziphosurine, rather than the previously supposed eurypterid affinity. Recent collecting at the site has yielded new and informative specimens of *Willwerathia laticeps* (STØRMER 1936). These vastly improve our knowledge of this rare chelicerate and help to clarify its systematic position.

The Willwerath locality lies north of Prüm in the north-west Eifel Mountains (Rhineland-Palatinate, Germany). The quarry which yielded the first fossils is situated 1 km north of Hermespannd (Fig. 1). Willwerath is part of the Hontheimer Sattel between the "Schneifel-Mulde" and

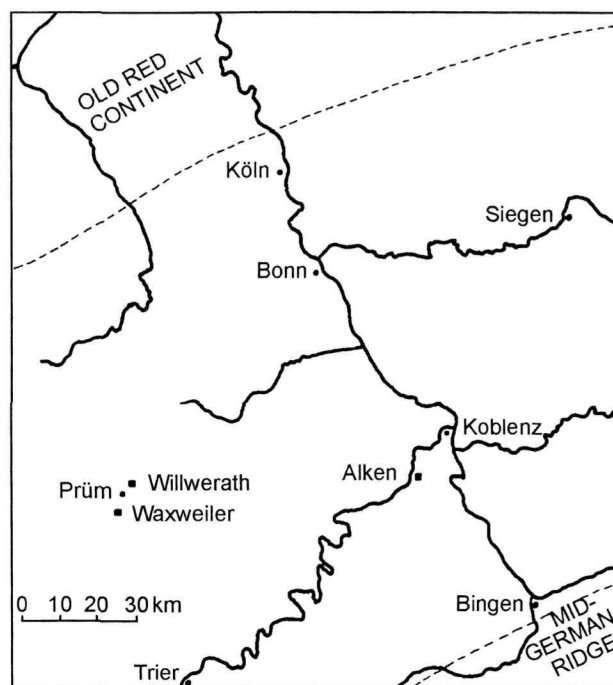


Fig. 1. General locality map showing the relative position of the Willwerath, Waxweiler and Alken sites (filled squares).

Addresses of the authors: LYALL I. ANDERSON, Department of Geology and Petroleum Geology, Meston Building, King's College, University of Aberdeen, AB24 3UE, Scotland; MARKUS POSCHMANN, Bussardweg 5, D-56075 Koblenz, Germany; CARSTEN BRAUCKMANN, Technische Universität Clausthal, Institut für Geologie und Paläontologie, Leibnizstraße 10, D-38678 Clausthal-Zellerfeld, Germany.

the “Prümer Mulde” (cf. WENTZCKE 1994). The sandstones of the Lower Devonian Klerf Beds (upper early Emsian) are sporadically worked for decorative stone in this area, whilst the fossiliferous mudstone and siltstones are deposited as spoil dump. The arthropod-bearing sequence has a thickness of about 150 cm, and is characterised by grey silty mudstones and muddy siltstones interbedded with fine sandstones.

The institutional and private collection abbreviations used in the text are as follows: AMNH (American Museum of Natural History, New York), D (M. POSCHMANN, Koblenz, private collection), PWL (Landessammlung für Naturkunde Rheinland-Pfalz, Mainz.), SLK (R. LEUNISSEN, Kreuzau, private collection), SMF (Forschungsinstitut und Naturmuseum Senckenberg, Germany), USNM (US National Museum, Smithsonian Institution, Washington DC), W (W. SIPPEL, Ennepetal, private collection).

### Palaeoecology of the Willwerath site

Willwerath is perhaps one of the most important Lower Devonian marginal marine fossil-bearing localities in the Rhenish Slate Mountains. Since the initial work of STØRMER (1936) the site has yielded exceptionally preserved arthropods, particularly eurypterids, of which five species have been described. Although volatiles (sensu ALLISON & BRIGGS 1991) have not been identified, refractory tissues such as the chitinous exoskeletons of arthropods are preserved in the minutest details. These include fine setae and pore canals identified in the integument of *Rhenopterus* (see STØRMER 1936). We therefore regard Willwerath as a Konservat-Fossilagerstätte as defined by SEILACHER (1970).

The fossil assemblage of Willwerath represents a mixture of marine, freshwater and terrestrial elements typical of a marginal marine setting (see MAPLES & SCHULTZE 1989). In this respect, it is comparable to other sites in the Lower Devonian of the Rhenish Slate Mountains, such as Alken an der Mosel (STØRMER 1976) and Waxweiler/Eifel (REBSKE et al. 1985). A terrestrial influence is indicated by the presence of the plants *Psilophyton burnotense*, *Sawdonia ornata*, *Drepanophycus spinaeformis* and *Zosterophyllum fertile* and a single arachnid of uncertain affinity (DUNLOP & POSCHMANN 1997). The presence of a small terrestrial arachnid closely parallels that identified by DUNLOP (1996) for the world's earliest terrestrial animal.

Ostracods (Leperditiida, *Rebskeella waxweilerensis*, *Poloniella* cf. *confluens*) are abundant, but show low species diversity. Along with the eurypterids, conchostracans and the highly abundant bivalve *Modiolopsis ekpempusa*, they indicate a brackish milieu, rich in oxygen. The bivalves are often preserved articulated, indicating autochthonous burial. The exceptional preservation of arthropods may be due to rapid burial by density flows originating from the delta front. Moreover, catastrophic burial has been suggested as distancing a carcass from scavengers and bioturbators (ALLISON & BRIGGS 1991).

Consequently, we classify Willwerath as an obrution deposit. BRETT (1990) suggested that the optimal areas for preservation of obrution deposits are relatively low energy environments slightly below normal storm wave base.

The palaeoecology of the agnathans and placoderms present at Willwerath is somewhat controversial. The relatively abundant arthrodire *Tiaraspis* was considered lacustrine by SCHÖLLMANN (1993: 37) whereas OTTO (1994: 80) suggested a marginal marine or fully marine environment for the vertebrates present in the Lower Devonian of the Rhenish Slate Mountains. Acanthodians and porolepiform crossopterygians are represented only by single, isolated skeletal elements and most likely represent allochthonous elements of the fauna. Remains of agnathans and arthrodiras are rarely partially articulated. One complete specimen of a pteraspid Waxweiler-form (sensu FRIMAN 1986) has also been found.

Fully marine invertebrates such as brachiopods and trilobites are unknown from this site further supporting the hypothesis that salinities were below normal marine levels. These observations fit well into a generalised picture of a marginal marine lagoon in a deltaic setting receiving influx of sediment in the form of density flows.

### Taphonomy of *Willwerathia*

The most interesting feature of the new material is that it demonstrates the unfused nature of the opisthosomal segments of synziphosurines. This has hitherto been suggested by ANDERSON (1996) and ANDERSON & SELDON (1997) but never conclusively proved. However, the pattern of disarticulation evident in specimen 471-D (Fig. 5a,b) lends considerable weight to this argument.

Eurypterid and *Willwerathia* fossils from the same bed show marked differences in their taphonomy and preservation. Firstly, the poor preservation of the integument in *Willwerathia* compared to that of eurypterids (see also BERGSTRÖM 1975). Most of the *Willwerathia* specimens are disarticulated and all lack traces of preserved appendages or any other part of the ventral anatomy. Conversely, the Willwerath eurypterids often preserve prosomal appendages. Secondly, eurypterid exoskeletons from Willwerath are extremely flattened due to sediment compaction (as they often are from other sites). *Willwerathia* on the other hand occurs as three-dimensionally preserved parts exhibiting their original convexity. Thirdly, brittle fracture of tergites is more often observed in *Willwerathia* than in the eurypterids.

How can these differences be explained? The majority of factors which determine flattening such as sediment grain size and timing of diagenesis affected both eurypterid and synziphosurine remains to the same extent. Thus the observed differences must be due to the different morphologies and mechanical strengths of the different cuticles.

The most obvious differences between the exoskeletons of xiphosurans and eurypterids is that in the

latter group, the opisthosomal appendages or 'book gills' are enclosed within a branchial chamber (see MANNING & DUNLOP 1995 for details). The opisthosomal chamber of xiphosurans is open. Consequently, upon death the ventral cavities of xiphosurans are more likely to be infilled by sediment than those of eurypterids. This results in a certain degree of resistance to compaction in xiphosurans and an extreme flattening in eurypterids, an effect compounded if the cuticle in question is a moult (Dr. N. H. TREWIN, University of Aberdeen, pers. comm.). Whether this causes the brittle fracture detailed above is open to question. Another difference between eurypterids and xiphosurans is that the prosomal appendages of eurypterids show modifications for a variety of functions such as paddles for swimming. In order to function properly, they are held outside the prosomal cavity. Xiphosuran appendages tend to be much simpler walking legs which occupy the prosomal cavity. Upon compression, these predominantly ventral structures can be seen lying outside the prosomal vault of eurypterids but are often hidden in xiphosurans.

An alternative but less plausible explanation is that the dorsal exoskeleton of *Willwerathia* was more reinforced by inorganic minerals such as calcium salts than that of the eurypterids. This would probably lead to an earlier decay of the non- or weakly mineralised intersegmental membranes and parts of the ventral anatomy, increasing the vulnerability to disarticulation prior to burial. After compaction and early diagenesis of the host sediment, the calcium salts were gradually dissolved and the refractory tissues were preserved as thin films of altered organic residues. However, mineralisation of the exoskeleton is unknown in any other xiphosuran, and as such, its presence here is speculative.

### Establishing opisthosomal tergite count in *Willwerathia*

Opisthosomal tergite count has found favour amongst previous workers (see ELDREDGE 1974; SELDEN & DRYGANT 1987 and ANDERSON & SELDEN 1997) in attempting to establish the relationships between different synziphosurines. It is a preservable and, for the most part, reliable morphological characteristic of the fossil. Therefore, to fit *Willwerathia* into the presently accepted scheme, it is vital to establish the total opisthosomal tergite count.

Unfortunately, the task is hindered by a lack of fully articulated specimens of *Willwerathia*. This is a result of the turbulent conditions which disarticulated and scattered the exoskeletons at the site of deposition. The specimen found to date which is closest to full articulation is in the private collection of Mr W. SIPPEL (Ennepetal). This specimen (W. 2297, Fig. 8) indicates nine opisthosomal tergites plus a tail spine. However, a noticeable gap exists between the third visible and fourth visible tergites. There is reason to believe that this is not the total count.

In the neotype, the tail spine along with three post-abdominal tergites are preserved (Fig. 3a-d). The angle at which the lateral epimera are projected out from the ninth tergite, relative to the axis of the tergite (Fig. 3d) is 40°. In 466-Db (Fig. 5), the most anterior of the two postabdominal tergites preserved also has epimera angled at 40°. The tergite posterior to this has epimera angled at 30°. Consequently, we believe that this is the tenth and final tergite in the opisthosoma of *Willwerathia*. As both specimens come from the same bed and have experienced the same degree of compression, it seems likely that this angle has not been affected by compression but actually reflects the original disposition of lateral epimera on these two tergites. In addition, there is no evidence of tectonic stretching of the rocks which contain these fossils.

### Phylogenetic position of *Willwerathia*

Synziphosurines represent a paraphyletic grouping of xiphosurans united by their shared possession of freely articulating opisthosomal tergites (a primitive character). So where in this group of organisms does *Willwerathia* fit? To answer this question, valid synapomorphies must be discovered between *Willwerathia* and other synziphosurines. Five possibilities are considered: the opisthosomal tergite count, the morphology of opisthosomal tergite one, the state of the second opisthosomal tergite, the width of the axial portion of the tergite relative to the lateral portion (see ANDERSON & SELDEN 1997) and the detailed morphology of the carapace (prosomal shield).

ANDERSON & SELDEN (1997) proposed *Legrandella* and *Weinbergina* as having eleven tergites in line with the views of ELDREDGE (1974), *Bunodes*, *Limuloides*, *Pasternakevia*, *Cyamocephalus* and *Pseudoniscus* as having ten (see ELDREDGE & PLOTNICK 1974) and *Kasibelinurus* as having only nine (in common with all xiphosurids). However, STÜRMEER & BERGSTRÖM (1981) reported only ten visible opisthosomal segments in *Weinbergina*. Re-examination of the X-ray photographs of *Weinbergina* in the light of investigation of the morphology of *Willwerathia* strongly suggests that STÜRMEER & BERGSTRÖM (1981) were in fact correct.

The characteristic morphology of opisthosomal tergite one observed in *Willwerathia* is shared by *Legrandella*, *Weinbergina*, *Limuloides*, *Bunodes*, *Cyamocephalus* and *Pseudoniscus*. *Kasibelinurus* has a much reduced opisthosomal tergite one in common with xiphosurids, whilst the character state in *Pasternakevia* is unknown (SELDEN & DRYGANT 1987). ELDREDGE (1974) suggested that opisthosomal tergite one was not visible in *Weinbergina*, as it was hidden below the posterior margin of the carapace, in an analogous manner to that seen in some xiphosurids. This prompted him to identify *Weinbergina* as having eleven opisthosomal tergites, the ten he could identify and a possible hidden one. We now believe that this interpretation is in fact incorrect. The first opisthosomal tergite in all of the above named forms is only

slightly narrower sagittally than the preceding second opisthosomal tergite, but this is a sufficient difference to enable its positive identification.

*Bunodes*, *Pasternakevia* and *Limuloides* all possess a second opisthosomal tergite modified by hypertrophy which is much larger than the first and third. *Willwerathia*, *Pseudoniscus*, *Weinbergina* and *Cyamocephalus* do not show this modification. *Cyamocephalus* possesses the autapomorphy of having the sixth and seventh opisthosomal tergites fused together (ELDRIDGE & PLOTNICK 1974; ANDERSON 1996). This character is not expressed in *Willwerathia*.

The axial region of the tergites of *Willwerathia* is much wider than the lateral regions. This configuration is recognised in *Bunodes*, *Limuloides* and *Weinbergina*. In *Pseudoniscus*, the axial region is much smaller than the adjoining lateral regions.

The detailed morphology of the carapace of *Willwerathia* consists of a distinctive arrangement of dorsal spine tubercles and a pair of postero-lateral carapace spines which is highly reminiscent of a form described by WOODWARD (1872: pl. 10, fig. 6) as *Hemiaspis limuloides* WOODWARD 1865. ANDERSON (1996) re-examined this material and concluded that the correct nomenclature for this species should be *Limuloides limuloides* WOODWARD 1865 on the following grounds. STÖRMER (1952) stated that the name *Hemiaspis* used by WOODWARD (1865) was preoccupied referencing a publication authored by NEAVE in 1940. However, the volume of Nomenclator Zoologicus dealing with the names *Hemiaspis* and *Limuloides* was published a year earlier (NEAVE 1939) than the date given by STÖRMER (1952). NEAVE (1939: 602) listed the name *Hemiaspis* as being used first by FITZINGER in 1861 for a genus of trilobite. Therefore, *Hemiaspis* WOODWARD 1865 falls, as it is a junior homonym. NEAVE (1939: 950) then continued by stating that *Limuloides*, which as published by SALTER (1857) was a nomen nudum, had been validated by WOODWARD (1865). For this reason, the name *Limuloides* should be attributed to WOODWARD (1865) rather than, as STÖRMER (1952) and ELDRIDGE (1974) stated SALTER in WOODWARD (1865). A distinctive autapomorphy of *Limuloides limuloides* WOODWARD (1865) is that the entire margin of the carapace is serrated with small outwardly facing spines. This serves to differentiate it from *Bunodes* and *Willwerathia*.

From the above discussion, we conclude that *Willwerathia* is not closely related to the taxa *Pseudoniscus*, *Cyamocephalus* or *Kasibelinurus*. The greatest similarities lie with the taxa *Bunodes* and *Limuloides* in terms of carapace morphology but *Weinbergina* in terms of overall body plan. However, *Bunodes* and *Limuloides* exhibit characters in an advanced state (e.g. hypertrophy of the second opisthosomal segment) in respect to the state observed in *Willwerathia*. Thus *Willwerathia*, although appearing stratigraphically later than these common Upper Silurian forms possesses a less derived body plan akin to that seen in *Weinbergina*, another Lower Devonian synzi-

phosurine. The lack of postero-lateral carapace spines and well-developed dorsal tubercles in *Weinbergina* serve to differentiate it from *Willwerathia*. Had *Weinbergina* possessed postero-lateral carapace spines, it is likely that they would have shown up in the X-ray photographs of STÖRMER & BERGSTRÖM (1981).

A consequence of this work is that the opisthosomal tergite count of *Legrandella* requires verification, either to remove it from Weinberginidae as a separate taxon or to rediagnose it to concur with the diagnosis of Family Weinberginidae in which it at present sits. This study recognises the need for further work on these problematic relationships between early synziphosurines.

## Systematic Palaeontology

Phylum Chelicerata HEYMONS 1901

Class Xiphosura LATREILLE 1802

Family Weinberginidae RICHTER & RICHTER 1929

Type genus: *Weinbergina* RICHTER & RICHTER 1929.

Diagnosis: Xiphosura with ten freely articulating opisthosomal tergites (seven pre-abdominal and three post-abdominal), the first tergite biconvex in shape, reduced slightly in size and with sharp outward facing lateral spines. Second tergite exhibits no modification by hypertrophy. Sixth and seventh segments freely articulating. The pre- and postabdominal division is slight. Prominent axial and lateral tergite spine nodes present on the first seven opisthosomal segments of the preabdomen, but lacking on the postabdomen.

Genus *Weinbergina* RICHTER & RICHTER 1929

Type species: *Weinbergina opitzi* RICHTER & RICHTER 1929; Lower Devonian (Emsian or Pragian) of Bundenbach, Germany. By original designation.

Diagnosis: Weinberginidae lacking postero-lateral carapace spines and spine-bearing tubercles on the lateral fields of the carapace.

*Weinbergina opitzi* RICHTER & RICHTER 1929

1929 *Weinbergina opitzi* n. sp. – RICHTER & RICHTER: 193-209, figs. 1-3.

1955 *Weinbergina opitzi* RICHTER & RICHTER – STÖRMER: fig. 11 (9), 15A.

1974 *Weinbergina opitzi* RICHTER & RICHTER – ELDRIDGE: 16, fig. 5, p. 38.

1981 *Weinbergina opitzi* RICHTER & RICHTER – STÖRMER & BERGSTRÖM: 237-255, figs. 2-7.

1984 *Weinbergina opitzi* RICHTER & RICHTER – FISHER: 199, fig. 2.

1987 *Weinbergina opitzi* RICHTER & RICHTER – SELDEN & SIVETER: 387.

1993 *Weinbergina opitzi* RICHTER & RICHTER – SELDEN: 299.

Type material: The holotype is SMF VIII 7a in the collections of the Forschungsinstitut und Naturmuseum Sencken-

berg, Germany. It consists of a complete specimen, viewed in dorsal and slightly lateral aspect.

Type stratum and locality: Lower Devonian (Emsian or Pragian), Hunsrückschiefer, Bundenbach, Germany (stratigraphic information from SELDEN 1993: 299).

Additional material: STÜRMEER & BERGSTRÖM (1981) noted that the prefix WS in their manuscript referred to radiographs in the archive of W. STÜRMEER rather than to actual museum numbers. They did, however, list the institutions from which they had borrowed specimens. WS 870 was previously unfigured and came from the Palaeontological Institute, University of Zurich. WS 10434 belonged to the Palaeontological Institute, University of Bonn, but STÜRMEER & BERGSTRÖM (1981) gave no museum number for this specimen.

#### Genus *Willwerathia* STØRMEER 1969

Type and only species: *Tarsopterus laticeps* STØRMEER 1936.

Diagnosis: Weinberginidae with a carapace possessing three pairs of spine bearing tubercles and a pair of postero-laterally directed carapace spines. Dense cuticular sculpture covers the entire dorsal surface.

Discussion: TOLLERTON (1989) placed *Willwerathia* along with a number of other suspected and/or poorly preserved eurypterids in Eurypterida incertae sedis. However, we recognise the synziphosurine nature of this fossil and remove it from the Eurypterida.

#### *Willwerathia laticeps* (STØRMEER 1936)

Figs. 2-9

- 1936 *Tarsopterus laticeps* – STØRMEER: 59, tab. 8, fig. 1.  
 1951 *Tarsopterella* nom. nov. (STØRMEER) – STØRMEER: 42.  
 1969 *Willwerathia laticeps* (STØRMEER) – STØRMEER: 26.  
 1989 *Willwerathia laticeps* (STØRMEER) – TOLLERTON: 655.

Type material: The holotype (see Fig. 2) was designated as No. 49 in the Geologisches Landesmuseum, Berlin by STØRMEER (1936). However, searching of the collections by one of us (MP) suggests that this specimen is no longer in existence. This was confirmed by Dr HELMS (Museum für Naturkunde der Humboldt-Universität, Berlin) and Dr LINDERT (Bundesanstalt für Geowissenschaften und Rohstoffe Hannover, Außenstelle Berlin) (pers. comms.). Without a type specimen for *Willwerathia*, any future work would be severely hindered. As our new specimens come from the same locality and horizon as the destroyed holotype, we feel justified in raising a neotype specimen for *Willwerathia laticeps*. The neotype is designated PWL 1997/2-LS in the Landessammlung für Naturkunde Rheinland-Pfalz, Mainz (Fig. 3).

Type horizon and locality: Willwerath, north of Prüm in the north-west Eifel Mountains, Lower Devonian Klerf Beds (upper Lower Emsian), Rhineland-Palatinate, Germany.

Additional material: SLK 1a-1b (part and counterpart) (Fig. 4a) and SLK 2 (Fig. 4b) (private collection of R. LEUNISSEN); 419-Db, 471-D, 472-D and 473-D (private collection of M. POSCHMANN); W 2241, W 2247, W 2297 and W 2298 (private collection of W. SIPPPEL).

Diagnosis: As for the genus.

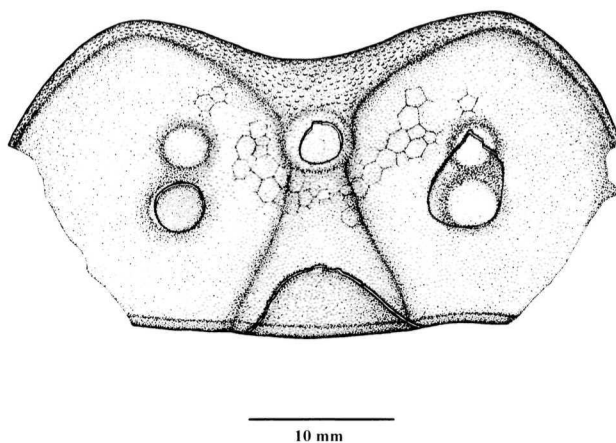
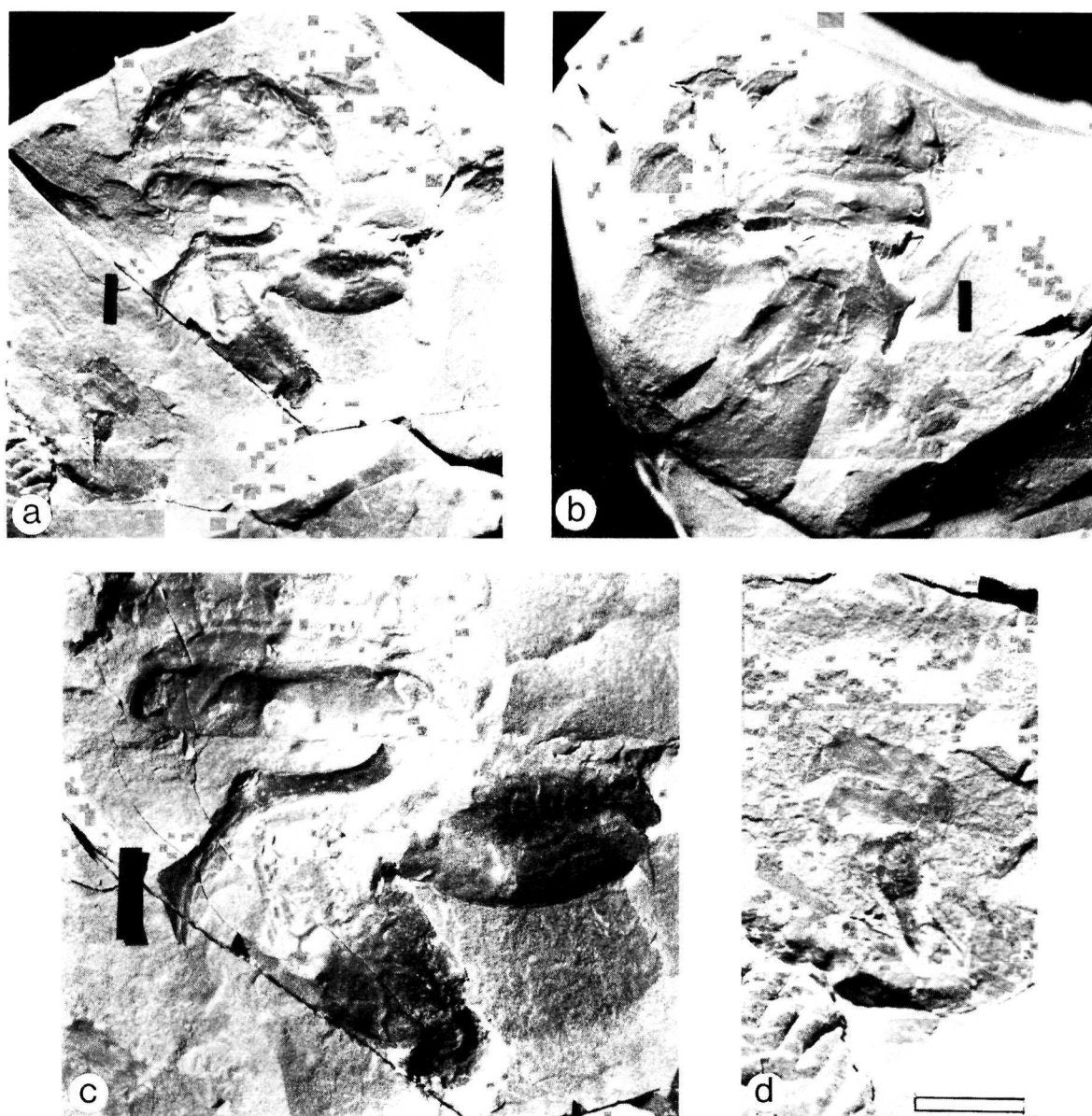


Fig. 2. *Willwerathia laticeps* (STØRMEER 1936). – Drawing of the destroyed holotype, specimen No. 49 previously housed in the Geologisches Landesmuseum, Berlin (after STØRMEER 1936).

Description of the neotype: Specimen PWL 1997/2-LS (Fig. 3a-d) is a relatively disarticulated exoskeleton comprised of the carapace (which is angled slightly down into the sediment and as a result, appears shorter than it would otherwise be), the reduced first opisthosomal segment, the second segment, three further segments displaced off to the right hand side and the postabdomen of three narrow opisthosomal segments followed by the tail spine. The three postabdominal segments are short (sag.) and decrease in width markedly between the eighth and tenth segment. The tail spine is wide-based and tapers rapidly. It is identical in morphology to many other synziphosurine tail spines cf. *Pasternakevia* SELDEN & DRYGANT 1987. All of the postabdominal tergites possess marked backward pointing lateral epimera.

Description of additional material: Specimen 471-D (Fig. 5b) consists of a bedding plane assemblage of nine disarticulated tergites. Considering the rarity of material assignable to *Willwerathia*, it is certain that all of these tergites belong to the same animal. The camera lucida drawing of this specimen (Fig. 5b) attempts to identify the opisthosomal tergites present in this assemblage. The other tergites can be roughly matched on account of their size to the preabdominal section. This is a vital observation as it suggests that the total opisthosomal segment count for *Willwerathia* is ten (seven pre-abdominal segments and the three postabdominal segments observed in specimen 466-Db). The anterior margin of some of the tergites which are preserved in an advantageous position relative to the bedding surface exhibit the presence of an anteriorly positioned ridge, presumably an articular surface.

Specimen 472-D is comprised of three articulated pre-abdominal tergites with a combined axial length of 55 mm (Fig. 4d). The most anterior tergite (identified from the position of the backward facing lateral epimera on the following tergites) is the largest of the series of three with a width of 58 mm. Interestingly, there appears to be an

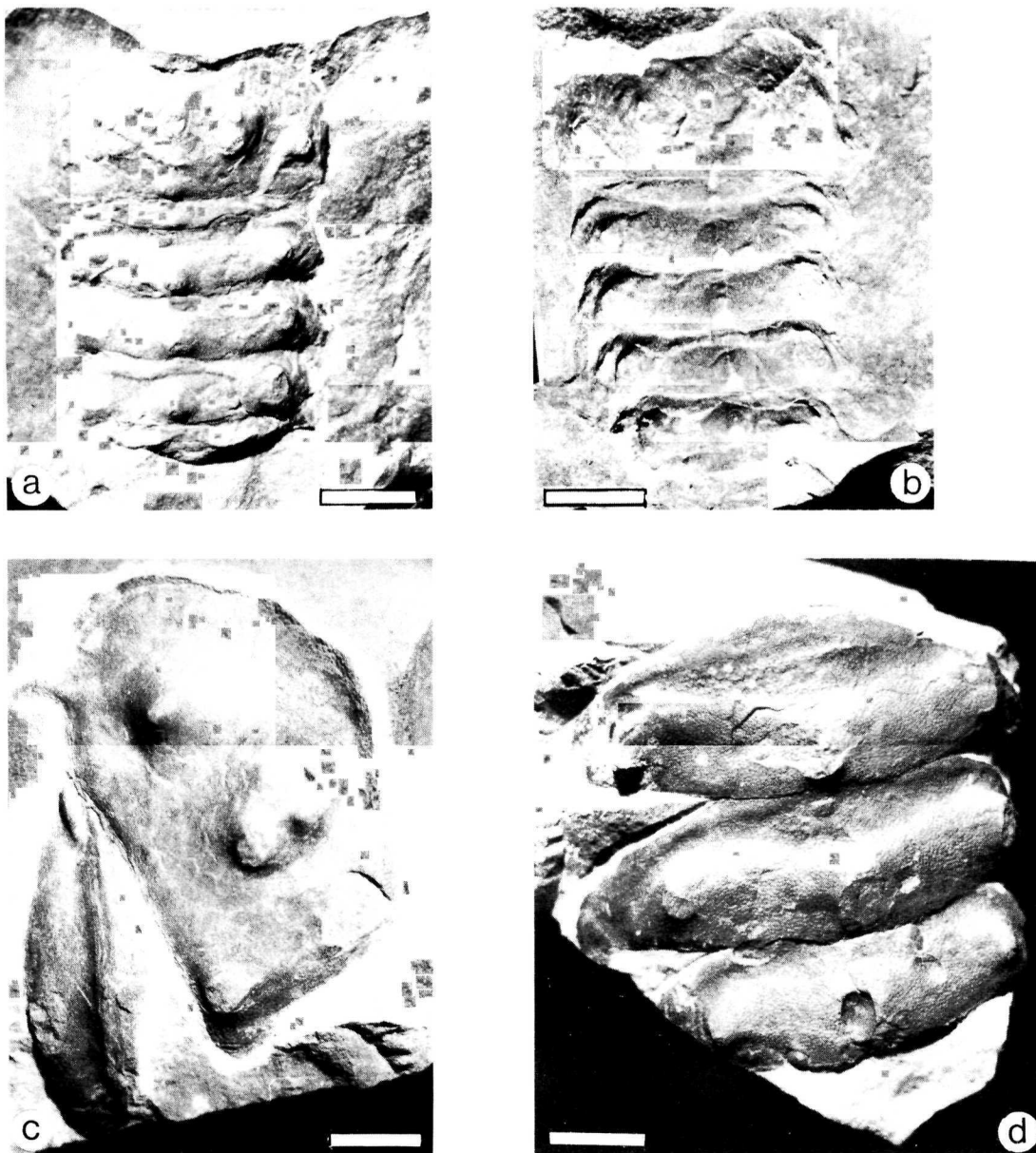


**Fig. 3.** *Willwerathia laticeps* (STØRMER 1936), neotype (PWL 1997/2 LS). – **a:** part. **b:** counterpart. **c:** close up of opisthosomal segment 23 with well-developed postero-lateral epimera. **d:** postabdominal region consisting of three opisthosomal tergites with posteriorly directed lateral epimera and a dart-shaped tail spine. – All scale bars: 10 mm.

impression of a leperditiid ostracod preserved approximately in the midline of the most posterior tergite in this series. The deep indentation of the ostracod (which was presumably calcified) suggests that upon compression, the cuticular exoskeleton of *Willwerathia* was relatively pliable. Once again, it is noted that the size of these fragments is overall much larger than that seen in many other synziphosurines. This may have been a contributory factor which influenced STØRMER (1936) to describe the original material as an eurypterid. The lateral spine nodes are well marked in this specimen but as with the other specimens, the tops are broken off. Slight nodes are also present on the axis of the tergites, displaced slightly to the posterior of each tergite. All three tergites exhibit the distinctive cuticular sculpture of *Willwerathia*.

Specimen 473-D (unfigured) is the smallest hitherto known specimen of *Willwerathia* with a total body length (including the tail spine) of 32 mm. This specimen is preserved along with an undetermined arthrodire plate, the bivalve *Modiolopsis* and the ostracodes *Hermannia* and *Poloniella*. Again, it is not possible to give a certain total tergite count as the region between the sixth (T6) and seventh (T7) visible segments is damaged. The opisthosomal tergites of this specimen possess prominent lateral epimera which are apparently relatively longer than in the larger individuals.

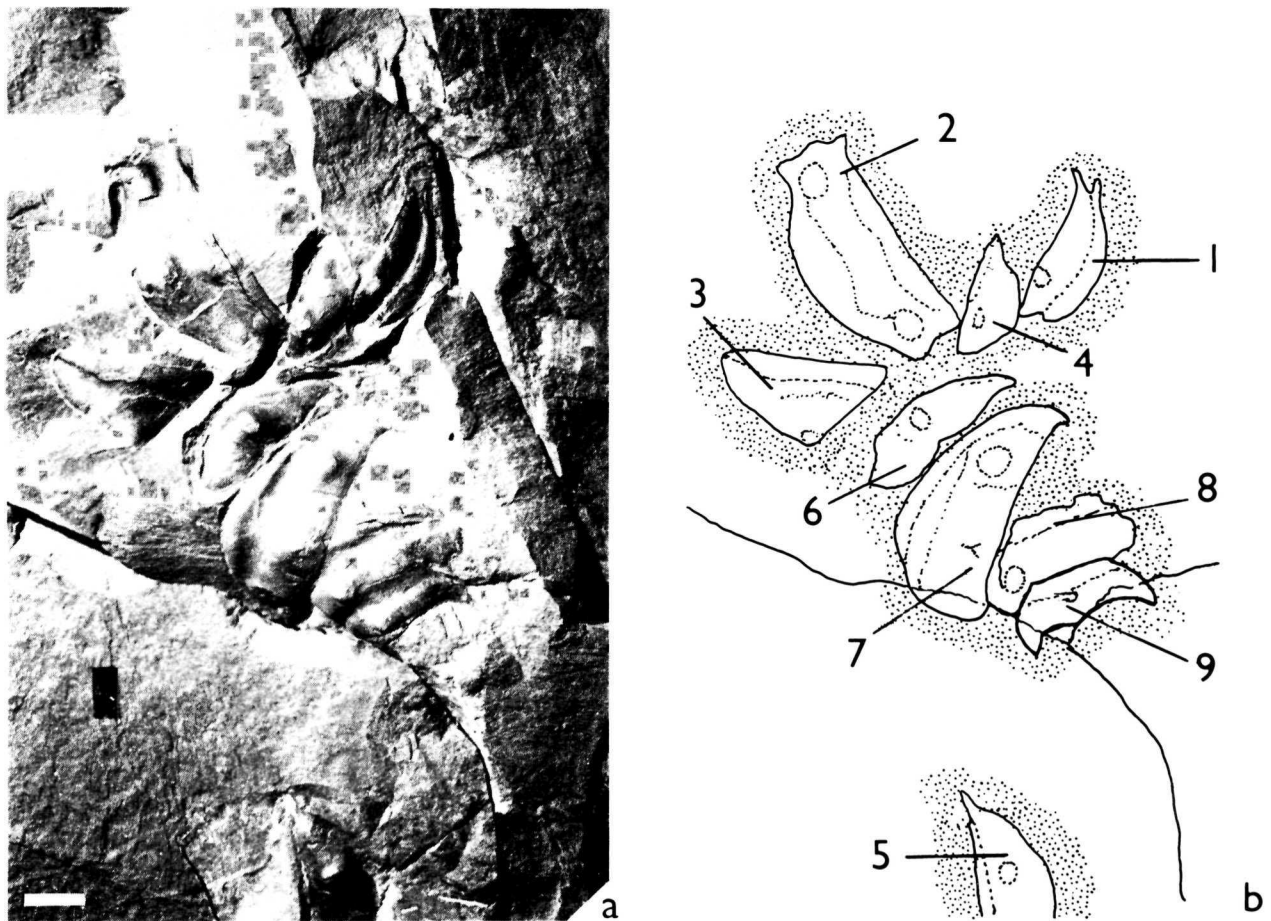
Specimen SLK 1a (Fig. 4a) consists of a well preserved carapace, with much of the dorsal topography apparent, followed by a small, reduced first opisthosomal segment (T1) and three equally size preabdominal segments (T2-



**Fig. 4.** *Willwerathia laticeps* (STØRMER 1936). – **a:** specimen SLK 1a (collection R. LEUNISSEN) showing the carapace, the reduced first opisthosomal segment and three full preabdominal opisthosomal segments. **b:** specimen SLK 1b (= counterpart to SLK 1a). **c:** specimen 419-D (collection M. POSCHMANN) showing a carapace with a well preserved postero-lateral carapace spine and reduced first opisthosomal segment. **d:** specimen 472-D (collection M. POSCHMANN) consisting of three preabdominal opisthosomal segments, the second of which bears the impression of an ostracod test. – All scale bars: 10 mm.

T4). The apparently concave anterior margin of the carapace is in fact the raised and tuberculate ophthalmic ridge. The true anterior carapace margin lies hidden below a small ridge of sediment. The ophthalmic ridges swing round and meet at the approximately two-thirds the way up its axial length. At the exact position at which they meet, a small rounded tubercle is positioned. A pair of slightly swollen ridges either side of the midline marks the position of the median dorsal ocelli in this specimen. Directly back from the median tubercle on the posterior margin of the carapace is another small spine bearing tubercle. This is analogous with similar structures seen in

Recent *Limulus* and other fossil xiphosurans such as *Bellinurus* and *Euproops*. Specimen SLK 1a is approximately 39 mm in length and possesses a rather unusual sculpture on the dorsal cuticular surface of the carapace. A series of polygonal raised areas cover the whole surface. The actual sculpture of the carapace consists of extremely small rounded tubercles. The ophthalmic ridges are also covered in tubercles. However, in this region, the tubercles are slightly larger and elliptical in outline, with the long axis of the ellipses running parallel with the lateral margins of the ophthalmic ridges. The cardiac lobe is well-marked and possesses an axially positioned spine



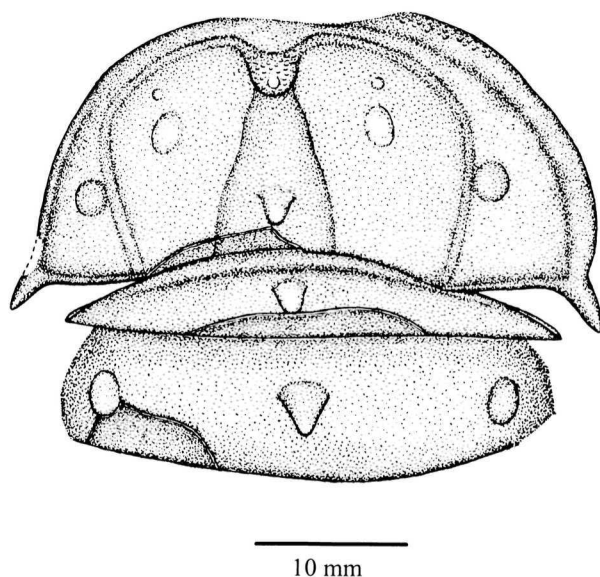
**Fig. 5.** *Willwerathia laticeps* (STÖRMER 1936). – **a:** specimen 471-D (collection M. POSCHMANN) showing the disarticulated array of opisthosomal segments. **b:** Camera lucida drawing of the same specimen with opisthosomal segments 1-9 identified. – Scale bar: 10 mm.

boss at its posterior intersection with the posterior carapace margin. The first opisthosomal segment is reduced in width relative to the following ones. It possesses a pair of lateral spines. The following three opisthosomal tergites are approximately the same size but narrow slightly in the posterior direction. A fifth opisthosomal segment is hinted at by the presence of a sharp ridge of cuticle directly posterior to the last opisthosomal segment. This segment is probably articulated with segment three, but is angled down into the sediment. Further segments may still be hidden and would only become visible upon excavation of this area.

SLK 1b (Fig. 4b) is the counterpart or negative to SLK 1a. It consists of a well preserved carapace, a reduced first opisthosomal segment and four complete and articulated preabdominal segments which taper very slightly towards the posterior of the animal. The total length of the preserved animal is approximately 45 mm. The anterior and left-hand antero-lateral margins of the carapace are broken away and cannot be seen. The position and morphology of the ophthalmic ridges and the cardiac lobe in this form are well marked in this specimen. The cardiac lobe is broadly triangular and tapers anteriorly. On the

posterior margin of the carapace, the cardiac lobe is 10 mm wide. At the anterior end of the cardiac lobe is a small node on which the median dorsal ocelli were positioned. The ophthalmic ridges are made distinct from the rest of the carapace by their slightly elevated topography and their slightly coarser cuticular sculpture. The ophthalmic ridges expand out from the ocellar node anteriorly and slightly laterally before swinging round to run towards the posterior margin of the carapace. The ophthalmic ridges intersect a small node on their lateral courses approximately two-thirds the way down the length of the carapace. These nodes positioned equidistant from the axis of the carapace probably mark the position of the lateral compound eyes. As in SLK 1A, the opisthosomal segments taper slightly towards the posterior. At the posterior margin of the fifth segment is the fractured anterior edge of the sixth pre-abdominal segment. The second opisthosomal segment is characterised by the presence of a concave anterior margin. The first opisthosomal segment is biconcave in shape and fits the concavity of the anterior margin of the second segment. Again, all opisthosomal segments possess an axially positioned spine and a pair of lateral spine bosses. The lat-



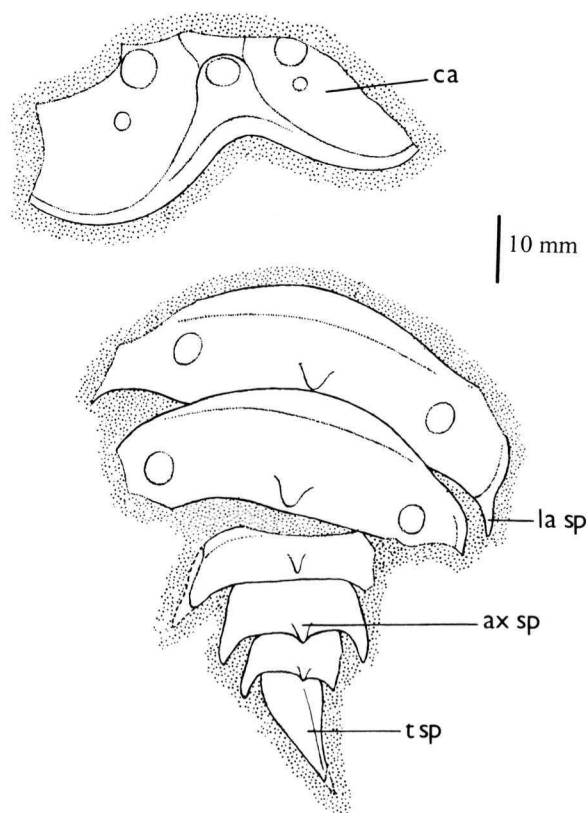


**Fig. 6.** *Willwerathia laticeps* (STØRMER 1936), drawing of specimen W 2411 (collection W. SIPPEL) well demonstrating the postero-lateral spines and the reduced first opisthosomal segment.

eral epimera of the segments following the reduced first segment are all posterior and slightly outward-facing and terminate in a sharp spine.

Specimen SLK 2 (unfigured) consists of an isolated carapace approximately 45 mm across. The left-hand lateral margin of the carapace dips into the sediment. The spine bearing tubercles of the carapace surface are well preserved in this specimen.

Specimen 419-Db (Fig. 4c) consists of a portion of a disarticulated carapace with a prominent postero-lateral spine produced from the left-hand lateral margin. The carapace is approximately 50 mm across and 30 mm long axially. A prominent spine boss is present in the left hand corner of the carapace, around which the ophthalmic ridge runs. The postero-lateral spine appears to be a continuation of the ophthalmic ridge in this specimen, and as such, may be considered to be an ophthalmic spine, although not in the same sense as in members of suborder Bellinurina (see ANDERSON & SELDEN 1997). In addition, lying posterior to, and slightly displaced to the left of the carapace is a well preserved first opisthosomal segment 40 mm wide and 13 mm long axially. This is the clearest view of opisthosomal segment one afforded by any of the material. The anterior articulating surface is well marked and is subdivided from the rest of the segment by a transverse ridge. At the left hand lateral margin of the transverse ridge is a small, outwardly facing spine. As only a little more of the width of the carapace is preserved (the whole of the cardiac lobe is present along with a small patch of cuticle on the right hand side of it), the entire width of the carapace must have been in the order of 95 mm across. This is by far the largest synziphosurine ever recorded. In fact, it outmatches many other occurrences

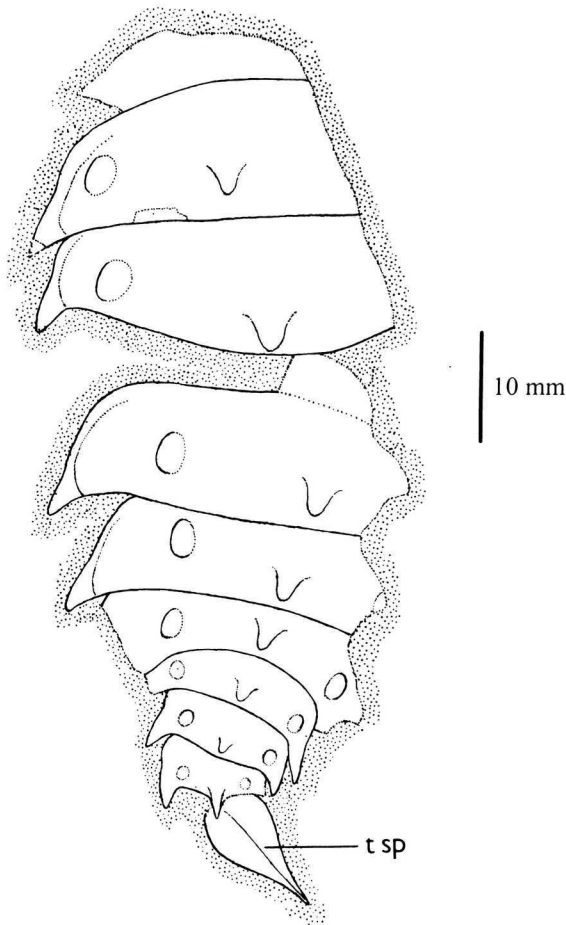


**Fig. 7.** *Willwerathia laticeps* (STØRMER 1936), camera lucida drawing of specimen W 2298 (collection W. SIPPEL) with prominent lateral (la sp) and axial spines (ax sp) on the opisthosomal segments. – ca = carapace; t sp = tail spine.

of fossil xiphosurans until the advent of the modern *Limulina* typified by *Xaniopyramis* SIVETER & SELDEN 1987.

Specimen W 2411 (Fig. 6) consists of a nearly complete carapace 36 mm wide, the distinctly reduced first opisthosomal tergite and the second opisthosomal tergite. The morphology and sculpture of the carapace is very similar to the neotype and even exhibits the postero-lateral carapace spines. The region lying outside the ophthalmic ridges (the extra-ophthalmic region) distinctly slopes down to the slightly raised border. The ophthalmic ridges and cardiac lobe are less distinctly marked than in other specimens but the tongue-shaped, granulated median sinus with the small rounded tubercle is clearly preserved. The first opisthosomal tergite (T1) is reduced in width and length in relation to the following one and laterally stretched out into a pair of spines. The morphology and sculpture of the second tergite (T2) is identical to that observed in the other specimens.

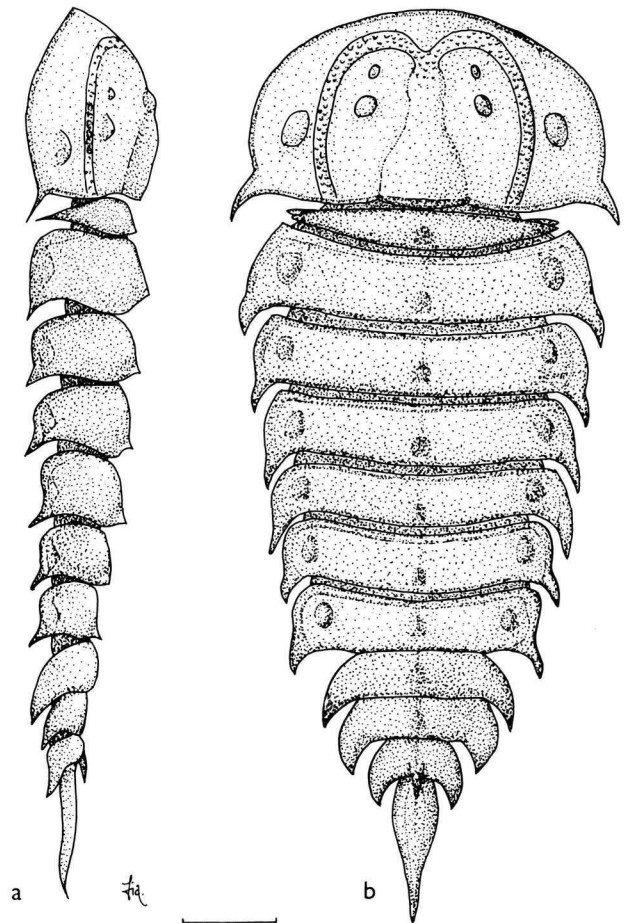
Specimen W 2298 (Fig. 7) is a disarticulated, fragmentary carapace and the posterior parts of the opisthosoma consisting of two preabdominal and three postabdominal tergites plus the anterior half of the tail spine. In comparison to the opisthosomal fragment, the carapace is inverted, with the anterior portion directed backwards. As



**Fig. 8.** *Willwerathia laticeps* (STØRMER 1936), camera lucida drawing of specimen W 2297 (collection W. SIPPEL) showing dart shaped tail spine (t sp) and prominent axial spine on the most posterior opisthosomal segment.

in the lost holotype and in specimen SLK 1A (see above), the true anterior margin is covered by a thin layer of sediment. The apparently concave border is in fact the raised and distinctly granulated ophthalmic ridge which is narrow laterally, but strongly broadened sagittally, forming a tongue-shaped median sinus including a small, rounded tubercle. At each side the ophthalmic ridges surround an area with two tubercles, a larger one close to the centre, and a smaller one in front of it. The opisthosomal fragment is partially disarticulated, two articulating preabdominal tergites and the three postabdominal tergites are separated by a noticeable gap. Due to the different size of both areas, there seems to be at least one or two tergites lacking between them. The shape and sculpture of both tergites and tail spine are similar to that described for W 2297. The total length of the fossil is about 113 mm.

Specimen W 2297 (Fig. 8) is one of the most complete specimens of this species. It indicates the presence of at least nine opisthosomal segments and a tail spine. There is a gap between the fourth and fifth visible tergites. It is not clear whether this is due to disarticulation or, what seems less likely, a tergite is lacking. Though the right margins of the anterior three preserved tergite are broken



**Fig. 9.** *Willwerathia laticeps* (STØRMER 1936), morphological reconstruction. – **a:** lateral view. **b:** dorso-ventral view. – Scale bar: 10 mm.

away, it can clearly be seen that the first visible opisthosomal tergite is approximately as broad as the following ones and thus cannot be the reduced first tergite (T1) but more likely the second one (T2). The posterior region of this tergite is largely missing whereas the anterior margin is preserved over the left half showing a rounded, articulating process and marginal wrinkled sculpture. The anterior three tergites (T2-T4 of our interpretation) are only very slightly tapering towards the posterior part, the next three tergites (T5-T7) a little bit stronger, whereas the posterior three (postabdominal) tergites (T8-T10) seem to taper more slightly again. Therefore the lateral margins of the whole opisthosoma are slightly bent sigmoidally in general. The posterior tergite (T10) laterally encloses the anterior portion of the tail spine which is dart-shaped in dorsal view with a sharp posterior tip and a median keel. Each tergite has a backwardly pointing median spine close to the posterior margin and, except for the three postabdominal tergites (T8-T10), two lateral tubercles placed exsagittally in about mid length. The length of the whole fossil is about 85 mm.

A morphological reconstruction of *Willwerathia laticeps* (STØRMER 1936) based on this material is presented

(Fig. 9). Differences in the length of tail spine between various specimens of *Willwerathia* may be due to sexual dimorphism, but equally, intraspecific variation in tail spine length in extant *Limulus* is quite marked.

## Discussion

The above descriptions denote the characteristics by which *Willwerathia* may be recognised amongst the Xiphosura. However, there are two other fossil organisms which *Willwerathia* might be confused with, particularly when the remains are disarticulated and incomplete. Both groups are found in strata of Lower Devonian age, in common with *Willwerathia*. The first of these is *Strigoproavus gruenenschladensis* described by SCHÖLLMANN (1983: 93, fig. 2).

Two of the authors (MP & LIA) has had the opportunity to restudy the material of SCHÖLLMANN (1983) as well as some newly collected material from the same site and the following differences are noted. Firstly, the exoskeleton of *Strigoproavus* is preserved as a thick dark coloured substance which was probably mineralised in life. This stands in marked contrast to the preservation of *Willwerathia* and synziphosurines in general. Secondly, the smallest specimen of *Willwerathia* is approximately 32 mm long. This is similar to a large *Strigoproavus*. Finally, the most striking difference between the two taxa is in the postabdominal region. In *Strigoproavus*, there are at least six segments and no elongate tail spine.

A second, recently described fossil organism bears more than a passing resemblance to *Willwerathia*. This is *Lophodesmus mirabilis* described by TESAKOV & ALEKSEEV (1992) from the Lower Devonian (? Emsian) of Bayan-Aul, Pavlodor region, Kazakhstan. TESAKOV & ALEKSEEV (1992) classified this organism as "Arthropoda Incertae sedis" but leaned towards a myriapod identity for it (the name *Lophodesmus* is preoccupied by an extant genus of millipede (Prof. W. SHEAR, Hampden-Sydney College Virginia, pers. comm.). We have been unable to study the type material at first hand, and thus base our comments on the figures given by TESAKOV & ALEKSEEV (1992). The superficial resemblance of the tergites is marked, down to the paired, sharp lateral epimera. There is even evidence that towards the anterior of each segment is an articulating surface similar to that in *Willwerathia*. However, we choose not to incorporate this material within *Willwerathia* due to the presence of a terminal segment with a fused median spine. Only discovery of better preserved and fully articulated specimens (including carapaces) will allow further comparisons to be made and any relationship between *Lophodesmus mirabilis* and *Willwerathia laticeps* to be considered.

## Palaeoecology of *Willwerathia*

The discovery of a synziphosurine in a depositional setting such as that indicated by the strata at Willwerath is not unusual. As ANDERSON (1996) discussed, the habitat

of synziphosurines appears to have been in close proximity to the depositional setting most likely to provide the conditions required to preserve their unmineralised exoskeletons. Evidence of interaction between *Willwerathia* and other faunal elements is scant. However, extant *Limulus* uses its leg gnathobases to grind up bivalves and perhaps *Willwerathia* exhibited similar feeding strategies. Synziphosurines such as *Kasibelinurus* have been shown to have interacted with the sedimentary substrate producing distinctive trace fossils (BABCOCK et al. 1995), but as yet, these have not been found at Willwerath.

The marked articulation surfaces present on each of the preabdominal segments suggests that *Willwerathia* could enrol in a sphaeroidal manner in much the same way as is evidenced by the holotype specimen of *Legrandella* (AMNH 29273) and a specimen of *Kasibelinurus* (USNM 484524) from the Upper Devonian of Pennsylvania, USA. Such flexibility of the opisthosomal segments may have been advantageous to the organism by allowing loose enrolment in response to predation, or, as an aid to excavating a shallow burrow. As BERGSTRÖM (1975) pointed out, the strong arching of the body in xiphosurans was probably a product of the need to accommodate the ventral appendages whilst the animal was in an enrolled state.

The highly vaulted carapace and convex tergites of *Willwerathia*, particularly in the anterior region of the opisthosoma do not point to a streamlined animal suited to a nektonic mode of life as has been proposed for some eurypterids. It is therefore most likely that *Willwerathia* led a bottom-dwelling, partly shallow burrowing mode of life feeding on benthic and semi-infaunal prey. The marginal rim of the carapace of *Willwerathia* may well have aided in covering the animal in sand in an analogous manner to that recorded in *Limulus* and hypothesised in phacopid trilobites (see ELDREDGE 1970). In this ecological niche, it would have escaped direct competition with the faster, more predatory eurypterids. Further collecting may yet shed light on the role of *Willwerathia* in the palaeoecology of the Willwerath deposit.

## Acknowledgments

We thank ROBERT LEUNISSEN (Kreuzau) and WOLFGANG SIPPEL (Ennepetal) for allowing us to study material in their private collections and Dr. HELMS and Dr. LINDERT (both Berlin) for their help in the search for the lost holotype.

## References

- ALLISON, P. A. & BRIGGS D. E. G. 1991. Taphonomy: Releasing the Data Locked in the Fossil Record. – 560 pp., New York, London (Plenum Press).
- ANDERSON, L. I. 1996. Taphonomy and Taxonomy of the Palaeozoic Xiphosura. – Unpublished Ph.D. thesis, Univ. of Manchester. – 413 pp.
- ANDERSON, L. I. & SELDEN, P. A. 1997. Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura. – *Lethaia* **30**: 19–31, Oslo.

- BABCOCK, L. E.; WEGWEISER, M. D.; WEGWEISER, A. E.; STANLEY, T. M. & MCKENZIE, S. C. 1995. Devonian horseshoe crabs from northern Pennsylvania. – *Pennsylvania Geology* **26**: 2-7.
- BERGSTRÖM, J. 1975. Functional morphology and evolution of the xiphosurids. – *Fossils and Strata* **4**: 291-305, Oslo.
- BRETT, C. E. 1990. Obrution Deposits. – [In:] BRIGGS, D. E. G. & CROTHER, P. R. [eds.] *Palaeobiology. A Synthesis*: 239-243, Cambridge/Massachusetts (Blackwell Science).
- DUNLOP, J. A. 1996. A trigonotarbid arachnid from the Upper Silurian of Shropshire. – *Palaeontology* **39**: 605-614, London.
- DUNLOP, J. A. & POSCHMANN, M. 1997. On the Emsian (Lower Devonian) arthropods of the Rhenish Schiefergebirge: 1. *Xenarachne*, an enigmatic arachnid from Willwerath, Germany. – *Paläontologische Zeitschrift* **71**: 231-236, Stuttgart.
- ELDRIDGE, N. 1974. Revision of the suborder Synziphosurina (Chelicerata, Merostomata), with remarks on merostome phylogeny. – *American Museum Novitates* **2543**: 1-41, New York.
- ELDRIDGE, N. & PLOTNICK, R. E. 1974. Revision of the pseudoniscine merostome genus *Cyamocephalus* CURRIE. – *American Museum Novitates* **2557**: 1-10, New York.
- FRIMAN, L. 1986. Die devonischen Agnatha des Rheinischen Schiefergebirges unter besonderer Berücksichtigung ihrer Histologie. – *Münstersche Forschungen zur Geologie und Paläontologie* **64**: 1-91, Münster.
- HEYMONS, R. 1901. Die Entwicklungsgeschichte der Scolopender. – *Zoologica* **13**: 1-244, Stuttgart.
- LATREILLE, P. A. 1802. Histoire naturelle, générale et particulière, des Crustacés et des Insectes. – **3**: 467 pp., Paris (Dufart).
- MANNING, P. L. & DUNLOP, J. A. 1995. Respiratory organs of eurypterids. – *Palaeontology* **38**: 287-297, London.
- MAPLES, C. G. & SCHULTZE, H. P. 1989. Preliminary comparison of the Pennsylvanian assemblage of Hamilton, Kansas, with marine and non-marine contemporaneous assemblages. – [In:] MAPES, G. & MAPES, R. H. [eds.] *Regional geology and palaeontology of the Upper Paleozoic Hamilton quarry area in southeastern Kansas*. – Kansas Geological Survey Guidebook Series **6**: 253-273, Lawrence/Kansas.
- NEAVE, S. A. 1939. *Nomenclator Zoologicus*. – **2**: 1025 pp., Bungay, Suffolk (Richard Clay and Company Ltd.).
- OTTO, M. 1994. Arthropodenfaunen (Vertebrata, Placodermi) aus dem Unter-Devon des Rheinischen Schiefergebirges: Morphologie, Taxonomie und Paläoökologie. – *Edition Wissenschaft* **50**: 1-98, Marburg (Tectum-Verlag).
- PICKETT, J. W. 1993. A Late Devonian xiphosuran from near Parkes, New South Wales. – *Memoirs of the Association of Australasian Palaeontologists* **15**: 279-287.
- REBSKE, W.; REBSKE, C.; BLESS, M. J. M.; PAPROTH, E. & STEEMANS, P. 1985. Over enkele Fossielen uit de Klerf-Schichten (Onder-Emsien) bij Waxweiler (Eifel, BRD) en hun Leefmilieu. – *Grondboor en Hamer* **5**: 142-155, Enschede.
- RICHTER, R. & RICHTER, E. 1929. *Weinbergina opitzi* n. g., n. sp., ein Schwerträger (Merost. Xiphos.) aus dem Devon (Rheinland). – *Senckenbergiana* **11**: 193-209, Frankfurt.
- SALTER, J. W. 1857. On some of the higher Crustacea from the British coal measures. – *Quarterly Journal of the Geological Society of London* **17**: 528-533, London.
- SCHÖLLMANN, L. 1993. Die Tonsteine der Keratophyrkomplexe 3 und 4 im Unterdevon (Ems) des Sauerlandes: Geochemische Milieuindikation, Fazies, Paläoökologie. – *Geologie und Paläontologie in Westfalen* **25**: 1-151, Münster.
- SEILACHER, A. 1970. Begriff und Bedeutung der Fossil-Lagerstätten. – *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* **1970**: 34-39, Stuttgart.
- SELDEN, P. A. & DRYGANT, D. M. 1987. A new Silurian xiphosuran from Podolia, Ukraine, USSR. – *Palaeontology* **30**: 537-542, London.
- SIVETER, D. J. & SELDEN, P. A. 1987. A new, giant xiphosurid from the lower Namurian of Weardale, County Durham. – *Proceedings of the Yorkshire Geological Society* **46**: 153-168, Wakefield.
- STÖRMER, L. 1936. Eurypteriden aus dem Rheinischen Unterdevon. – *Abhandlungen der Preußischen Geologischen Landesanstalt, Neue Folge* **175**: 1-74, Berlin.
- 1951. A new eurypterid from the Ordovician of Montgomeryshire. – *Geological Magazine* **88**: 409-422, London.
- 1952. Phylogeny and taxonomy of fossil horseshoe crabs. – *Journal of Paleontology* **26**: 630-640, Tulsa/Oklahoma.
- 1969. Eurypterids from the Lower Devonian of Willwerath, Eifel. – *Senckenbergiana lethaea* **50**: 21-35, Frankfurt am Main.
- 1976. Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 5: Myriapoda and additional forms, with general remarks on fauna and problems regarding invasion of land by arthropods. – *Senckenbergiana Lethaea* **57**: 87-183, Frankfurt am Main.
- STÜRMER, W. & BERGSTRÖM, J. 1981. *Weinbergina*, a xiphosuran arthropod from the Devonian Hunsrück Slate. – *Paläontologische Zeitschrift* **55**: 237-255, Stuttgart.
- TESAKOV, A. S. & ALEKSEEV, A. S. 1992. Myriapod-like arthropods from the Lower Devonian of Central Kazakhstan. – *Paleontological Journal* **26**: 18-23, New York.
- TOLLERTON, V. P. 1989. Morphology, taxonomy and classification of the Order Eurypterida BURMEISTER, 1843. – *Journal of Palaeontology* **63**: 642-657, Ithaca/New York.
- WENTZCKE, M. 1994. Die Geologie des Raumes Neuendorf-Willwerath unter besonderer Berücksichtigung der Sedimentologie und Paläoökologie der Klerf-Schichten (Steinbruch bei Willwerath). – Unveröffentlichte Diplomarbeit an der Rheinischen Friedrich-Willhelms-Universität. - 136 pp., Bonn.
- WOODWARD, H. 1865. On a new genus of Eurypterida from the Lower Ludlow rocks of Leintwardine, Shropshire. – *Quarterly Journal of the Geological Society* **21**: 490-492, London.
- 1872. Notes on some British Palaeozoic Crustacea belonging to the order Merostomata. – *Geological Magazine* **9**: 433-441, London.

Eingang des Manuskriptes am 20. November 1997;  
Annahme durch die Schriftleitung am 5. August 1998.