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THE EARLIEST EUROPEAN STREBLOCHONDRIID BIVALVES (PTERIOMORPHIA; LATE FAMENNIAN)

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(7 figures & 4 tables)

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ABSTRACT. Revision of the Late Famennian bivalve fauna from the southern coast of Laurussia has revealed that various groups of bivalves, up to now regarded as appearing in the Early Carboniferous, are now proved to range back into the Late Famennian. Streblochondriid bivalves can be traced back into the Late Famennian, through their oldest members, *Streblopteria piltonensis* (Whidborne, 1896) and *Streblopteria lepis* (Whidborne, 1896), both occurring in the clastic shelf facies of the Latest Famennian. They form part of the highly diversified shelf fauna of the last transgression-regression subcycle of the Devonian. The origin of streblochondriids has to be dated back in the Early Famennian after the Frasnian/Famennian Crisis, whereas the main development and diversification of the group occurred in the shelf region of the marine Carboniferous. Streblochondriids are one of the rare groups of bivalves that show palaeogeographical and palaeoecological relations to the fauna of the „basinal" facies of the Upper Devonian and Lower Carboniferous. In the introductory part of this paper the taxonomical value of morphological features and the taxonomical state of knowledge is discussed. In the systematic part *Streblopteria piltonensis* and *Streblopteria lepis* are described and revised in detail.

KEYWORDS: Bivalvia, Streblochondriidae, taxonomy, stratigraphy, Famennian, Europe.

ZUSAMMENFASSUNG. **Die ältesten europäischen Streblochondriiden (Pteriomorphia, Spätes Famennium).** Die Revision der spät-famennischen Bivalvenfauna am Südrand von Laurussia hat gezeigt, daß zahlreiche Bivalvengruppen, deren Ursprung bisher im tieferen Unterkarbon angenommen wurde, bis in das höhere Famennium zurückreichen. Dies gilt auch für Streblochondrien, deren älteste Vertreter, *Streblopteria piltonensis* (Whidborne, 1896) und *Streblopteria lepis* (Whidborne, 1896), in der Fazies des klastischen Schelfes im Ober-Famennium („Strunium") vorkommen. Sie bilden damit einen Anteil an der hoch diversen Schelffauna während des letzten Transgressions-Regression-Subzyklus im Devon. Der Ursprung der Streblochondrien muß im frühen Famennium nach der Frasnes/Famenne-Krise gesucht werden, während die Hauptentwicklung und Diversifizierung in den Schelfmeeren des Karbons erfolgte. Streblochondrien gehören zu den wenigen Bivalvengruppen, die paläogeographische und paläoökologische Beziehungen zur „Beckenfazies" im Oberdevon und Unterkarbon zeigen. Im einführenden Teil dieser Arbeit wird der taxonomische Stellenwert morphologischer Eigenschaften und der taxonomische Kenntnisstand der Streblochondrien diskutiert; im systematischen Teil werden *Streblopteria piltonensis* und *Streblopteria lepis* ausführlich beschrieben und diskutiert.

SCHLÜSSELWÖRTER: Bivalvia, Streblochondriidae, Taxonomie, Stratigraphie, Famennium, Europa.

RESUME. **Les bivalves streblochondriens européens anciens (Pteriomorphia, Famennien récent).** La révision de la faune à bivalves du Famennien récent du bord sud de Laurussia a démontré que beaucoup de groupes à bivalves, dont la première apparition était supposée dans le Carbonifère ancien jusqu'à ce jour, descendent jusqu'au Famennien récent. Des bivalves streblochondriens sont retrouvés dans le Famennien récent sous la forme de leur représentants les plus anciens, *Streblopteria piltonensis* (Whidborne, 1896) et

Streblopteria lepis (Whidborne, 1896), tous les deux apparaissent dans le faciès clastique de plateau continental du Famennien récent („Strunien"). Ils font partie de la faune très diversifiée de plateau continental du dernier sous-cycle de transgression-régression du Dévonien. L'origine des streblochondriens doit être recherchée dans le Famennien ancien après la crise Frasnien/Famennien, leur développement majeur et la diversification du groupe a eu lieu dans les mers du plateau continental du Carbonifère. Les streblochondriens sont un des rares groupes de bivalves qui montrent des relations paléogéographiques et paléoécologiques avec la faune du faciès „basinal" du Dévonien supérieur et du Carbonifère inférieur. La valeur taxonomique des caractères morphologiques et l'état des connaissances de la classification des streblochondriens est discutés dans l'introduction du présent travail; *Streblopteria piltonensis* et *Streblopteria lepis* sont décrits en détail et révisé dans la partie systématique.

MOTS-CLES: Bivalvia, Streblochondriidae, taxonomie, stratigraphie, Famennien, Europe

1. INTRODUCTION

Late Palaeozoic aviculopectinaceans and pectinaceans form an extensive group of bivalves which is strongly oversplit into species of different taxonomical value. Consequently, there is a chaotic wealth of names, species, nomina nuda and nomina dubia. One of the reasons is that the shell morphology and sculpture patterns of the right and left valves of a single species can differ markedly. A second reason is the separate naming of different preservational states of the same species. Other reasons include lack of study on variability, stratigraphical and geographical distribution or the erection of taxa based on insufficiently preserved specimens. These problems have hindered accurate taxonomic treatment of this important group. However, familiarity with the essentials of recent or well preserved fossil bivalve material illustrating variability, distribution and ontogeny (comp. Davenport, 1900; Fedotov, 1932; Smith, 1991; Waller, 1993; Waloszek, 1984), leads to a picture of - Late Palaeozoic - taxa that has gained in precision, provided that types have been studied. Hence, it seems most likely that more than 50% of the Devonian and Carboniferous „species" may prove to be synonymous, if a palaeobiological basis is used.

Within this group streblochondriids represent a small, compact subgroup with a relatively weak sculpture pattern. It is already represented in the Early Carboniferous by the genera Streblochondria Newell, 1938, Striochondria Waterhouse, 1983 and Streblopteria McCoy, 1851. Species belonging to these taxa were formerly assigned to Pecten, *Lima, Aviculopecten, Pleuronectites, Crenipecten, Palaeolima, Streblopteria,* or especially *Pseudamusium (=Pseudamussium).* Several combinations of genera and species have been proposed according to a subjective understanding and extension of taxa (see Newell, 1938; Paul, 1941). As mentioned above, many species show broadly overlapping morphology or only slight differences, but different stratigraphical or geographical occurrence has led to new names, mostly based on insufficient type material.

The streblochondriids described in this paper belong to the neritic fauna of the Latest Famennian („Strunian") clastic shelf area at the Southern margin of Laurussia (SW-England, Belgium, W-Germany). The bivalves of this facies have been revised and described by the author (Amler, 1993a, 1993b, 1995).

Up to now streblochondriids were regarded as ranging from Early Carboniferous to Permian time (Newell & Boyd, 1985b). But revision of the Late Famennian bivalve fauna has revealed that the ancestors of the Early Carboniferous taxa can be traced back at least to the Famennian (see chapter on Evolution). The Late Famennian streblochondriids described in this paper were distributed along the northern margin of the Rheic Ocean (comp. McKerrow & Ziegler, 1972) during the last subcycle of sea level rise in the Devonian (IIf), according to Johnson *et al.* (1985, 1986; comp. Dreesen *et al.*, 1988; Amler, 1993a). Only the streblochondriids and karadjaliids (the former *Posidonia venusta* group) occur in more than one facies in the Famennian, whereas most of the associated bivalves do not occur in other facies (for example the Upper Cypridina Shales or the Wocklum Beds; Schmidt, 1924). Together with streblochondriids many other pteriomorphs, up to now believed to appear successively at the beginning of the Carboniferous, have Late Famennian ancestors.

Repository. The studied specimens from the Late Famennian of Europe are housed in several scientific and private collections. Throughout the text the following prefixes to specimen numbers are used: SM - Sedgwick Museum, Cambridge; NDM - North Devon Museum, Barnstaple; GSM - Geological Survey Museum, Keyworth; IRSNB - Institut Royal des Sciences Naturelles de Belgique,

Bruxelles; GPIG - Geologisch-Paläontologisches Institut und Museum der Universität Göttingen; Mbg. - Institut für Geologie und Paläontologie der Philipps-Universität Marburg; BGR - Bundesanstalt für Geowissenschaften und Rohstoffe Hannover, Außenstelle Berlin. Amateur collections are abbreviated as follows: ET - Erich Thomas, Witten; KW - Klaus M. Weber, Solingen; SW - Stephan Wehking, Velbert (all Germany).

2. VALUE OF MORPHOLOGICAL FEATURES IN STREBLOCHONDRIID BIVALVES

During recent years several bivalve taxonomists have tried to solve the problem of weighting morphological characters. But, even in Recent bivalves, taxonomical concepts are different or contradictory. Even though the use of the characters of external shell sculpture patterns alone for separating taxa on species or generic level has been criticized, research on Recent and Caenozoic pectinoids (Fleming, 1958; Light, 1988; Smith, 1991; Waller, 1993) has validated rib count, as well as rib form, as good species specific characters. This supports the use of further taxonomically relevant features such as the mode of rib number increase and the development of ribs in different shell regions, the differing sculpture patterns on right and left valves and, last but not least, the ornament development on the anterior auricle of the right valve. In addition, shell colour patterns are very often a distinguishing feature of Recent pectinid species (Fleming, 1957), but, even though Carboniferous streblochondriids, especially the genus *Streblopteria*, are one of the most common pteriomorphs with preserved colour patterns (Mapes & Benstock, 1988) it appears to be impractical to use former colour markings as diagnostic features for separating species. Notwithstanding that complicated statistical and mathematical programs may serve taxonomical concepts (but sometimes they do not, comp. Hajkr *et al.*, 1974), basic shell sculpture patterns as well as simple valve measurements and valve proportions, lead to and assist species definitions (comp. Amler, 1994, in prep. a; Waller & Marincovich, 1992). Combined with ontogeny and variation analysis these characters are commonly sufficient in separating species of pectinoids or aviculopectinoids. Statistics are generally used for repetition or for convincing others about what a professional, palaeobiologically trained eye of the palaeontologist has discovered through observations and experience.

Besides the basic types of shell sculpture patterns some valve dimensions and valve proportions are important (Fig. 1).

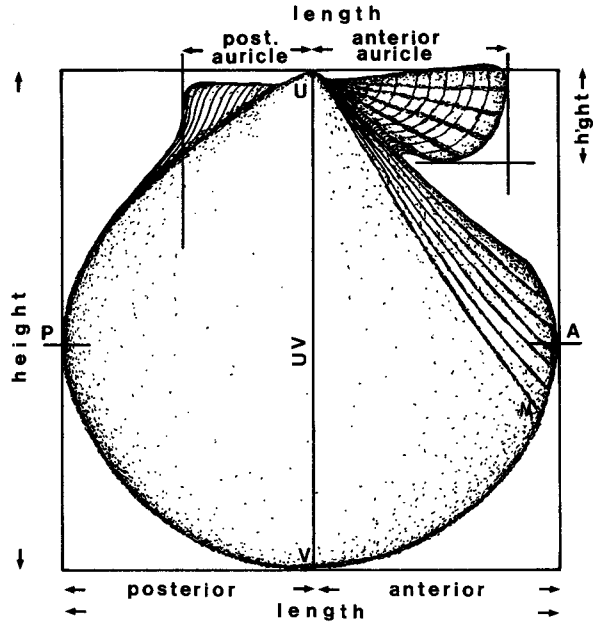

Figure 1. Scheme of dimensions and measurements in streblochondriid bivalves. For discussion and explanation see text. A = anteriormost point of valve; P = posteriormost point of valve; U = top of umbo; V = most ventral point of shell; UV = umbonal vertical.

Valve length (L). The total length (Ltot) of the valve body parallel to the hinge margin measured between two tangents perpendicular to hinge margin, touching the valve at the anteriormost (A) and posteriormost (P) points. The total valve length is split into an anterior (Lant) and a posterior (Lpost) part, limited by the tangents respectively and the umbonal vertical (UV), running from the top of the umbo (U) to the ventral margin (V).

Valve height (H). The total height of the valve body measured parallel to the umbonal vertical between two tangents touching the top of the umbo (U) parallel to the hinge line and the most ventral point (V) of the shell.

Auricle length (LA). The length of the anterior auricle (LAA) parallel to the hinge line between the umbonal vertical and a tangent touching the anteriormost point of the anterior auricle, perpendicular to the hinge line. The length of the posterior auricle (LPA) is only approximately determinable: it is the length measured between the umbonal vertical and a second vertical fixed at the posteriormost point of the hinge line (posterodorsal angle).

Height of anterior auricle. The maximum height of the anterior auricle of the right valve, measured parallel to the umbonal vertical, between two tangents drawn parallel to the hinge line, touching the ventralmost and dorsalmost points of the auricle.

The length of the auricles of the left valve are measured in a similar way to the dimensions of the posterior auricle.

All measurements and angles match largely with the terms used by Waller & Marincovich (1992) for modern pectinids. Throughout the text the term „commarginal" instead of concentric is used for the description of growth lines.

3. CURRENT KNOWLEDGE OF STREBLOCHONDRIIDS

In his painstaking and pioneering work on Late Palaeozoic pectinaceans Newell (1938) separated a group of aviculopectinid shells with weakly developed or missing radial sculpture pattern and unequal auricles. He created the subfamily Streblochondriinae Newell, 1938 for these shells, including *Streblochondria* Newell, 1938, type species *Streblochondria sculptilis* (Miller, 1891). He placed the genera *Streblopteria* and *Obliquipecten* in a closely related position.

As part of an extensive compilation „Die Fauna des deutschen Unterkarbon" H. Paul wrote a monograph on Early Carboniferous bivalves in Germany which was never published but destroyed during the Second World War (comp. Weyer, 1964). Only the synonymy lists of the different taxa were published as part of the „Fossilium Catalogus I. Animalia" (Paul, 1941). It is obvious that Paul followed Newell in dividing streblochondriid aviculopectinaceans into smooth or exclusively commarginal ornamented taxa grouped in *Streblopteria* and forms with radial ornament assigned to *Streblochondria*.

Only a few authors have dealt with the aviculopectinacean and Palaeozoic pectinacean bivalves since, and no comprehensive revision has been carried out. In recent years I have studied several hundreds of streblochondriids and compared streblochondriid morphology with that of modern pectinids. Considering the results of other works on Palaeozoic aviculopectinaceans and pectinaceans some basic data can be emphasized. Now upgraded to family rank (Newell & Boyd, 1985b) seven genera are currently assigned to the Streblochondriidae:

- *Streblochondria* Newell, 1938 (Early Carboniferous to Late Permian)
- *Striochondria* Waterhouse, 1983 (Late Carboniferous to Middle Permian)
- *Streblopteria* McCoy, 1851 (Late Devonian to Middle Permian)
- *Guizhoupecten* Chen, 1962 (Middle to Late Permian)
- *Eocamptonectes* Newell, 1969 (Early to Late Permian)
- *Pleuronectites* Schlotheim, 1820 (Middle to Late Triassic)
- *Obliquipecten* Hind, 1903 (Early Carboniferous to Early Permian).

As diagnostic features of family rank shells have two opisthocline valves of nearly equal inflation, always markedly shorter posterior auricles, a calcitic outer shell layer composed of a radial fibrous microstructure and an alivincular ligament with - as far as is known - strengthened borders to the resilifer on the hinge plate. In general, genera differ predominantly in external shell ornamentation, but it has to be mentioned that transitional development of shell characters is exceptionally variable and very often strongly dependent on preservation. One of the problematic characters is the development of very fine radial ribs on a narrow shell region adjacent to the anterior margin and parallel to the byssal notch, whereas all the rest of the valve remains smooth. Interestingly, this feature is combined with strong radial and commarginal ornament on the anterior auricle of the right valve. The Carboniferous genera are characterized as follows:

- *Streblochondria* (type species *Aviculopecten sculptilis* Miller, 1891) is slightly to moderately opisthocline in valve outline, the auricles are unequal in length - the anterior auricles of both valves are generally about twice as long as the posteriors, the anterior auricle of the right valve possesses a distinct, deeply indented byssal notch. Both valves are ornamented with radial ribs or costae, crossed by commarginal costae of equal strength, resulting in an almost regular reticulate sculpture pattern; the auricles, too, are radially and commarginally ornamented.
- *Striochondria* (type species *Streblochondria auriocosta* Waterhouse, 1982) is similar to *Streblochondria* but reticulate sculpture pattern is developed very delicately on both valves.
- *Streblopteria* (type species *Meleagrina laevigata* McCoy, 1844) is acline to slightly opisthocline in valve outline; both the anterior and posterior auricles are equal in length or the anterior auricle is longer than the posterior; the external shell surface is largely smooth or ornamented with commarginal growth lines only. The anterior auricle of the right valve is additionally covered with distinct radial ribs or costae.
- *Obliquipecten* (type species *Obliquipecten laevis* Hind, 1903) is very similar to *Streblopteria*; its posterior auricles are distinctly reduced to a narrow fringe, the anterior auricle of the right valve is broadly spoon-shaped.
- *Guizhoupecten* (type species *Guizhoupecten wangi* Chen, 1962) is very similar to *Streblochondria* in general outline, but possesses strong radial ribs and plications in which the entire shell is radially folded. Consequently, this feature is also visible on the internal surface of the shell. In some species the number of ribs increases by bifurcation on right valves and implantation on left valves. Commarginal

ornament occurs in the growth lamellae on the ribs and interspaces. In general habitus *Guizhoupecten* resembles modern pectinids, but - like all other streblochondriids - it is lacking the presence of a ctenolium which remains a striking difference between Palaeozoic aviculopectinacean and modern pectinacean pteriomorphs.

All the above mentioned characters are insufficient for a solid palaeobiological diagnosis. They commonly overlap in their development and they are more or less subject to the state of preservation. At present, the taxonomical basis of the Streblochondriidae, i.e. the revision of the type species, is incomplete. Therefore, it remains impossible, for the moment, to distinguish precisely between the different genera and to decide, whether the presence of a set of delicate radial ribs on the anteriormost region of the shell body is a character of *Streblopteria*, of *Striochondria*, or a separate, new genus.

An important morphological feature of the Streblochondriidae is the shell microstructure. According to Newell (1938), Newell & Boyd (1985a, b) and Carter (1990a, b) the calcitic outer shell layer in streblochondriids is radial fibrous prismatic in both valves and only the juvenile right valves show regular simple prismatic structure. In adult right valves the microstructure varies from radial fibrous prismatic to irregular sphaerulitic prismatic. In adult left valves it may be homogenous with traces of an irregular simple prismatic structure. The middle and inner shell layers of left valves are composed of an aragonitic crossed lamellar structure to the exterior and interior of the pallial line. According to Carter (1990a) this type of shell microstructure reflects a more advanced stage in the evolution of the shell microstructure within the Pectinacea. The presence of radial fibrous prisms in the outer shell layer and the lack of nacreous structures in the middle and inner layers are derived characters which separate streblochondriids from most aviculopectinaceans. All these microstructural data have been observed in Late Carboniferous and Permian taxa, but are not confirmed in Early Carboniferous or Late Famennian forms - partly for preservational reasons. Therefore, no answer can be given at present whether or not Late Devonian streblochondriids possessed a more plesiomorph stage in shell structure than Late Carboniferous and Permian taxa. It appears doubtful to me that this advanced type of shell microstructure could have evolved from the ancestral Pterinopectinidae, Aviculopectinidae or Entoliidae without intermediate forms.

The history of taxonomical grouping has been summarized by Carter (1990a). For some reason the systematic position of the family Streblochondriidae remains uncertain. Newell & Boyd (1985b, 1987) removed the family from the Aviculopectinacea and placed it in the Pectinacea on account of the transitional position of the ligament between the Aviculopectinacea and the Pectinacea. With regard to shell microstructure - as far as known today - the Streblochondriidae share with the Pectinacea the more advanced grade of calcitic fibrous prismatic outer shell layer. On the other hand, a ctenolium which is regarded as a fundamental derived character for modern pectinaceans (Waller, 1984) is not developed in the Streblochondriidae.

4. SYSTEMATIC PALAEONTOLOGY

? Superfamily Aviculopectinacea Meek & Hayden, 1864 (Waller, 1978)

Family Streblochondriidae Newell, 1938

Streblopteria McCoy, 1851

Type species. *Meleagrina laevigata* McCoy, 1844 (SD Meek & Worthen, 1866).

Diagnosis. A genus of the family Streblochondriidae (see Waterhouse, 1982; Newell & Boyd, 1985b) with the following characters: shell very slightly inequivalve; valves acline to opisthocline, outline orbicular, transversely oval or suboval and slightly oblique; umbo only slightly swollen; auricles of different size: anterior auricle markedly separated from median shell body, about twice as long as posterior auricle; posterior auricle indistinctly separated from shell body, short, narrow, marginally attached to shell body. Surface of central shell body and posterior auricle smooth or ornamented with very faint commarginal lines of growth; anterior auricles ornamented additionally with few radiating ribs. Both valves nearly equally inflated.

Remarks. Phylogenetic relations between *Streblopteria*, *Streblochondria* Newell, 1938 and *Striochondria* Waterhouse, 1983 as well as *Obliquipecten* Hind, 1903 are unresolved. A detailed study on the morphology, systematics, ontogeny and variability of members of *Streblochondria* s. l. is being carried out by me (Amler, in prep. b). Several species of the genera *Streblopteria*, *Striochondria* and *Streblochondria* are distributed world-wide in marine sediments of Carboniferous and Permian age. Since being established and first revised by Newell (1938), various authors have attributed a variety of „species" of aviculopectinids to these genera due to their differing thoughts on palaeozoology (i.e. Paul, 1941; Demanet, 1938, 1941; Nicolaus, 1963), without ever having analyzed the systematics and evolution of the genera. Especially the separation at generic level has been inconsistently applied by different authors which has caused a vast host of names („species") and assignments. The reason for this excessive splitting

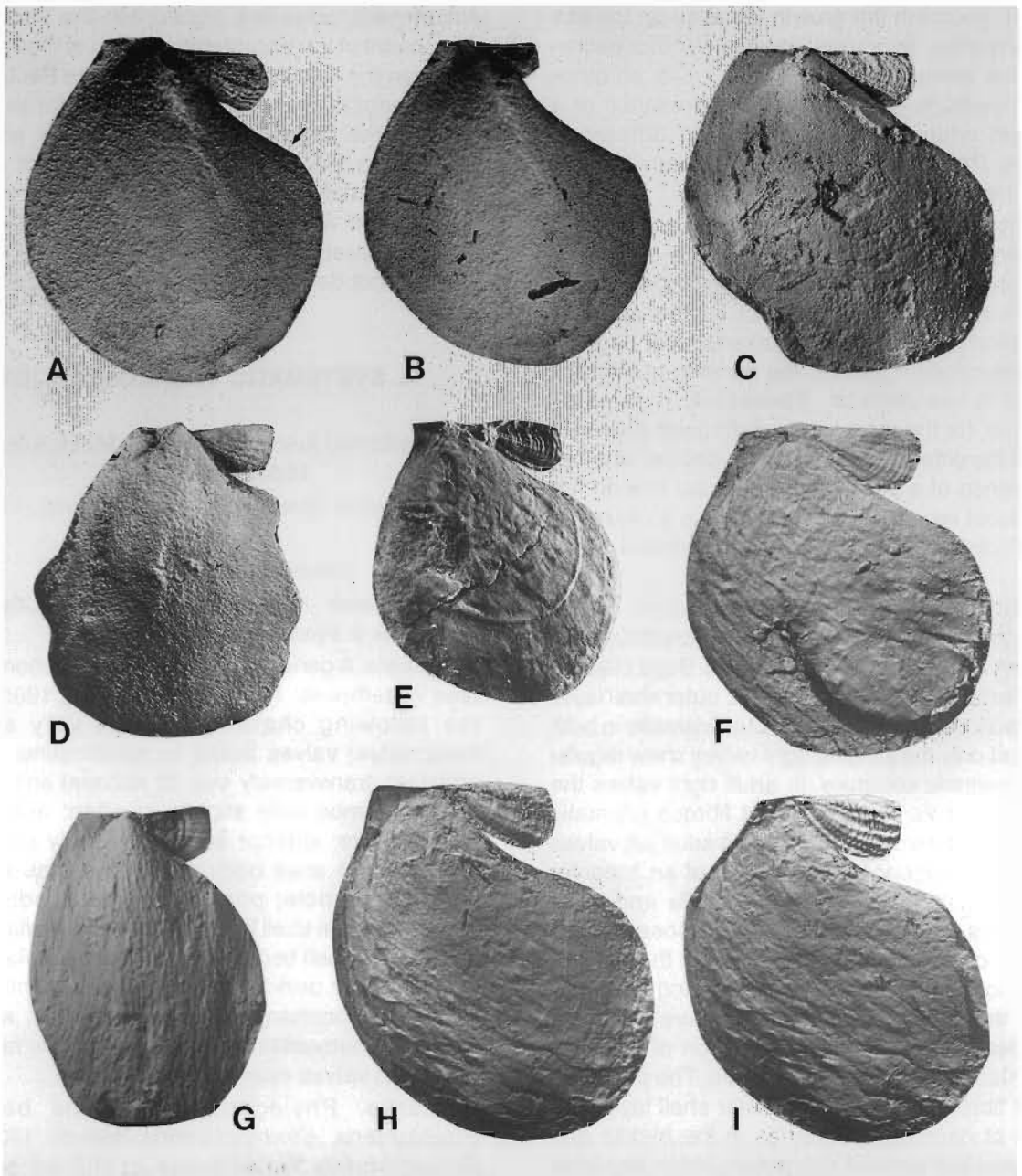

Figure 2. *Streblopteria piltonensis* (Whidborne, 1896). Right valves.
A: Lectotype, SM.H.327, Porter Coll., silicone cast of external mould, coated with MgO. Note delicate radial threads on anteriormost portion of valve. Figured in Whidborne, 1896: Pl. 16 Fig. 7. x4,0 [#9744#].
B: Lectotype, SM.H.327, Porter Coll., internal mould, defective in anterodorsal region, coated with MgO. Figured in Whidborne, 1896: Pl. 16 Fig. 7. x3,9 [#9742#].
C: Paralectotype, SM.H.238, Porter Coll., silicone cast of external mould, coated with MgO. Figured in Whidborne, 1896: Pl. 16 Fig. 8. x2,5 [#9748#].
D: Paralectotype, NDM.648, Hall Coll., internal mould, defective in anterior and posterior region, coated with MgO. Figured in Whidborne, 1896: Pl. 16 Fig. 9. x3,1 [#291702#].
E: Specimen BGR not registered, Paul Coll., internal mould, defective in posterocentral region. x4,0 [#5411#].
F: Specimen ET.Wa.283, Thomas Coll., internal mould, coated with MgO. x5,7 [#9751#].
G: Specimen SW.1329, Wehking Coll., internal mould, coated with MgO. x3,9 [#9752#].
H: Specimen SW.1334, Wehking Coll., internal mould, coated with MgO. x5,5 [#9756#].
I: Specimen SW.1334, Wehking Coll., silicone cast of external mould, defective in posterodorsal region, coated with MgO. x5,5 [#9758#].

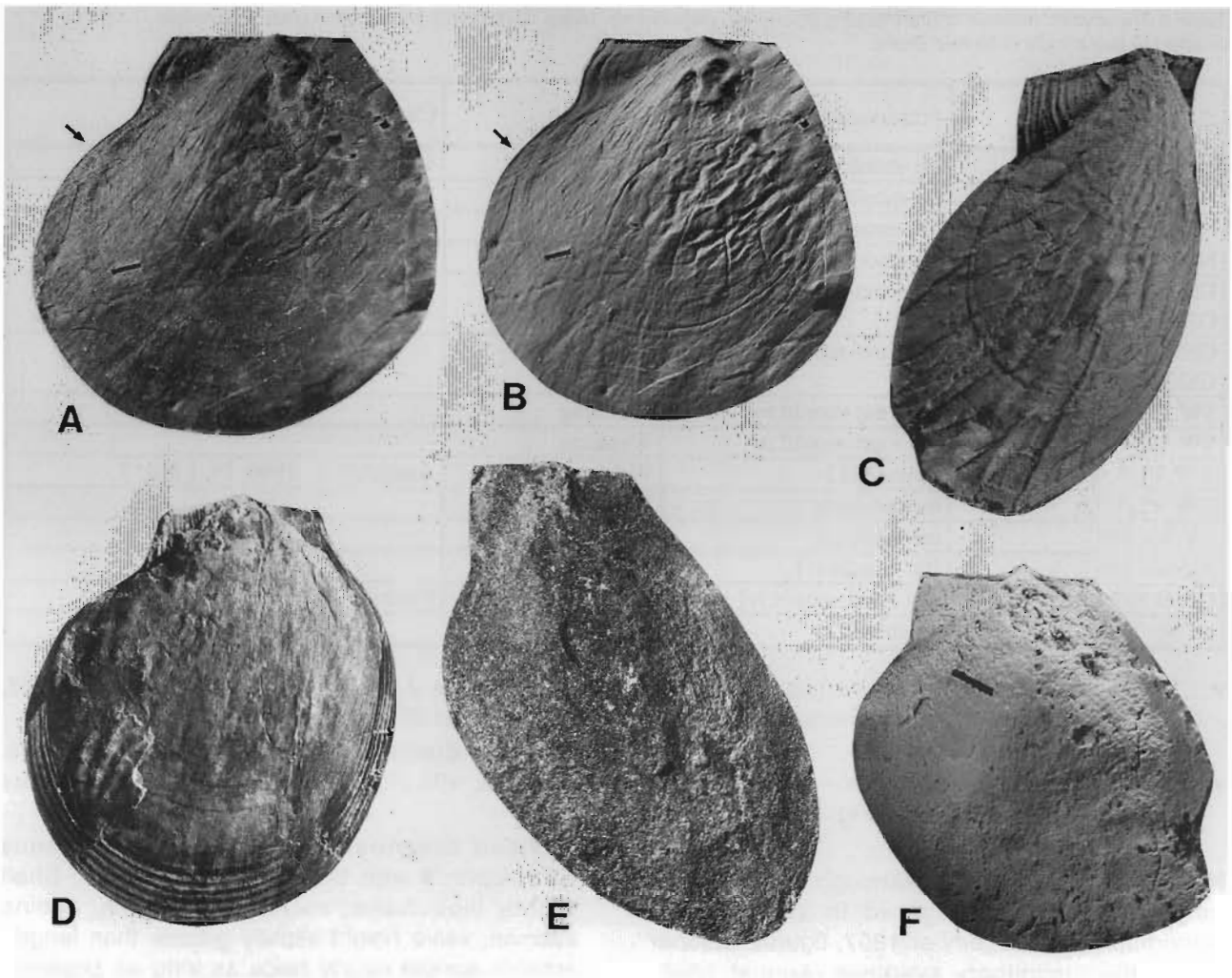

Figure 3. *Streblopteria piltonensis* (Whidborne, 1896). Left valves.
A: Specimen KW.VLA.66, Weber Coll., internal mould. Note delicate radial threads on anteriormost portion of valve. x3,6.
B: Specimen KW.VLA.66, Weber Coll., internal mould, coated with MgO. Note delicate radial threads on anteriormost portion of valve. x3,6.[#9746#].
C: Specimen GPIG.912.4.105, Michels Coll., internal mould, tectonically damaged, coated with MgO. x5,0 [#9734#].
D: Specimen BGR not registered, Paul Coll., internal mould, defective in umbonal region. x3,9 [#5416#].
E: Paralectotype, NDM.660, Hall Coll., internal mould, tectonically damaged. Figured in Whidborne, 1896: Pl. 16 Fig. 10. x3,0 [#21539#].
F: Paralectotype, NDM.661, Hall Coll., internal mould, defective in posterior region, coated with MgO. Figured in Whidborne, 1896: Pl. 16 Fig. 11. x3,0 [#291738#].

into morphospecies is the poor knowledge on taxonomically relevant morphological characters and especially their variability. Whereas some authors have stressed a supposed stratigraphical restriction, Newell & Boyd (1985b) demonstrated the broad intraspecific plasticity within Permian members of the Streblochondriidae.

Streblopteria piltonensis (Whidborne, 1896)

Figs. 2-4, Tabs. 1-2

v* 1896 *Pleuronectites Piltonensis* Whidborne, Preliminary Synopsis: 375.

v 1896/97 *Pleuronectites Piltonensis*. – Whidborne, Devonian fauna South England, 3: 140, Pl. 16 Fig. 7-9, 10?, 11?

vpt 1896/97 *Pleuronectites Hicksii*. – Whidborne, Devonian fauna South England, 3: 142; non Pl. 16 Fig. 14, 14a.

v 1902 *Streblopteria ? piltonensis*. – Drevermann, Etroeungt-Stufe: 508, Pl. 14 Fig. 21.

? 1924 *Streblopteria* cf. *piltonensis*. – Schmidt, Cephalopodenfaunen Devon-Carbongrenze: 143.

pt 1941 *Streblochondria piltonensis*. – Paul, Lamellibranchiata infracarbonica: 232.

v 1986 *Prosochasma procrescens*. – Michels, Ober-Devon von Velbert: 76.

v 1990 *Streblopteria piltonensis*. – Amler *et al.*, Bivalven Oberdevon Bergisches Land: 51, Pl. 3 Fig. 7.

Table 1. The studied material of Streblopteria piltonensis *(Whidborne, 1896). Specimen's preservation given in brackets [ ] refer to crushed or tectonically deformed shells.*

Specimen	Preservation	Collection	Citation
SM.H.328 (PLT)	ext-mould.rv	Porter	Whidborne, 1896: Pl. 16 Fig. 8
NDM.648 (PLT)	int-mould.rv	Hall	Whidborne, 1896: Pl. 16 Fig. 9
NDM.660 (PLT)	[int-mould.lv]	Hall	Whidborne, 1896: Pl. 16 Fig. 10
NDM.661 (PLT)	[int-mould.lv]	Hall	Whidborne, 1896: Pl. 16 Fig. 11
GSM.DEA.2602-GSM.DEA.2603	int + ext-mould.lv	GSM	
GSM.DEB.8008-GSM.DEB.8009	int + ext-mould.rv	GSM	
SW.1329	int + ext-mould.rv	Wehking	
SW.1334	int + ext-mould.rv	Wehking	
KW.VLA.66	int-mould.lv	Weber	Amler *et al.*, 1990: Pl. 3 Fig. 7
KW.VLA.72	int-mould.rv	Weber	
ET.Wa.283	int-mould.rv	Thomas	
ET.Wa.526	[int-mould.rv]	Thomas	
GPIG.912.4.105	[int + ext-mould.lv]	Michels	Michels, 1986: 76
no No. (Berlin)	int-mould.rv	Paul	

v 1993 *Streblopteria piltonensis*. – Amler, Bivalvenfauna des Oberen Famenniums: 112, Pl. 7 Fig. 5-8.

v 1993 *Streblopteria piltonensis*. –Amler, Shallow marine bivalves: 415, Pl. 2 Fig. 11-13.

Nomenclatorial remarks. Although the species is fully described and figured in Whidborne's monograph (text December 1897, figures October 1896), the preliminary synopsis (August 1896) preceds through its short description according to ICZN, Articles 11-12.

Lectotype (designated here). The type series comprises about 15 specimens, only some of which have been located. Whidborne was aware of the high shell shape plasticity and selected two specimens as „types" (Whidborne, 1896/97: 141, Pl. 16 Fig. 7 und 8), one of which - an internal mould of a right valve with external counterpart (SM.H.327) - from the Porter Collection, figured by Whidborne, 1896: Pl. 16 Fig. 7 and housed in the Sedgwick Museum Cambridge, is here designated as lectotype.

Paralectotypes. The remaining specimens mentioned by Whidborne (1897: 141, PLT, see below).

Studied material. See Tab. 1.

Type locality. Pilton near Barnstaple (nowadays a suburb of Barnstaple), Devon; Great Britain.

Type stratum. Pilton Shales of the Pilton Formation; according to Goldring (1955, 1970) and Edmonds *et al.* (1985) the only possible localities at the Northwestern periphery of Barnstaple (= suburb Pilton) belong in part or completely to the Pilton A; approximately *costatus*-zone, Late Famennian („Strunian").

Occurence. Late Famennian of SW-England, Belgium and W-Germany.

Original diagnosis (Whidborne, 1896a: 375). „Smooth, with striated wing and produced anterior side."

Revised diagnosis. Characters of the genus *Streblopteria* with the following features: Shell slightly inequivalve; valves opisthocline, outline suboval; valve height slightly greater than length; anterior auricle nearly twice as long as posterior auricle; outer valve surface smooth or sculptured with delicate commarginal growth lines, anterior part of shell body ornamented with 3-6 extremely fine radial capillae/lirae parallel to byssal notch; dorsal portion of anterior auricle without radial ribs, ventral portion sculptured with 3-4 fine costae or plicae.

Morphology (Fig. 4). Shell slightly inequivalve with respect to auricles; valves opisthocline, inequilateral, ratio Lant : Lpost about 1.3-1.5; auricles unequal, more distinctly separated from shell body on the right valve than on the other, anterior auricles nearly twice as long as posterior auricles; outline of median shell body obliquely suboval-pectiniform; angle of obliquity about 15°. Valve length: valve height ratio about 0.85-0.95.

Right valve (Figs. 2A-I and 4). Umbo orthogyrate, small and inconspicuous, pointed, triangular, not swollen, hardly raised above hinge margin; umbonal angle about 80-90°. Hinge margin straight, reaching about 50-60% of total valve length. Auricle sulci narrow; anterior auricle sulcus sharply furrowed and passing into deeply indented, V-shaped byssal notch. Anterior auricle lobate, its anterior margin tightly convex in outline and meeting the anterodorsal margin at an obtuse angle. Posterior auricle small, triangular, indistinctly separated from

the shell body, without distinct auricular sulcus, posterior margin of the posterior auricle straight or slightly concave in outline, meeting the posterodorsal margin at an obtuse, right or acute angle. Anterior margin of the median shell body in dorsal region (= parallel to byssal notch) slightly concave in outline until anteriormost point of the shell, then bluntly rounded towards ventral direction; ventral portion of the anterior margin, complete ventral margin and ventral portion of the posterior margin continuously convex arched; anteroventral margin very slightly elongated (obliquity !) and therefore slightly more convex in outline; median and dorsal portion of the

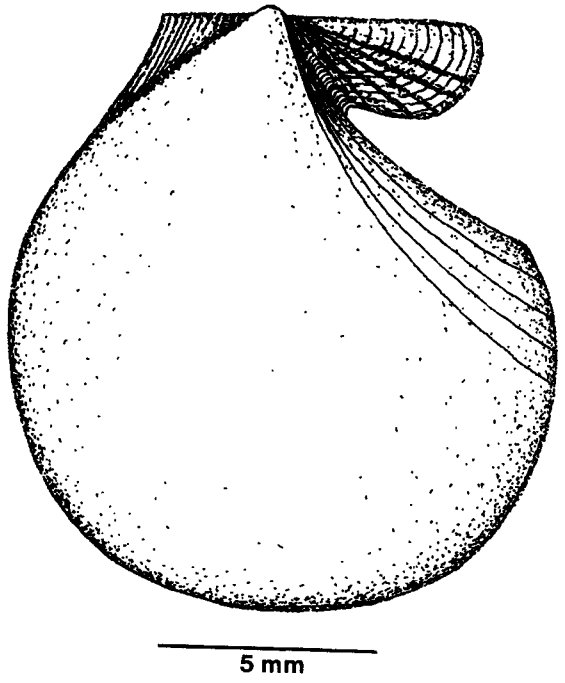

Figure 4. *Streblopteria piltonensis* (Whidborne, 1896). Reconstruction of the right valve external morphology based on the lectotype (compare Fig. 2A and B) and paralectotypes

posterior margin including auricular sulcus less convex rounded in outline; dorsal portion of the posterior margin inconspicuously passing into the concave portion of the posterior margin of the posterior auricle; posterior auricle very indistinctly separated from the posterior region of the shell body.

Sculpture pattern. Median shell body smooth or extremely fine commarginal striated; growth lines very rarely slightly strengthend to form concentric wrinkles or rugae. Anterodorsal fringe region near anterior slope towards byssal sulcus or byssal notch covered with 3-6 extremely thin, radial threads. Anterior auricle bipartite: dorsal portion without radial costae, ventral portion, except on byssal fasciole, sculptured with 3-4 thin, radial costae; anterior auricle additionally covered with strong, fine, sharply raised growth lines. Posterior auricle, like the median shell body, smooth or striated with faint commarginal growth lines.

Valves inflated with medium convexity, greatest in the central region. Auricles very gently convex or flat, anterior auricular sulcus deeply furrowed; posterior auricular sulcus very inconspicuously marked by the flattening of the posterior auricle.

Left valve (Fig. 3A-F). The outline of the median shell body corresponds to that of the right valve; umbo less inflated. Anterior auricular sulcus very shallow, passing into a small byssal sinus. Anterior auricle triangular, anterior margin of the anterior auricle gently convex rounded and joining the anterodorsal margin at an obtuse angle. Posterior auricle small, elongated, triangular, even less distinctly separated from the central shell body than on the right valve due to its very slight inflation; Hinge plate edentulous; elongated, triangular ligamental area preserved on internal mould of a left valve; central resilifer not visible due to tectonic crushing of the umbo. No internal mould available showing proper impressions of muscle scars and pallial line.

Measurements: see Tab. 2.

Remarks. The great variety of „species" established by deKoninck (1885) for the Carboniferous seems to be phaenotypic. Therefore, ontogenetic analysis and variation statistics are necessary to establish a solid discrimination on species level.

A diagnostic character of *S. piltonensis* is the ornament on the right anterior auricle, characterized by a bipartition into a radially ornamented ventral region and a dominantly commarginal sculptured dorsal field. This character distinguishes *S. piltonensis* from all subsequent taxa and from *S. lepis* (Whidborne, 1896), from the latter even more by a differing shell height/shell length ratio. Members of *Streblochondria* and *Striochondria* Waterhouse, 1983 are covered, at least on one valve, with radial or reticulate sculpture patterns. But it has to be stressed that some specimens of *S. piltonensis*, including the lectotype, show a narrow anterior shell region with minutely developed radial threads.

Localities. Vicinity of Barnstaple (SW-England); vicinity of Ratingen and Velbert (W-Germany).

Streblopteria lepis (Whidborne, 1896)

Figs. 5-6, Tabs. 3-4

v* 1896 *Pleuronectites lepis* Whidborne, Preliminary Synopsis: 375.

v 1896/97 *Pleuronectites lepis*. – Whidborne, Devonian fauna South England, 3: 142, Pl. 16 Fig. 12, 13.

v 1902 *Aviculopecten* sp. – Drevermann, Etroeungt-Stufe: 504.

pt 1941 *Streblochondria piltonensis*. – Paul, Lamellibranchiata infracarbonica: 232.

Table 2. Measurements [in mm] of *Streblopteria piltonensis* (Whidborne, 1896). Ltot = total length; Lant = length of valve anterior to umbo; Lpost = length of valve bejond umbo; LAA = length of anterior auricle (anterodorsal margin); LPA = length of posterior auricle (posterodorsal margin); H = greatest height of valve; obliquity = angle of divergence between vertical of valve and direction of maximum growth; (LT) = lectotype; (PLT) = paralectotype.

Specimen	Valve	Preservation	Ltot	Lant	Lpost	LAA	LPA	H	Obliquity°
SM.H.327 (LT)	rv	int-mould	12,5	7,5	5,0	4,0	2,0	14,0	~15
SM.H.328 (PLT)	rv	ext-mould	22,0	13,0	9,0	6,5	3,5	23,0	~20
NDM.659 (PLT)	rv	int-mould	12,5+	5,5+	7,0	4,0	1,6	16,0	~10
NDM.661 (PLT)	lv	[int-mould]	15,0	7,0	8,0	4,0	2,0	15,8	~0
SW.1329	rv	int-mould	11,5+	6,5+	5,0	3,0	1,5	16,0	~20
SW.1334	rv	int-mould	10,0	7,0	3,0	3,0	1,0	10,5	~20
KW.VLA.66	lv	int-mould	15,5	9,5	6,0	4,0	2,0	17,0	~17
ET.Wa.283	rv	int-mould	9,0	6,0	3,0	3,0	1,3	10,0	~25
ET.Wa.526	rv	[int-mould]	8,0	4,5	3,5	2,5	1,0	9,5	~5

Table 3. Studied material of *Streblopteria lepis* (Whidborne, 1896).

Specimen	Preservation	Collection	Citation
SM.H.326(PLT)	int-mould.rv	Porter	Whidborne, 1896: Pl. 16 Fig. 12
Mbg. 4763	int + ext-mould.rv	Drevermann	Drevermann, 1902: 504
Mbg. 3040	int + ext-mould.dv	Drevermann	Drevermann, 1902: Pl. 14 Fig. 21
ET.Wa.258	int + ext-mould.rv	Thomas	
GSM.Za.3864	ext-mould.lv	GSM	
BGR.5247 (Berlin)	int-mould.rv	Paul	

v 1993 *Streblopteria lepis*. – Amler, Bivalvenfauna des Oberen Famenniums: 114, Pl. 8 Fig. 7-9.

Nomenclatorial remarks. Although the species is fully described and figured in Whidborne's monograph (text December 1897, figures October 1896) the preliminary synopsis (August 1896) preceds through its short description according to ICZN, Articles 11-12.

Lectotype (designated here). The syntype series consists of four specimens (Whidborne, 1897: 142); from these the internal mould of a left valve (NDM.656), Hall Collection, figured in Whidborne, 1896: Pl. 16 Fig. 13 is being chosen as lectotype; it is kept in the North Devon Museum Barnstaple.

Paralectotypes. The remaining three specimens mentioned by Whidborne (1897), only one of which (SM.H.326) has been localized.

Studied material. See Tab. 3.

Type locality. Top Orchard Quarry [= former quarry on eastern road side of A39 opposite junction with B3230, 2 km north of Barnstaple, Devon, Great Britain].

Type stratum. Pilton Shales, Pilton Formation; Pilton A according to Goldring (1955, 1970); approximately *costatus*-Zone, Late Famennian („Strunian").

Occurrence. Late Famennian of SW England and W Germany.

Original diagnosis (Whidborne, 1896a: 375). „Smooth, sub-orbicular, slightly oblique, with sub-equal wings."

Revised diagnosis. Characters of the genus *Streblopteria* with the following features: Shell slightly inequivalve; valves slightly opisthocline or acline, outline of valves subcircular to transversely oval. Valve height smaller or equal to valve length; anterior auricle twice as long as posterior auricle; external shell surface covered with fine commarginal growth lines, anterior region of median shell body adjoining to byssal notch without radial lines; anterior auricle ornamented with 4-5 fine radial ribs.

Morphology (Figs. 5 and 6). Shell slightly inequivalve in auricular region; valves opisthocline, almost equilateral, ratio Lant : Lpost about 1; auricles of different size, more distinctly separated from the shell body on the right valve, anterior auricles about twice as long as posteriors; outline of the median shell body subcircular-transversely oval, pectiniform; angle of obliquity about 5-10°. Ratio of valve length to valve height about 1,0-1,1.

Right valve (Figs. 5C, E, F, G, H and 6). Umbo orthogyrous, small, bluntly triangular, not swollen, not raised above the hinge margin; umbonal angle 90-100°. Hinge margin straight, reaching about 50-60% of the total valve length. Anterior auricular sulcus sharply furrowed, narrow and passing into a

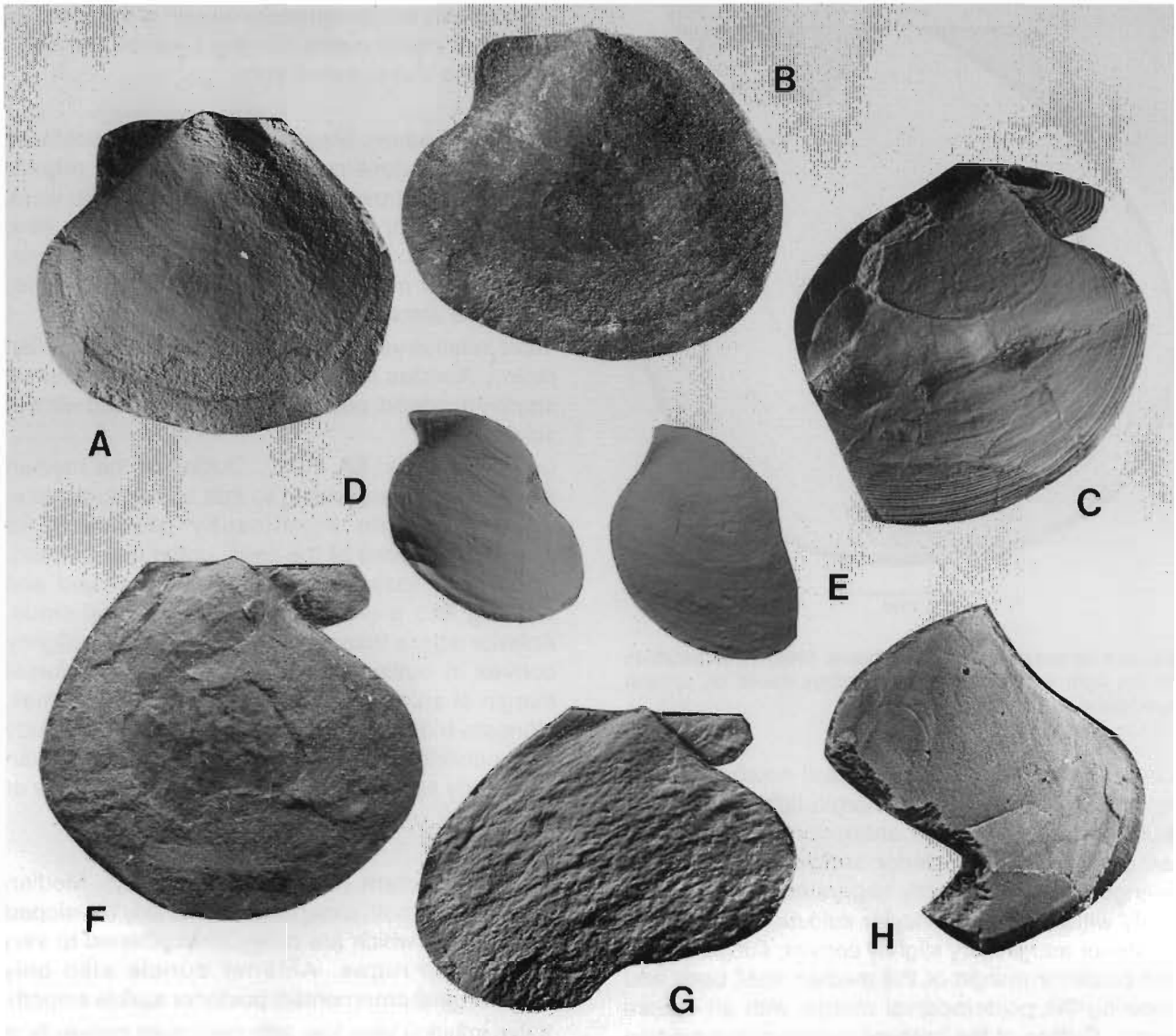

Figure 5. *Streblopteria lepis* (Whidborne, 1896).
A: Lectotype, NDM.656, Hall Coll., internal mould of left valve, coated with MgO. Figured in Whidborne, 1896: Pl. 16 Fig. 13. x3,0 [#21726#].
B: Lectotype, NDM.656, Hall Coll., internal mould of left valve. Figured in Whidborne, 1896: Pl. 16 Fig. 13. x3,3 [#21719#].
C: Specimen Mbg. 4763, Drevermann Coll., internal mould of right valve, defective in posterior region, coated with MgO. x3,2 [#5819#].
D: Specimen Mbg. 3040, Drevermann Coll., internal mould of left valve, defective in anterior and dorsal region, coated with MgO. x3,5 [#97389#].
E: Specimen Mbg. 3040, Drevermann Coll., internal mould of right valve, defective in posterior and dorsal region, coated with MgO. x3,8 [#9739#].
F: Specimen BGR.5247, Paul Coll., internal mould of right valve, defective in anterodorsal region. x6,0 [#5641#].
G: Specimen ET.Wa.258, Thomas Coll., internal mould of right valve, defective in ventral region, coated with MgO. x4,0 [#5821#].
H: Paralectotype, SM.H.326, Porter Coll., internal mould, defective in posteroventral and dorsal region, coated with MgO. Figured in Whidborne, 1896: Pl. 16 Fig. 12. x6,0 [#3942#].

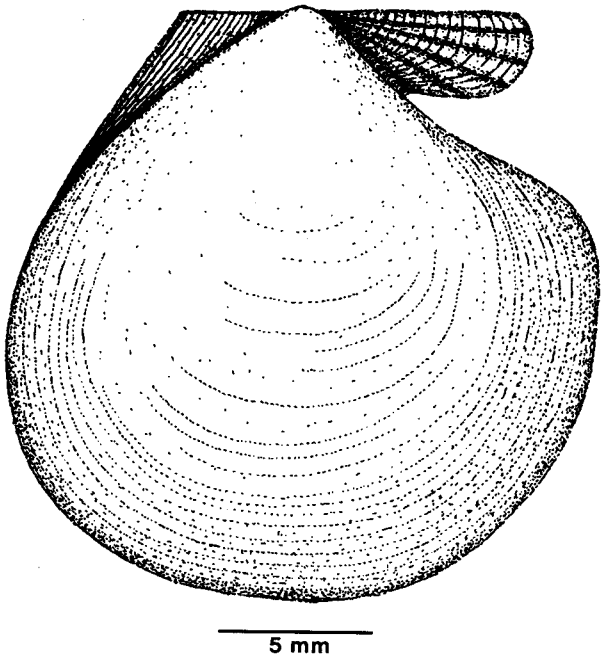

Figure 6. *Streblopteria lepis* (Whidborne, 1896). Reconstruction of the right valve external morphology based on several specimens.

deeply indented V-shaped byssal notch. Anterior auricle lobate, its anterior margin tightly convex in outline and meeting the anterodorsal margin with an obtuse angle. Posterior auricle small, narrow, triangular, and indistinctly separated from the shell body without a real auricular sulcus, outline of the posterior margin very slightly convex, subparallel to the posterior margin of the median shell body and meeting the posterodorsal margin with an obtuse angle. Outline of the anterior margin of the median shell body parallel with byssal notch slightly concave up to the projecting anteriormost point of the shell, then tightly bent in ventral direction; ventral section of the anterior margin, complete ventral margin and ventral section of the posterior margin continuously and regularly broadly convex in outline; dorsal section of the posterior margin including auricular sulcus again very gently convex in outline or passing continuously into the posterior margin of the posterior auricle; posterior auricle forming a narrow, adherent tract to the median shell body.

Sculpture pattern. Median shell body and posterior auricle both covered with very fine and regular commarginal growth lines, rarely thickened to weak rugae. Anterior auricle with 4-5 fine radial ribs; additionally covered with fine, sharp growth lines. On internal moulds only growth rugae visible, otherwise smooth.

Valve inflation very low; maximum inflation in median region. Auricles flattened, anterior auricular sulcus sharply furrowed; posterior auricle separated without sulcus.

Left valve (Figs. 5A, B, D). Outline of the median shell body corresponding to that of the right valve, anterior margin significantly protruding to anteriormost point of the shell; umbo less inflated. Anterior auricular sulcus markedly furrowed and passing into a small and shallow byssal sinus. Anterior auricle triangular, its anterior margin slightly convex in outline and meeting the anterodorsal margin at an obtuse angle. Posterior auricle small, elongate-triangular, separated from the shell body very indistinctly due to the low inflation of the median shell body and the missing of an auricular furrow or sulcus.

Sculpture pattern (internal moulds only). Median shell body smooth except for very weakly developed growth lines which are rarely strengthened to very low growth rugae. Anterior auricle also only commarginal ornamented; posterior auricle smooth.

Valve inflation very low, with maximum convexity in median region; flattening of inflation continuous in posterior direction, abrupt and steep in anterior direction; auricles flat.

Hinge plate, ligamental area, adductor muscle scars and pallial line not visible on any specimen. Some impressions visible only on internal moulds are regarded as preservational artefacts.

Measurements: see Tab. 4.

Table 4. Measurements [in mm] of *Streblopteria lepis* (Whidborne, 1896). Ltot = total length; Lant = length of valve anterior to umbo; Lpost = length of valve bejond umbo; LAA = length of anterior auricle (anterodorsal margin); LPA = length of posterior auricle (posterodorsal margin); H = greatest height of valve; obliquity = angle of divergence between vertical of valve and direction of maximum growth; (LT) = lectotype; (PLT) = paralectotype.

Specimen	Valve	Preservation	Ltot	Lant	Lpost	LAA	LPA	H	Obliquity°
NDM.656 (LT)	lv	int-mould	18,0	9,0	9,0	4,0	2,5	17,0	~90
SM.H.326 (PLT)	rv	int-mould	7,2+	3,7	3,5+	-	-	8,0	~85
Mbg. 4763	rv	int-mould	17,0	9,0	8,0	4,5	-	17,0	-
ET.Wa.258	rv	int-mould	13,5	6,5	7,0	3,5	1,5	10,0+	~90
GSM.Za.3864	lv	ext-mould	10,0+	4,5+	5,5	3,0	1,5	7,0+	~90
BGR.5247 (Berlin)	rv	int-mould	9,8	5,1	4,7	3,7	1,3	9,3	~90

Remarks. There are only very few specimens of this species and it seems doubtful to separate *S. lepis* from *S. piltonensis* on the basis of very slight differences in shell morphology. But, the differing proportions in shell dimensions and the missing radial filae on the anterodorsal shell region are visible on the studied specimens and distinguish both taxa (see *S. piltonensis*).

Localities. Vicinity of Barnstaple (SW-England); vicinity of Velbert (W-Germany).

Streblopteria hicksi (Whidborne, 1896)

Fig. 7

v* 1896 *Pleuronectites Hicksii* Whidborne, Preliminary Synopsis: 375.
v 1896/97 *Pleuronectites hicksii*. – Whidborne, Devonian fauna South England, 3: 142, Pl. 16 Fig. 14, 14a.
v 1993 *Streblopteria hicksi*. – Amler, Bivalvenfauna des Oberen Famenniums: 116, Pl. 7 Fig. 13.

Nomenclatorial remarks. Although the species is fully described and figured in Whidborne's monograph (text December 1897, figures October 1896) the preliminary synopsis (August 1896) preceds through its short description according to ICZN, Articles 11-12.

Type material. The type series consists of four insufficiently preserved syntypes, none of which show detailed morphology for complete diagnosis (see below).

Lectotype (here selected, Fig. 7A-B). Internal mould of a left valve, severely damaged (NDM.662), Hall Collection, figured in Whidborne (1896: Pl. 16 Fig. 14, 14a), kept in the collection of North Devon Museum Barnstaple.

Paralectotypes. The remaining three specimens mentioned in Whidborne (1897: 143) from the Porter and Whidborne collections, housed in the Sedgwick Museum Cambridge.

Type locality. Bradford, Devon. This expression may be a spelling error of the village Bradiford, 1 km northwest of Barnstaple, Devon, Great Britain.

Type stratum. Pilton Shales, Pilton Formation; according to Goldring (1955, 1970) and Edmonds *et al.* (1985) generally all possible localities in the northwestern peripherie of Barnstaple belong mainly to Pilton A; approximately *costatus* Zone, Late Famennian („Strunian").

Original diagnosis (Whidborne, 1896a: 375). „Short, ovate with minute concentric striae."

Remarks and **resemblances**. Without exception all the studied syntypes are fragments which do not allow a definitive diagnosis. Only a few details of the shell morphology are visible, some of which had to be reconstructed from the internal moulds only. The lectotype steinkern (Fig. 7A-B) shows few radial lines on the anterior half of the valve which distinguishes it from *S. piltonensis* and *S. lepis*. The other syntypes are indeterminable or fit within the variation of *Streblopteria piltonensis*. Until further material has been collected the taxon *Pleuronectites hicksii* Whidborne, 1896 should be confined to the type material!

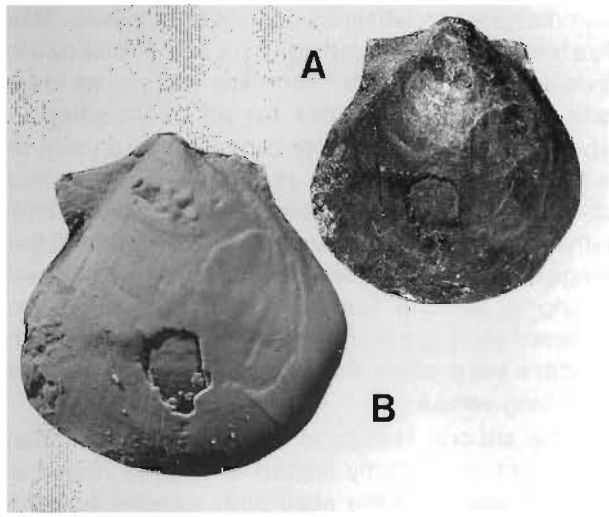

Figure 7. *Streblopteria hicksi* (Whidborne, 1896).
A: Lectotype, NDM.662, Hall Coll., internal mould of left valve, damaged. Figured in Whidborne, 1896: Pl. 16 Fig. 14. x4,9 [#21619#].
B: Lectotype, NDM.662, Hall Coll., internal mould of left valve, damaged, coated with MgO. Figured in Whidborne, 1896: Pl. 16 Fig. 14. x6,0 [#292056#].

5. DISCUSSION ON LATE FAMENNIAN STREBLOCHONDRIIDS

The generic position of the three described species presents a multifold problem on taxonomical, nomenclatorial, eco-morphological and preservational grounds. Yet, this problem cannot be solved satisfactorily, because some of the mentioned reasons are difficult to judge, some may be unsolvable. The most serious difficulty arises with the already established genera *Streblopteria* and *Streblochondria*, the former being completely smooth according to its original description by McCoy (1851, 1855), the latter being ornamented with radial and commarginal ribs of equal strength on the complete shell. But even though Waterhouse (1983) added a third genus *Striochondria*, recognized by thin radial fila, two major morphological characters seen in several specimens with streblochondriid features cannot be grouped.

The first one is the taxonomical treatment of species with different valve morphology, as can be seen in the Viséan *Streblochondria praetenuis* (v. Koenen, 1879). This species shows radial and commarginal sculpture patterns on left valves and

commarginal growth lines only on right valves. This feature is very common in Late Palaeozoic aviculopectinids and euchondriids and seems to be one of the main reasons for an overloading in species names in aviculopectinacean taxonomy. In a few cases species can readily be distinguished due to their complete preservation of both valves either lying opposite to each other connected at the hinge line or being preserved with both valves closed in original position. But the vast majority of species is based on single or fragmentary valves only which hinders very often the accurate assignment of matching valves.

The second feature is the restriction of radial ornament to a strictly limited shell area near the anterior margin of the shell body parallel with the byssal sulcus and byssal notch. The rest of the shell body of these shells is left smooth or ornamented with commarginal growth lines only. This character is also a widely distributed phenomenon (comp. Newell 1938) observed in many Carboniferous specimens but very often obscured by the insufficient state of preservation. As this morphological feature may have been a character influenced by environment or mode of life, it either could distinctly be developed or it could be obscured, if, respectively, the ecological stress had not been present. The above mentioned features can be observed in Recent analogues in the Pectinacea, without ever having been analysed adequately.

6. EVOLUTION

During Devonian time several evolutionary trends in pterinopectinids and aviculopectinids show a parallel development. A general tendency in the evolution from predominantly conservative pterinopectinid forms to the more modern aviculopectinid types is visible, without a sudden extinction of the conservative stock (Amler, 1993, 1995, in press). Obviously, rapid evolution is visible within the aviculopectinids in the Late Devonian, increasing in importance after the Frasnian Crisis or the *annulata*-event (Becker, 1992).

Aviculopectinids reach a first acme in the limestone facies of the Carboniferous Anglo-Brabant shelf area. But radiation must have started parallel to the development of varied shelf environments during Latest Devonian time, because several different groups occur separately and simultaneously in the earliest Carboniferous and can be traced back to the Late Famennian. The central group may be formed by *Aviculopecten*, which could have been derived from erect, upright forms of *Pterinopecten* or *Pseudaviculopecten*. Newell (1938) regarded *Streblochondria* (and allies) as a primitive aviculopectinid, because of the poor development of its auricles recapitulated in early growth stages of some aviculopectinids. But no true ancestor with streblochondriid morphology is known in the Early Famennian which leads to the contrary assumption that streblochondriids evolved from *Aviculopecten* by a successive reduction of valve ornamentation and posterior auricle size.

At present, we only know *Streblopteria piltonensis*, *S. lepis* and *S. hicksii* as the oldest members of this group with a distinct, reduced morphology. Once developed, this type of morphology diversified throughout the Carboniferous and persisted into the Permian (Waterhouse, 1982, 1987).

Whereas most of the morphological structures were reduced, the development and sculpture of the anterior auricle and the anterior marginal region of the right valves seem to play an important role due to - at present unknown - environmental or functional reasons.

A comparable trend is developed in pernopectinids and early entoliids, which seemed to arise at the same time as streblochondriids in the Famennian. As already mentioned in a previous chapter, a major difficulty in the search for possible ancestors of Late Devonian and Early Carboniferous streblochondriids arises in the lack of preserved fossil shell material in Late Famennian siltsones, where all fossils are preserved as external and internal moulds. The complete observations and thoughts on streblochondriid evolution will be discussed after completition of the study on the family Streblochondriidae (Amler, in prep. b).

7. MODE OF LIFE IN STREBLOCHONDRIID BIVALVES

Streblochondriids like most aviculopectinids, some other pectinids and few pterinopectinids possess a more or less asymmetrical shell. The presence of a byssal organ is known in nearly all taxa. According to Stanley (1968) and later authors these animals should have been epibyssate attached to any erect substrate or byssally attached lying with the left valve upside on the seafloor. Different kinds of substrate could have served for attachment, i.e. crinoidal stems, erect bryozoan branches and fronds, other molluscan shells and - especially - algal thalli in the „kelp areas" within the photic zone. The strong and heavily ornamented anterior auricles combined with the peculiar ornament on the anteriormost region of the shell body are suggestive of a fixed byssal attachment during most of adult life in various and differing life positions.

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