

SYSTEMATIC REVISION OF THE MIDDLE AND LATE DEVONIAN BRACHIOPODS *Schizophoria* (*Schizophoria*) AND '*Schuchertella*' FROM NORTH AMERICA

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SYNOPSIS *Schizophoria* and '*Schuchertella*', two common genera of Devonian brachiopods from North America, are systematically revised based on cladistic analysis. Several Early Devonian schizophoriid species are placed within *S. (Eoschuchertella)*, while all other North American Devonian and Mississippian species studied are placed within *S. (Schizophoria)*. *Schizophoria meeki* Fenton & Fenton is synonymised with *S. macfarlanii* Meek. Ancestral forms of *Schizophoria (Schizophoria)* were present in Europe and the Appalachian basin and inhabited outer platform environments through the Frasnian. Several independent lineages of *S. (Schizophoria)* persisted through the Late Devonian biodiversity crisis and subsequently colonised nearshore environments. Most cladogenetic events within North American species of *S. (Schizophoria)* occurred via dispersal mechanisms, while vicariant speciation was rare. Cladistic analysis of North American species assigned to '*Schuchertella*' revealed that all species through the Frasnian belong to *Floweria*, an impunctate genus, while Famennian and later species belong to *Schuchertella*. The generic placement of the Devonian 'schuchertellids' is revised accordingly. *Schuchertella* and *Floweria* are superficially similar and exhibit an analagous (albeit temporally offset) evolutionary transition from free-resting ancestors to descendants with attached pedicle valves. *Floweria* also exhibits reduced rates of vicariant speciation compared to speciation by dispersal. The relative reduction in vicariant speciation has been documented for other Devonian taxa (bivalves, phyllocarids and trilobites) and may be an important control on faunal dynamics in North America during the Late Devonian biodiversity crisis.

KEY WORDS Mass extinction, Phylogeny, Brachiopods, Laurentia, Speciation, Biogeography

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INTRODUCTION

Orthid and orthotetid brachiopods were among the most common organisms in Devonian shallow marine benthic communities. Both of these brachiopod groups persisted through the Frasnian–Famennian (Late Devonian) biodiversity crisis,

while experiencing both extinction and speciation. Investigation of the patterns and processes involved with Middle to Late Devonian diversity patterns may provide further insight into the controls on faunal dynamics during the Frasnian–Famennian crisis, such as the effect of geographical range on biotic turnover. In spite of the potential importance of

these groups, little has been published previously regarding species-level phylogenetic relationships and biogeographical patterns of orthid and orthotetid brachiopods during the Devonian. This paper presents species-level phylogenetic revisions of representative orthid and orthotetid genera, *Schizophoria* King, 1850 and '*Schuchertella*' Girty, 1904, respectively. The phylogenies derived here are also used to examine biogeographical patterns of these taxa in North America during the Middle and Late Devonian.

REVISION OF *SCHIZOPHORIA* (*SCHIZOPHORIA*)

Background

Schizophoria King, 1850 is a species-rich, cosmopolitan genus that persisted from the Early Devonian through the Early Carboniferous. The Middle to Late Devonian is a key interval in the history of this taxon as it encompasses the maximal diversity increase of the largest subgenus, *Schizophoria* (*Schizophoria*) King, 1850. This interval also encompasses a dramatic biotic turnover and important changes in the geographical range of *Schizophoria* during the Late Devonian. Several studies have revised aspects of schizophoriid taxonomy (e.g. Lazarev 1976; Jansen 2001), but a comprehensive taxonomic revision of Middle and Upper Devonian *Schizophoria* from North America has not been undertaken previously. This paper presents a phylogenetic analysis of Middle and Late Devonian *Schizophoria*, primarily members of *S. (Schizophoria)* from North America, to assess species validity, taxonomy and evolution within this subgenus.

Schizophoria is a common and significant Paleozoic genus that is readily distinguished by its transversely ovate, biconvex, uniplicate shell ornamented with fine striae. The ventral muscle field is bilobate to obcordate and includes both median and bounding ridges extending from the dental plates (Williams & Harper 2000). Although specimens are readily assignable to genus, specific assignments are more difficult due to character convergence. Numerous species have been assigned to *Schizophoria*, but most of these species are restricted in geographical and/or stratigraphical occurrence.

Although many published accounts of *Schizophoria* involve either erecting new species or documenting specific occurrences within species lists, several studies have attempted revision and synthesis of whole faunas (i.e. Struve 1965; Pocock 1966, 1968; Lazarev 1976; Cooper & Dutro 1982; Jansen 2001). Most have struggled with the vast number of species involved and attempted to alleviate this problem by either establishing species groups (e.g. Pocock 1966, 1968) or erecting subgenera (Lazarev 1976; Jansen 2001). In the recent revision of the *Treatise on Invertebrate Paleontology*, Williams & Harper (2000) delineated three subgenera, *S. (Schizophoria)* King, 1850 (Lower Devonian to Lower Carboniferous) *S. (Paraschizophoria)* Lazarev, 1976 (Lower Devonian to Lower Carboniferous) and *S. (Pocockia)* Lazarev, 1976 (Lower Carboniferous), and elevated a formerly proposed Lower Devonian subgenus *S. (Eoschizophoria)* Rong & Yang, 1980 to generic status. Williams & Harper (2000) also noted that the diagnostic features of each of the other subgenera are present in the *S. (Schizophoria)* lineage, which restricts the utility of its subgeneric usage. The

problem with overlapping morphological features between subgenera was also noted by Jansen (2001) who described two new Lower Devonian subgenera, *S. (Rhenoschizophoria)* and *S. (Pachyschizophoria)*. In particular, *S. (Schizophoria)* encompasses such a wide variety of forms that most of the diagnostic characteristics of the other subgenera are incorporated into one or more species of *S. (Schizophoria)*. However, these character convergences tend to be at disparate stratigraphical horizons. For example, Lower Devonian forms of *S. (Schizophoria)* tend to be small in size, while Middle and Upper Devonian species can approach a large size, such as that considered to be characteristic of the Lower Devonian subgenera *S. (Pachyschizophoria)* or *S. (Rhenoschizophoria)* (Jansen 2001).

The validity of *S. (Schizophoria)* as a useful taxon is considered in this paper and presented along with the first phylogenetic revision of *S. (Schizophoria)*. The estimated phylogeny is also used to examine biogeographical changes in North American *S. (Schizophoria)* during the Middle and Late Devonian.

Phylogenetic analysis

Taxa analysed

Specimens representing 23 species of *Schizophoria* were analysed. Most species known from the Middle and Upper Devonian and several Lower Devonian species from North America (those for which sufficient morphological information exists) were included in the phylogenetic analysis. Several taxa lacking sufficient morphological data for character analysis, which can result in spurious cladistic reconstructions, were excluded. Because the focus of this analysis was on evolutionary and biogeographical patterns of Middle and Late Devonian species of *Schizophoria* (*Schizophoria*), most species of *Schizophoria* attributed to other subgenera in older and younger strata were excluded. However, several Early Devonian species attributed to other subgenera and Early Mississippian species attributed to *Schizophoria* (*Schizophoria*) were included, to help constrain the ages of ancestral speciation events and to determine which lineages persisted through the Late Devonian biodiversity crisis. *Schizophoria* (*Rhenoschizophoria*) *provulvaria* (Maurer, 1886) was chosen as the outgroup for character polarisation. This taxon was selected because it is a well-characterised member of the subgenus *S. (Rhenoschizophoria)*, a potential sister group to *S. (Schizophoria)* (Jansen 2001). *Schizophoria* (*Rhenoschizophoria*) is known only from the Lockhovian to Emsian of Europe, North Africa and Turkey (Jansen 2001).

Type specimens were examined for analysis whenever possible. Examination of type specimens is essential for determining character states since these are the name bearers of the species; additional specimens can provide further information but do not carry equivalent taxonomic status (International Commission on Zoological Nomenclature 1999) and, thus, are not as critical for character analysis. The type series of many species comprises multiple specimens, which allow the range of variation within a species to be determined. When possible additional non-type specimens and specimens illustrated in the literature were also examined. Only specimens interpreted to represent adult individuals were included. Ontogenetic variation, therefore, is not considered within this analysis and all character codings represent the adult condition.

The paratype series of *S. iowensis* (Hall, 1858) included two distinguishable morphotypes: subcircular versus transversely ovoid forms. The two morphotypes were coded individually and analysed separately as *S. iowensis* 'A' and *S. iowensis* 'B' to determine whether they grouped together and formed a single species or belonged within two distinct species.

Specimens were examined from the following collections: American Museum of Natural History (AMNH); Carnegie Museum of Natural History (CM); Cincinnati Museum Center (CMC); Field Museum of Natural History (FMNH); Geological Survey of Canada (GSC); New York State Museum (NYSM); Ohio State University Orton Museum (OSU); Smithsonian Institution (USNM); University of Michigan Museum of Paleontology (UMMP); and Yale Peabody Museum (YPM).

Characters and character states

Parsimony analysis was conducted using 36 morphological characters. Although higher-level brachiopod relationships have been the subject of phylogenetic revision (e.g. Williams & Brunton 1993; Carlson 1995; Jaecks & Carlson 2001; Leighton & Maples 2002), only one species-level brachiopod phylogeny based on morphological characters has been previously published (i.e. Monks & Owen 2000). Both internal and external characters were included in this analysis because both have been proven to be useful in both species-level taxonomy of this group (Williams & Harper 2000; Jansen 2001) and in phylogenetic studies of other brachiopod clades (i.e. Monks & Owen 2000; Leighton & Maples 2002).

Due to the limited amount of discrete character variation within *Schizophoria*, *Schizophoria* species are typically distinguished by relative differences in size, shape, or expression of features such as ornamentation or muscle scars (Jansen 2001). Consequently, although a number of discrete characters, such as presence or absence of an anteromedian ridge on the interior of the dorsal valve (character 34), can be coded, many characters represent relative proportions, such as the relative inflation of the dorsal valve (character 2). Relative character states are common in phylogenetic analyses of many invertebrate clades (e.g. arthropods: Lieberman 2002; Rode & Lieberman 2002; bivalves: Monari 2003; Rode 2004; brachiopods: Monks & Owen 2000; bryozoa: Pachut & Anstey 2002; crinoids: Kammer & Ghan 2003). Some relative character states include morphometric values and may appear quasi-continuous when normalised to produce a ratio. Continuous characters have been shown to possess significant phylogenetic signal (Thiel 1993; Morton & Kincaid 1995); characters that appear continuous, therefore, should not be excluded from analyses *a priori*. Approximately one half of the morphological characters included within this analysis are based on morphometric measurements. Measured values for each morphometric character per species are shown in Table 1. Character states were determined following the suggestions of Morton & Kincaid (1995), who advise visual inspection of the data distribution followed by analysis of variance (ANOVA) to determine the distinctness or overlap of prospective character states. Measurements were divided into character states by examining univariate and histogram plots of the data from each specimen and dividing values into classes based on natural breaks. Natural breaks within the quasi-continuous data series were located on the basis of

gaps or changes of slope within the distribution. Data values within each class were compared using ANOVA using Minitab (Minitab Inc. 1996). The distribution of morphometric data by character state is presented in Table 2. In all cases, the 95% confidence intervals of the mean values of each character state are non-overlapping, which suggests character states are discrete.

Morphometric character coding for each species is based on the distribution of data in Table 1. The entire range of values exhibited by a species in Table 1 was considered during character coding. When morphometric measurements for a species include values within the expected range (mean \pm 1 standard deviation) of multiple character states, the species was coded as polymorphic for that character. In cases where the morphometric measurements for a species ranged outside the bounds of a single character state but not within the range of the next character state, the species was coded with only the first character state. Characters were coded in this way because the range values (mean \pm 1 standard deviation) represent 67% of the expected values for each character state; additional overlap, particularly within the boundary of mean \pm 2 standard deviations is expected within the distribution at a lower frequency (Sokal & Rohlf 1995). It is most probable, therefore, that the species exhibits only the first character since it falls within the expected range of that character only and species were coded accordingly.

Characters are arranged into external, ventral valve internal and dorsal valve internal groups. (0) represents the presumed primitive state. Morphological terminology follows Williams & Brunton (1997). Character codings for analysed taxa are presented in Table 3. Species that exhibited multiple states for a character – whether a morphometric character (as described above) or discrete – were coded as polymorphic for that character. The locations of key morphological measurements are illustrated in Fig. 1.

External characters

All measurements in millimeters.

1. Size. Determined by measuring the maximum shell width parallel to the hinge line (Fig. 1.1a): (0), large (≥ 32.1 mm); (1), medium ($22.4 \leq x \leq 28.5$ mm); (2), small (≤ 17.9 mm).
2. Relative inflation of the dorsal valve. The ratio of the maximum dorsal valve height, measured perpendicular to the commissural plane, divided by the maximum width, measured parallel to the hinge line (Fig. 1.1e): (0), low (≤ 0.228); (1), moderate ($0.257 \leq x \leq 0.333$); (2), high (≥ 0.479).
3. Relative inflation of the ventral valve. The ratio of the maximum ventral valve height, measured perpendicular to the commissural plane, divided by the maximum width, measured parallel to the hinge line (Fig. 1.1e): (0), low (≤ 0.215); (1), moderate ($0.260 \leq x \leq 0.309$); (2), high (≥ 0.338).
4. Relative length of the hinge line. The ratio of the length of the hinge divided by the maximum width, measured parallel to the hinge line (Fig. 1.1b): (0), long (≥ 0.638); (1), short (≤ 0.688).
5. Depth of the sulcus. The ratio of the depth of the sulcus, measured as the vertical distance between the commissure at the centre of the sulcus and the commissure at the break in the slope at the side of the sulcus,

Table 1 Data range of morphometric characters of species in *Schizophoria* analysis.

	1	2	3	4	5	6	7	8	11	12	15	16	21	27	28	29	31	32	33
<i>S. (Rhenoschizophoria) provulvaria</i>	30.0– 40.4	0.121– 0.210	0.159– 0.216	0.696– 0.773	0.163	0.490	1.030	0.558– 0.773	0	0.369	0.145	0	?	0.497– 0.605	0.354– 0.393	0.184– 0.207	0.349– 0.551	0.343– 0.368	0.114– 0.161
<i>S. (Eoschizophoria) oriskania</i>	20.3– 20.8	0.183– 0.296	0.202– 0.296	0.433– 0.542	0.080	0.543– 0.704	1.000– 1.105	0.889– 0.980	0.795	0.472	0.122– 0.164	0.100– 0.109	0	0.514	0.240	0.207	0.519	0.351	0.183
<i>S. (Eoschizophoria) parafragilis</i>	15.9	0	0.434	0.591	0	0	?	1.151	0	0.318– 0.449	0.105– 0.223	0.130	0.219	0	1	1	0	0	0
<i>S. (Eoschizophoria) paraprima</i>	4.6– 10.0	0.554	0.210– 0.268	0.652– 0.690	0	0	0	0.845– 0.920	0	0.409– 0.714	0.167– 0.245	0	0.146	0.307– 0.400	0.211– 0.300	0.154– 0.241	0.353	0.243	0.122
<i>S. (Schizophoria) amanaensis</i>	18.9– 28.4	0.222– 0.366	0.175– 0.176	0.606– 0.709	0.457	0.616– 0.629	0.481– 0.786	0.817	0.422	0.660	0.060– 0.180	0.030– 0.076	0.106	0	1	0	1	1	1
<i>S. (Schizophoria) australis</i>	37.0– 65.4	0.289– 0.326	0.120– 0.178	0.519– 0.648	0.210– 0.444	0.412– 0.527	0.371– 0.617	0.703– 0.826	0.705– 0.713	0.242	0.073	0.036	0.065	0.424	0.254	0.104	0.513	0.399	?
<i>S. (Schizophoria) choteueauensis</i>	14.4– 34.0	0.255– 0.360	0.334– 0.435	0.433– 0.634	<0.174	0.502– 0.550	0.817– 1.11	0.843– 0.946	>0.838	0.236– 0.448	0.112– 0.152	0.080– 0.118	0.240– 0.250	0.404– <0.493	0.281– <0.323	<0.298	0.520	0.417	0.185
<i>S. (Schizophoria) ferronensis</i>	25.7	0.268	0.191	0.554	0.358	0.642	0.710	0.825	0.632	0.612	0.209	0.155	0.202	1	1	0	?	?	?
<i>S. (Schizophoria) impressa</i>	14.7– 43.4	0.136– 0.217	0.093– 0.213	0.479– 0.626	0/1	0	0/1	0.835– 0.864	0.440– 0.530	0	0.070	?	0	0.349– 0.474	0.220– 0.387	0.181– 0.230	0.518– 0.567	0.415– 0.435	0.109– 0.176
<i>S. (Schizophoria) iowensis 'A'</i>	25.7– 29.9	0.482– 0.600	0.239– 0.301	0.452– 0.669	0.250– 0.422	0.436– 0.608	0.477– 0.741	0.730– 0.820	0.484– 0.670	0.250– 0.775	0.094– 0.140	0.081– 0.190	0.113	0.367	0.276	0.195	0.549	0.366	0.290
<i>S. (Schizophoria) iowensis 'B'</i>	18.4– 27.1	0.225– 0.239	0.144– 0.171	0.468– 0.672	0.229– 0.279	0.444– 0.467	0.705– 0.762	0.832– 0.957	0.480– 0.665	0.511– 0.711	0.040– 0.052	0	0.067– 0.163	0.374– 0.455	0.241– 0.257	0.158– 0.207	?	?	?
<i>S. (Schizophoria) macfarlanii</i>	23.5– 27.1	0.480– 0.513	0.250– 0.307	0.435– 0.502	0.291– 0.464	0.762– 0.827	0.487– 0.640	0.882– 0.887	0.540– 0.585	0.309– 0.393	0.153– 0.220	0.280– 0.381	0.070	?	?	?	0.678	<0.504	<0.135
<i>S. (Schizophoria) magna</i>	25.4– 31.5	2	0.175– 0.198	0.574– 0.653	1/ 2	1	1	0.836– 0.854	0.565– 0.698	0.582– 0.764	0.123– 0.133	0	0	0.434– 0.488	0.252– 0.336	0.224– 0.313	?	?	?
<i>S. (Schizophoria) marylandica</i>	13.9– 17.9	0	0	0.496– 0.588	0.250	0.400	1	0.669– 0.772	0.575	0	1	0	0	0.425	0.277	0.155	0.387	0.324	0.187
<i>S. (Schizophoria) meeki</i>	23.0– 31.1	0.269– 0.600	0.176– 0.315	0.461– 0.634	0.117– 0.242	0.590– 0.918	0.303– 0.670	0.894– 10.118	0.606– 0.688	0.294– 0.592	0.103– 0.194	0.128– 0.357	0.066– 0.234	?	?	?	?	?	?
<i>S. (Schizophoria) mesacarina</i>	27.6	0.428	0.134	0.492	0.241	0.511	0.712	0.822	0.705	0.648	0.154	0.125	0.211	1	1	0	0	1	1
<i>S. (Schizophoria) multistriata</i>	18.3– 30.2	0.222– 0.283	0.137– 0.240	0.430– 0.656	0.078– 0.259	0.494– 0.619	0.513– 0.900	0.821– 0.880	0.430– 0.806	0.313– 0.622	0.083– 0.143	0.020– 0.114	0.063– 0.113	0.433– 0.472	0.245– 0.282	0.164– 0.224	0.425– 0.507	0.408– 0.439	0.199– 0.293
<i>S. (Schizophoria) resupinata</i>	14.3– 26.7	0.237– 0.264	0.164– 0.203	0.468– 0.594	0.039– 0.240	0.453– 0.572	0.622– 0.863	0.790– 0.825	0.682– 0.673	0.241– 0.574	0.068– 0.071	0.054– 0.071	0	0.379	0.157	0.105	0.493	0.363	0.202
<i>S. (Schizophoria) subelliptica</i>	9.1– 14.2	0.158– 0.187	0.199– 0.231	0.589– 0.669	0	0.396– 0.400	0.124– 0.133	0.780– 0.801	0	0.476– 0.600	0.066– 0.123	0.063– 0.066	0.235	0.366– 0.373	0.231– 0.232	0.158– 0.198	0.490– 0.547	0.368– 0.374	0.209– 0.211
<i>S. (Schizophoria) sulcata</i>	21.7– 25.9	0.358– 0.595	0.239– 0.309	0.525– 0.654	0.363– 0.443	0.560– 0.714	0.519– 0.667	0.873– 0.982	0.467– 0.583	0.089– 0.192	0.063– 0.080	<0.063	0	0.434– 0.459	0.251– 0.288	1	0.544	0.442	0.327
<i>S. (Schizophoria) swallowi</i>	31.1– 50.4	0.148– 0.181	0.137– 0.161	0.633– 0.714	0	0.373– 0.391	0.791– 10.087	0.736– 0.807	0	0.600– 0.735	0.026– 0.062	0.072– 0.110	0	0.354– 0.414	0.248– 0.260	0.106– 0.160	0.495– 0.599	0.349– 0.366	0.228– 0.248
<i>S. (Schizophoria) traversensis</i>	41.1– 45.2	0.217– 0.219	0.134	0.516– 0.650	0.236– 0.348	0.478– 0.584	0.618	0.796– 0.852	0.180– 0.200	0.842	0.092– 0.175	0.146	0.134	0.414	0.303	0.219	?	?	?
<i>S. (Schizophoria) tulliensis</i>	19.9– 28.1	0.258– 0.527	0.165– 0.204	0.506– 0.650	0.081– 0.330	0.474– 0.801	0.331– 0.836	0.792– 0.904	0.463– 0.769	0.490– 0.580	0.092– 0.222	0.092– 0.175	0.068– 0.093	0.383– 0.430	0.255– 0.274	0.142– 0.197	0.408– 0.581	0.362– 0.431	0.176– 0.251

Table 2 Statistical separation of morphometric characters in *Schizophoria* analysis.

Character	Mean	S.D.	Range (mean \pm 1 S.D.)	ANOVA results
1. Maximum width				
(2) small	13.79	4.09	$x \leq 17.9$	$P < 0.001$
(1) medium	25.46	3.07	$22.4 \leq x \leq 28.5$	
(0) large	39.85	7.78	$x \geq 32.1$	
2. Dorsal valve inflation				
(0) low	0.191	0.037	$x \leq 0.228$	$P < 0.001$
(1) moderate	0.295	0.038	$0.257 \leq x \leq 0.333$	
(2) high	0.531	0.053	$x \geq 0.479$	
3. Ventral valve inflation				
(0) low	0.176	0.039	$x \leq 0.215$	$P < 0.001$
(1) moderate	0.285	0.025	$0.260 \leq x \leq 0.309$	
(2) high	0.390	0.052	$x \geq 0.338$	
4. Relative hinge length				
(1) short	0.564	0.074	$x \leq 638$	$P < 0.001$
(0) long	0.699	0.011	$x \geq 0.688$	
5. Sulcus depth				
(0) low	0.120	0.046	$x \leq 0.166$	$P < 0.001$
(1) moderate	0.247	0.024	$0.223 \leq x \leq 0.271$	
(2) high	0.403	0.053	$x \geq 0.350$	
6. Relative total height				
(0) low	0.488	0.064	$x \leq 0.552$	$P < 0.001$
(1) high	0.712	0.106	$x \geq 0.606$	
7. Comparative concavity of dorsal and ventral valves				
(1) dorsal concavity greater	0.604	0.140	$x \leq 0.745$	$P < 0.001$
(0) subequal	0.972	0.110	$0.862 \leq x \leq 1.082$	
(2) ventral concavity greater	1.365	0.106	$x \geq 1.259$	
8. Relative shell depth				
(0) low	0.769	0.065	$x \leq 0.832$	$P < 0.001$
(1) high	0.912	0.081	$x \geq 0.833$	
11. Start of sulcus				
(1) proximal	0.534	0.138	$x \leq 0.672$	$P < 0.001$
(0) distal	0.753	0.045	$x \geq 0.709$	
12. Height of ventral cardinal area				
(0) low	0.322	0.097	$x \leq 0.419$	$P < 0.001$
(1) high	0.609	0.111	$x \geq 0.498$	
15. Extension of ventral umbo across hinge				
(1) low	0.061	0.017	$x \leq 0.078$	$P < 0.001$
(0) high	0.146	0.042	$x \geq 0.104$	
16. Extension of dorsal umbo across hinge				
(0) small	0.084	0.030	$x \leq 0.114$	$P < 0.001$
(1) large	0.230	0.094	$x \geq 0.136$	
21. Size of dorsal cardinal area				
(0) small	0.105	0.039	$x \leq 0.143$	$P < 0.001$
(1) large	0.243	0.061	$x \geq 0.182$	
27. Length of ventral muscle scars				
(1) short	0.387	0.031	$x \leq 0.418$	$P < 0.001$
(0) long	0.474	0.043	$x \geq 0.431$	
28. Max width of ventral muscle scars				
(1) narrow	0.257	0.031	$x \leq 0.288$	$P < 0.001$
(0) wide	0.359	0.025	$x \geq 0.333$	
29. Min width of ventral muscle scars				
(1) narrow	0.098	0.009	$x \leq 0.108$	$P < 0.001$
(0) wide	0.196	0.040	$x \geq 0.156$	
31. Length of dorsal muscle scars				
(0) short	0.384	0.033	$x \leq 0.418$	$P < 0.001$
(1) long	0.529	0.046	$x \geq 0.453$	
32. Max width of dorsal muscle scars				
(0) narrow	0.344	0.038	$x \leq 0.383$	$P < 0.001$
(1) wide	0.433	0.034	$x \geq 0.400$	
33. Min width of dorsal muscle scars				
(0) narrow	0.155	0.036	$x \leq 0.191$	$P < 0.001$
(1) wide	0.239	0.039	$x \geq 0.200$	

For all classes, the 95% confidence intervals are non-overlapping. S.D., standard deviation.

Table 3 Character state distribution for taxa in the phylogenetic analysis of *Schizophoria*.

	12345 6789	1111111111 0123456789	2222222222 0123456789	33333333 0123456
<i>S. (Rhenoschizophoria) provulvaria</i>	00000 0000	0000000000	0?X0000000	0X00000
<i>S. (Eoschizophoria) oriskania</i>	1XX10 X010	0010000010	0001101010	110010?
<i>S. (Eoschizophoria) parafragilis</i>	20210 0?11	0001000110	11X1101011	000000?
<i>S. (Eoschizophoria) paraprima</i>	22X00 0011	00X000001?	1001111110	000010?
<i>S. (Schizophoria) amanaensis</i>	1X002 1101	11110X0110	0000000010	0111001
<i>S. (Schizophoria) australis</i>	0101Y 0101	1000110000	10110X0111	111??0?
<i>S. (Schizophoria) choteueauensis</i>	11210 0000	1000100011	1101010X10	0110100
<i>S. (Schizophoria) ferrenensis</i>	11012 1100	0111001010	010?010110	???????
<i>S. (Schizophoria) impressa</i>	X001X 0X11	110011?110	1001X0XXX0	1110100
<i>S. (Schizophoria) iowensis 'A'</i>	110YY X100	11X100X110	1001000110	0101000
<i>S. (Schizophoria) iowensis 'B'</i>	10011 011?	1110110110	1001000X10	0??????
<i>S. (Schizophoria) macfarlanii</i>	12112 1110	1101101011	000???????	?110010
<i>S. (Schizophoria) magna</i>	1201Y 1111	1110100110	10010000X0	0??????
<i>S. (Schizophoria) marylandica</i>	20011 0101	1100?10?00	1000000110	0000000
<i>S. (Schizophoria) meeki</i>	1YX1X 1110	11X1001010	1X0???????	?????1?
<i>S. (Schizophoria) mesacarina</i>	12011 0100	0010000010	1100010110	101110?
<i>S. (Schizophoria) multistriata</i>	1101X XXXX	XXX0000010	1000000010	0X11101
<i>S. (Schizophoria) resupinata</i>	1101X 0X00	11X0010010	0001100111	010110?
<i>S. (Schizophoria) subelliptica</i>	20010 0200	00100X0100	1101000111	010110?
<i>S. (Schizophoria) sulcata</i>	12112 1111	X100?10010	0000000011	0111000
<i>S. (Schizophoria) swallovi</i>	00000 0000	1010110100	1000001110	010110?
<i>S. (Schizophoria) traversensis</i>	0001Y 01X0	1110001110	0000001110	0??????
<i>S. (Schizophoria) tulliensis</i>	1Y00X XXX0	XX1100X01X	0001000110	1XXX000
<i>S. (Schizophoria) macfarlanii</i> [rev.]	1YX1W 1110	11X1X0101X	XX0???????	?110010
<i>S. (Schizophoria) magna</i> [rev.]	1Z01Y X111	11101X0110	1001000XX0	0??????

Missing data are indicated by '?'.
Character states listed as W, X, Y and Z are polymorphic, where W = (0 & 1 & 2), X = (0 & 1), Y = (1 & 2) and Z = (0 & 2).

Character numbers are listed across the top of the table.

rev., revised.

divided by shell thickness (total height) of the brachiopod (Fig. 1.1c): (0), low (≤ 0.166); (1), moderate ($0.223 \leq x \leq 0.271$); (2), high (≥ 0.350).

- Relative shell height. The ratio of the shell thickness (total height) of the individual and the maximum width, measured parallel to the hinge line (Fig. 1.1d): (0), low (≤ 0.552); (1), high (≥ 0.606).
- Comparative convexity of the valves. The ratio of the ventral valve height, measured as the maximum vertical height of the ventral valve perpendicular to the commissural plane and the dorsal valve height, measured as the maximum vertical height of the ventral valve perpendicular to the commissural plane (Fig. 1.1e): (0), subequal ($0.862 \leq x \leq 1.082$); (1), dorsal convexity greater (≤ 0.745); (2), ventral convexity greater (≥ 1.259).
- Depth of the shell. Ratio of the maximum shell length, measured perpendicular to the hinge line, divided by the maximum shell width, measured parallel to the hinge line (Fig. 1.1a): (0), low (≤ 0.832); (1), high (≥ 0.833).
- Dorsal umbonal angle. The angle observed between the two limbs of the umbo when the dorsal valve is lying on the commissural plane (Fig. 1.1a): (0), narrow ($\leq 95^\circ$); (1), wide ($\geq 100^\circ$).
- Ventral umbonal angle. The angle observed between the two limbs of the umbo when the ventral valve is lying on the commissural plane (Fig. 1.1b): (0), narrow ($\leq 100^\circ$); (1), wide ($\geq 110^\circ$).
- Start of the sulcus. Ratio of the distance, measured perpendicular to the hinge line, from the ventral umbo to

the beginning of a perceptible concave deflection in the ventral valve divided by the maximum length of the valve, measured perpendicular to the hinge line: (0), distal (≥ 0.709); (1), proximal (≤ 0.672).

- Height of the ventral cardinal area. Ratio of the vertical distance from the hinge line to the top of the ventral interarea, measured perpendicular to the hinge line, divided by the ventral valve height, measured as the maximum vertical height of the ventral valve perpendicular to the commissural plane (Fig. 1.1e): (0), low (≤ 0.419); (1), high (≥ 0.498).
- Angle of the ventral cardinal area. The angle observed between the lateral boundaries of the ventral interarea (Fig. 1.1e): (0), high ($> 125^\circ$); (1), low ($\leq 120^\circ$).
- Angle of the delthyridium. The angle observed between the lateral edges of the delthyrial opening (Fig. 1.1e): (0), low ($\leq 60^\circ$); (1), high ($> 65^\circ$).
- Posterior extension of the ventral umbo across the hinge line. Ratio of the distance of extension of the ventral umbo, measured perpendicular to the hinge line, divided by the length of the hinge line (Fig. 1.1d): (0), high (≥ 0.104); (1), low (≤ 0.078).
- Posterior extension of the dorsal umbo across the hinge line. Ratio of the distance of extension of the dorsal umbo, measured perpendicular to the hinge line, divided by the length of the hinge line (Fig. 1.1d): (0), low (≤ 0.114); (1), high (≥ 0.136).
- Angle between the ventral interarea and the hinge line. The angle at which the deltidial plates diverge from the

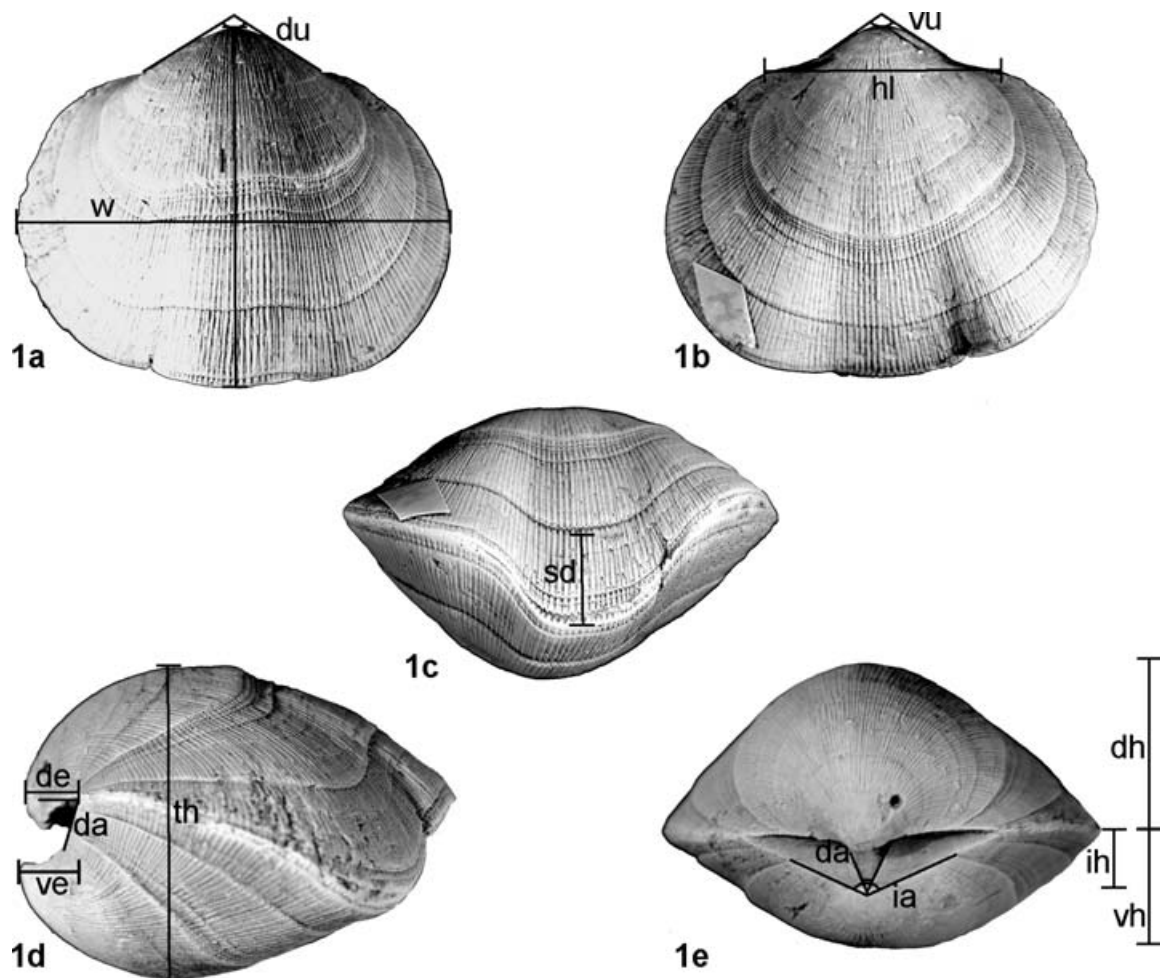


Figure 1 Location of morphological measurements illustrated on *Schizophoria ferronensis*, USNM 124322. **1a**, dorsal view, $\times 2.3$; **1b**, ventral view, $\times 2.3$; **1c**, anterior view, $\times 2.3$; **1d**, lateral view, $\times 2.7$; **1e**, posterior view, $\times 2.3$. Abbreviations; da, the delthyrial angle (angle between hinge line and ventral interarea); de, extension of dorsal umbo over hinge line; dh, height of the dorsal valve; du, dorsal umbonal angle; hl, hinge length; ia, the angle of the interarea; ih, interarea height; l, valve length; sd, sulcus depth; th, total shell height; ve, ventral extension over hinge line; vh, height of the ventral valve; vu, ventral umbonal angle; w, maximum width.

- commissural plane prior to incurving (Fig. 1.1d): (0), inclined ($\leq 60^\circ$); (1), upright ($\geq 70^\circ$).
18. Termination of the cardinal extremities: (0), extended, corners are sharp (as in Fig. 4.4); (1), truncated, corners are rounded (as in Fig. 1.1b).
 19. Maximum convexity of the dorsal valve. The location where the maximum curvature of the dorsal valve occurs: (0), posterior to midline; (1), anterior to midline.
 20. Convexity of the flanks dipping away from the dorsal umbo. The slope at which the lateral flanks of the dorsal valve dip away from the umbo at the location of the maximum curvature of the dorsal valve: (0), steeply dipping ($> 45^\circ$); (1), gently sloping ($< 30^\circ$).
 21. Height of the dorsal cardinal area. The ratio of the vertical distance from the hinge line to the top of the dorsal interarea, measured perpendicular to the hinge line, divided by the ventral valve height, measured as the maximum vertical height of the ventral valve perpendicular to the commissural plane (similar to character 12): (0), small (≤ 0.142); (1), large (≥ 0.182).
 22. Costal density. Number of costae per 5 mm at the anterior margin: (0), average (13 or more); (1), few (up to 12).

Internal characters of the ventral valve

23. Outline of the ventral muscle area: (0), obcordate, diductors diverge; (1), bilobate, parallel diductors (see Fig. 4.1a).
24. Development of the dental plate ridge around muscle scars: (0), entirely, dental plates form an elevated ridge that encloses the muscle field (see Fig. 5.2a); (1), laterally, dental plates form an elevated ridge medially, but ridges do not connect anteriorly (see Fig. 4.2a).
25. Longitudinal division of the ventral muscle scars by median septum: (0), throughout, the entire muscle field is divided by a median septum (see Fig. 5.2a); (1), anterior only, only the anterior portion of the muscle field is divided by a median septum (Fig. 4.2a).
26. Relief of the dental plate ridge enclosing the muscle scars: (0), high relief, distinctly elevated above the valve

- floor (see Fig. 5.2a); (1), low relief, moderately raised above the valve floor (see Fig. 4.1a).
27. Length of the ventral muscle scars. The ratio of the maximum length of the ventral muscle field, measured perpendicular to the hinge line, divided by the maximum shell length, measured perpendicular to the hinge line: (0), long (≥ 0.431); (1), short (≤ 0.418).
 28. Maximum width of the ventral muscle scars. The ratio of the maximum width of the ventral muscle field, measured parallel to the hinge line, divided by the maximum valve width, measured parallel to the hinge line: (0), wide (≥ 0.333); (1), narrow (≤ 0.288).
 29. Width of the ventral muscle scars directly anterior of hinge teeth. The ratio of the width of the ventral muscle field, measured parallel to the hinge line immediately anterior of the hinge teeth, divided by the maximum valve width, measured parallel to the hinge line: (0), wide (≥ 0.156); (1), narrow (≤ 0.108).
 30. Continuation of the median septum beyond the muscle field: (0), absent, the median septum terminates at the anterior edge of the muscle field (see Fig. 5.2a); (1), present, the median septum continues beyond the anterior edge of the muscle field (see Fig. 4.1a).

Internal characters of the dorsal valve

31. Length of the dorsal muscle scars. The ratio of the maximum length of the dorsal muscle field, measured perpendicular to the hinge line, divided by the maximum shell length, measured perpendicular to the hinge line: (0), short (≤ 0.418); (1), long (≥ 0.453).
32. Maximum width of the dorsal muscle scars. The ratio of the maximum width of the dorsal muscle field, measured parallel to the hinge line, divided by the maximum valve width, measured parallel to the hinge line: (0), narrow (≤ 0.383); (1), wide (≥ 0.400).
33. Width of the dorsal muscle scars directly anterior to the brachiphores. Ratio of the width of the dorsal muscle field, measured parallel to the hinge line immediately anterior to the brachiphores, divided by the maximum valve width, measured parallel to the hinge line: (0), narrow (≤ 0.191); (1), wide (≥ 0.200).
34. Antero-median ridge of the dorsal valve. Well-developed ridge subdividing the dorsal muscle field laterally: (0), present (see Fig. 5.6); (1), absent (see Fig. 4.1b).
35. Umbonal region thickened. Increased carbonate deposition within the umbonal region of the dorsal valve: (0), absent; (1), present (see Fig. 5.6).
36. Palial markings. Number of major vascular branches of the mantle canal system: (0), 4 trunks (see Fig. 5.6); (1), 6 trunks.

Parsimony analysis

Phylogenetic analysis used PAUP* 4.0b10 (Swofford 2002). The data set was subjected to a heuristic search using a random addition sequence of 100 replications with tree-bisection-reconnection used as the branch-swapping algorithm. Taxa containing multiple states for a character were treated as polymorphic for that state. All characters were treated as unordered because there was no consistent criterion on which to order them. Characters were optimised using the accelerated transformation (ACCTRAN) option for analysis of character evolution.

A single most parsimonious tree with a length of 197 steps was recovered. This tree is presented in Fig. 2. The consistency index (CI) is 0.52 and the retention index (RI) is 0.48. This observed consistency index exceeds those derived from sets of similarly sized matrices constructed from random data (CI = 0.18) at the 0.05 level of significance (Klassen *et al.* 1991). The phylogenetic analysis was also performed following removal of the species synonymised in the systematic paleontology section of this paper. The character coding of *S. macfarlanii* in the revised analysis was determined by merging the character states of *S. macfarlanii* and *S. meeki* in the original analysis using MacClade 3.04 (Maddison & Maddison 1992). The revised character coding for *S. magna* was determined by merging the original character codings of *S. magna* and *S. iowensis* 'B'. Using the branch-and-bound search option of PAUP*, a single most parsimonious tree was recovered and is presented in Fig. 3. The tree length = 193 steps. The CI = 0.57 and the RI = 0.48. The consistency index exceeds consistency indices constructed from random data of similar sized matrices (CI = 0.18) at the 0.05 level of significance (Klassen *et al.* 1991).

The amount of support for the recovered cladogram was characterised by bootstrap and jackknife analyses. Both of these analyses provide information about the stability of a branch position when a portion of the data set is eliminated (Felsenstein 1985; Sanderson 1989). Due to constraints imposed by the size of the data set, the bootstrap analysis was performed using a 'fast' stepwise-addition search with 10 000 replicates. Groups compatible with the single most parsimonious tree were retained. The confidence values for the nodes duplicated in the bootstrap analysis are presented in Fig. 3. Jackknife analysis was accomplished using the 'fast' stepwise addition search with 10 000 replicates and 5% deletion of characters (equivalent to 3 characters). As in the bootstrap analysis, groups compatible with the single most parsimonious tree were retained. The confidence values for the nodes duplicated in the jackknife analysis are also presented in Fig. 3.

Support for the cladogram was further constrained by calculation of the g_1 statistic, a measure of the skewness of tree length distributions as an indicator of phylogenetic signal (Hillis 1991; Hillis & Huelsenbeck 1992). The g_1 value obtained from a distribution of 10 000 trees constructed from this data set is -0.214 , markedly higher than in random data and significant at the $P = 0.01$ level (Hillis & Huelsenbeck 1992), indicating considerable phylogenetic structure within the data.

Results and Taxonomic Implications

Recognition of clades within the genus

Several patterns are apparent from inspection of the cladograms in Figs 2 and 3. First, members of the ingroup (i.e. North American schizophoriids) are divided into two clades at the basal ingroup node. One clade is composed of *S. oriskania* Schuchert, 1913, *S. parafragilis* Johnson, 1970, and *S. paraprimita* Johnson *et al.*, 1973 (Fig. 4). This clade exhibits the characteristics of *S. (Eoschizophoria)* and is referred to that taxon. The other clade comprises the remainder of the ingroup taxa and is referred to *S. (Schizophoria)*. Within this second clade, additional phylogenetic structure is uncovered. The five basal-most members branch in a pectinate pattern as follows: *S. (Schizophoria)*

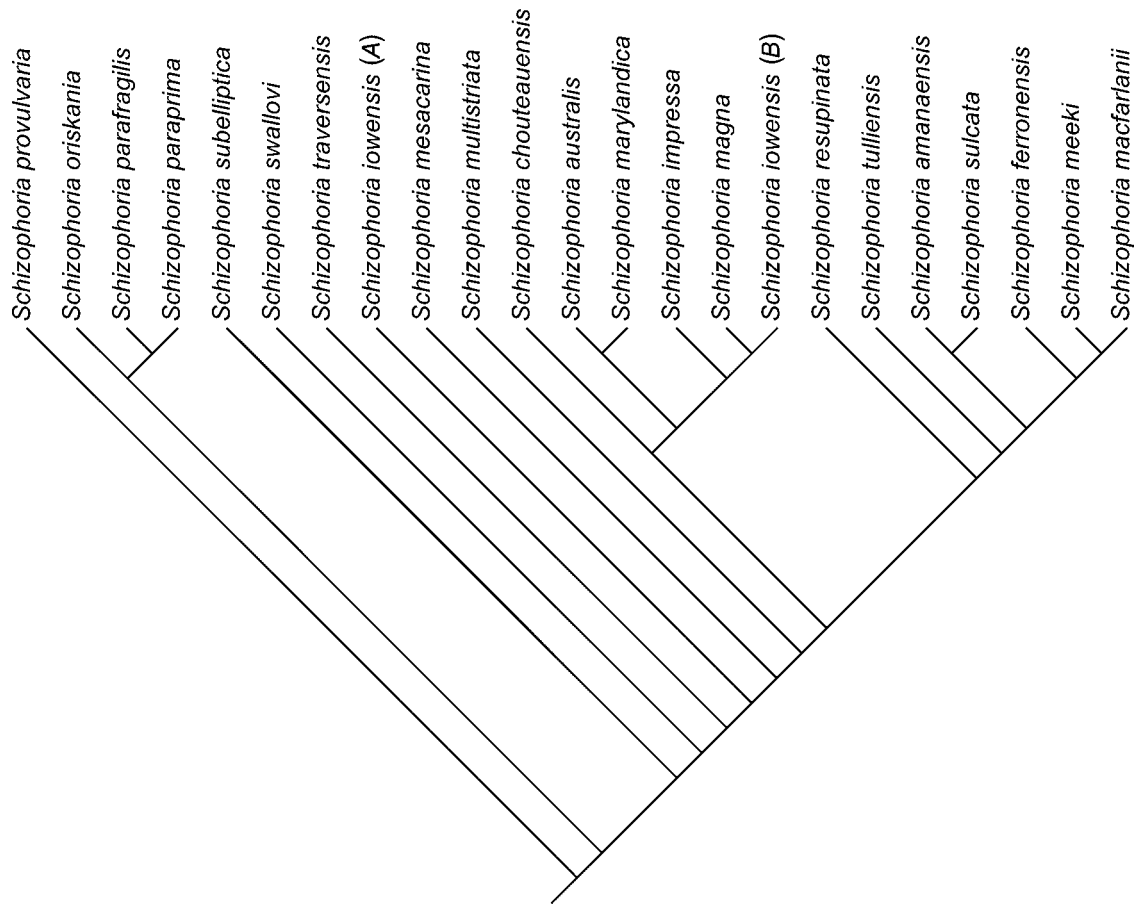


Figure 2 Single most parsimonious tree produced from analysis of character data given in Table 3 using PAUP* 4.ob10 (Swofford 2002). Tree length is 197 steps. The retention index is 0.52 and the consistency index is 0.48.

subelliptica (White & Whitfield, 1862), *S. (Schizophoria) swallowi* (Hall, 1858), *S. (Schizophoria) traversensis* Grabau, 1931, *S. (Schizophoria) iowensis* (Hall, 1858) [including members of the paratype series of form 'A'], *S. (Schizophoria) mesacarina* Imbrie, 1959 and *S. (Schizophoria) multistriata* (Hall, 1857). The remaining taxa form two clades. The first of these clades includes *S. (Schizophoria) chouteauensis* Weller, 1914, *S. (Schizophoria) australis* Kindle, 1909, *S. (Schizophoria) marylandica* Clarke & Schwartz, 1913, *S. (Schizophoria) impressa* (Hall, 1843), *S. (Schizophoria) iowensis* (Hall, 1858) [including members of the paratype series of form 'B'] and *S. (Schizophoria) magna* Fenton & Fenton, 1924 (Fig. 4). The second clade includes *S. (Schizophoria) resupinata* (Martin, 1809), *S. (Schizophoria) tulliensis* (Vanuxem, 1842), *S. (Schizophoria) amanaensis* Stainbrook, 1945, *S. (Schizophoria) sulcata* Johnson & Perry, 1976, *S. (Schizophoria) ferrenensis* Imbrie, 1959, *S. meeki* Fenton & Fenton, 1928 and *S. (Schizophoria) macfarlanii* Meek, 1868 (Fig. 5).

Each of these clades is supported by specific character evidence. The monophyly of the *S. (Eoschuchertella)* clade consisting of *S. oriskania*, *S. paraprima* and *S. parafragilis* is supported by a high shell depth ratio, rounded cardinal extremities and dental ridges that bound the ventral muscle field only on the lateral edges (characters 8, 18 and 24). In addition, the sister taxon relationship between *S. paraprima* and *S. parafragilis* is supported by shared wide dorsal

umbonal angle and short dorsal muscle scars (characters 9 and 31). Tree support for these branches is strong, as indicated by the jackknife and bootstrap values in Fig. 3.

The monophyly of the *S. (Schizophoria)* clade, comprising the remaining ingroup species, is supported by the short ventral muscle field, wide dorsal muscle field and an upright attitude of the delthyrial plates (characters 17, 27 and 33). The placement of each taxon within the basal, pectinate portion of the *S. (Schizophoria)* clade is supported by further character evidence. The monophyly of members of *S. (Schizophoria)* exclusive of *S. subelliptica* is evidenced by a wide pedicle umbonal angle (character 10). Synapomorphies of moderate sulcus depth, dorsi-biconvex shape, proximal sulcus origination and truncated cardinal extremities (characters 5, 7, 11 and 18) support the monophyly of the taxa above *S. swallowi*. Species above *S. traversensis* share a medium body size and highly inflated dorsal valve (characters 1 and 2). The monophyly of species including *S. mesacarina* crownward is supported by inclined delthyrial plates, high relief of the ridge bounding the ventral muscle field and wide dorsal muscle scars (characters 17, 26 and 32). The placement of *S. multistriata* as sister to the remainder of the *S. (Schizophoria)* species is supported by the shared reduced inflation of the dorsal valve (character 2).

Following the pectinate portion of the *S. (Schizophoria)* lineage, two clades are recovered, referred to below as the *S. chouteauensis* and *S. resupinata* clades. The sister

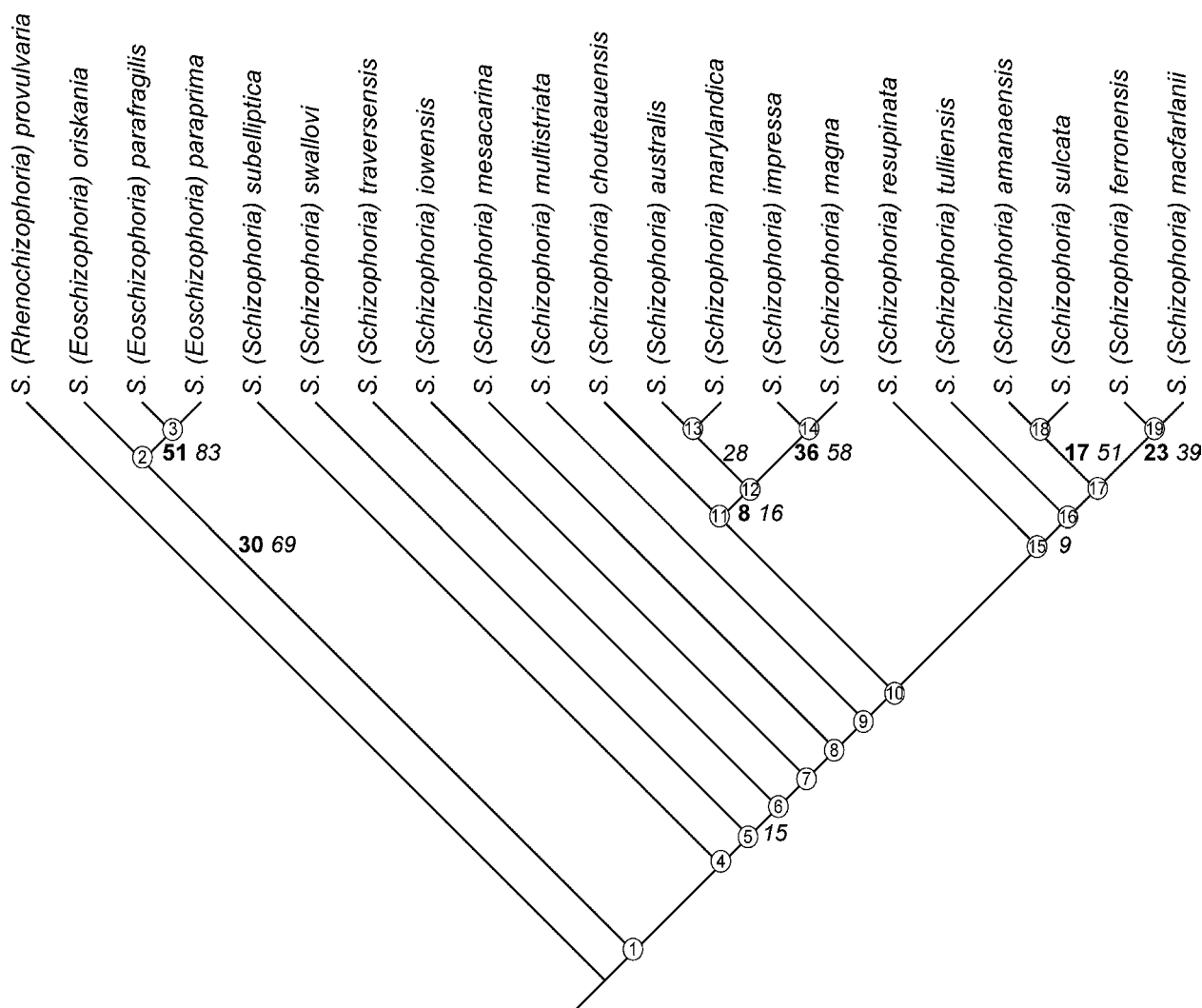


Figure 3 Single most parsimonious tree produced from analysis of character data given in Table 3 using PAUP* 4.0b10 (Swofford 2002) when *Schizophoria* (*Schizophoria*) *macfarlanii* and *S. (Schizophoria) magna* are revised following the synonymy proposed in the text. Tree length is 193 Steps. The retention index is 0.57 and the consistency index is 0.48. The g_i statistic for the tree is -0.214 . Bootstrap and jackknife values are indicated next to the nodes that they support, in bold and italic numerals, respectively. Character states were placed at the nodes using MacClade 3.04 (Maddison & Maddison 1992) under ACCTRAN optimisation. Node numbers are circled on the cladogram. Apomorphic characters that change unambiguously below nodes are listed in parentheses. Node 2, 8(1), 18(1), 24(1); Node 3, 9(1) 31(0); Node 4, 17(1), 27(1), 33(1); Node 5, 10(1); Node 6, 5(1), 7(1), 11(1), 18(1); Node 7, 1(1), 2(2); Node 8, 17(0), 26(0), 32(1); Node 9, 2(1); Node 10, 23(1); Node 11, 12(0), 14(1), 33(0); Node 12, 9(1); Node 13, 15(1), 18(0); Node 14, 8(1), 17(1); Node 15, 20(0); Node 16, 13(1), 34(0); Node 17, 5(2); Node 18, 9(1), 27(0); Node 19, 16(1).

relationship of these two clades is supported by a bilobate, parallel outline to the ventral muscle field (character 23). The monophyly of the *S. chouteauensis* clade is supported by low ventral cardinal area, high delthyrial angle and narrow dorsal muscle scars (characters 12, 14 and 33), while the monophyly of the *S. resupinata* clade is supported by the shared development of steeply dipping lateral flanks of the dorsal valve (character 20).

The topology within the *S. chouteauensis* clade is strongly supported by character evidence and bootstrap and jackknife values (Fig. 3). The monophyly of *S. australis*, *S. marylandica*, *S. impressa* and *S. magna*, is supported by a wide brachial umbonal angle (character 9). The sister relationship of *S. australis* and *S. marylandica* is further supported by cardinal extremities that extend laterally and a significant extension of the pedicle umbo across the hinge

line (characters 15 and 18). The sister relationship of *S. impressa* and *S. magna* is supported by high valve depth ratio and upright delthyrial plates (characters 8 and 17). The initial analysis (Fig. 2) placed part of the *S. iowensis* paratype series (type 'B') in a sister group relationship with *S. magna*. Comparison of the character coding for these two forms indicated that they were identical in all but three continuous characters, brachial inflation, overall shell height and extension of pedicle umbo across the hinge line (characters 2, 6 and 15), representing a mean character difference (as calculated with PAUP) of 0.103. Specimens of the type 'B' of the *S. iowensis* paratype series are, therefore, synonymised with *S. magna* in the systematic paleontology section below.

Tree topology within the *S. resupinata* clade is also well constrained by character evidence and supported by bootstrap and jackknife analyses. The monophyly of *S. tulliensis*,

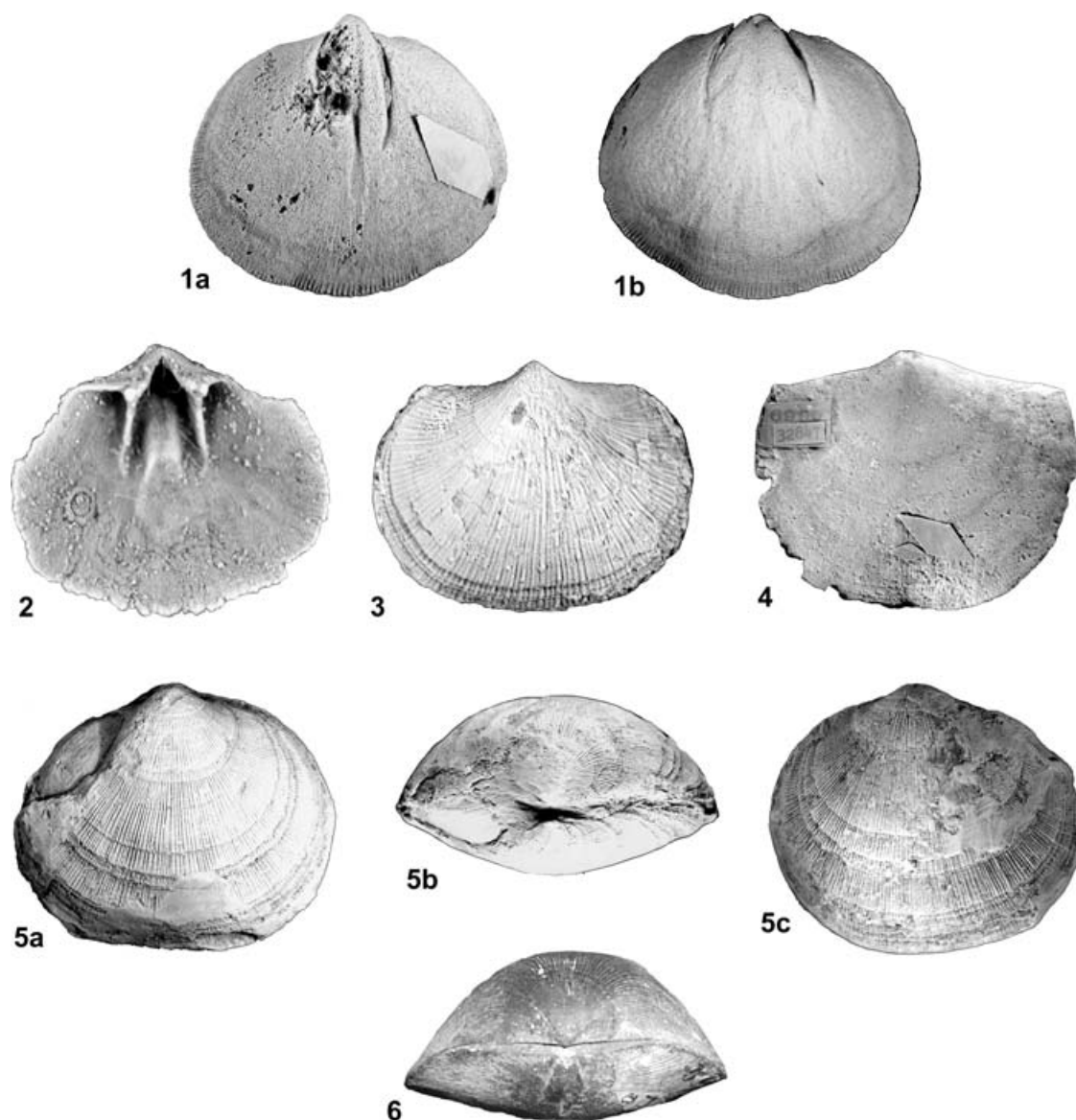


Figure 4 1, *Schizophoria* (*Eoschizophoria*) *oriskania* Schuchert, 1913; YPM S1413B (lectotype), 2.4×; 1a, internal mold of ventral valve; 1b, internal mold of dorsal valve. 2, *Schizophoria* (*Eoschizophoria*) *paraprima* Johnson et al., 1973; USNM 171386 (lectotype); ventral valve interior, 5.5×. 3, *Schizophoria* (*Schizophoria*) *subelliptica* (White & Whitfield, 1862); FMNH 14227, ventral view, 4.5×. 4, *Schizophoria* (*Schizophoria*) *swallowi* (Hall, 1858; AMNH 32847 (lectotype), ventral view), 1.0×. 5, *Schizophoria* (*Schizophoria*) *chouteauensis* Weller, 1914; FMNH 9689a (lectotype), 1.7×; 5a, ventral view, 5b, posterior view, 5c, dorsal view. 6, *Schizophoria* (*Schizophoria*) *australis* Kindle, 1909; USNM 62005c (lectotype), posterior view, 1.3×.

S. amanaensis, *S. sulcata*, *S. ferronenesis* and *S. macfarlanii* is supported by the low angle of the ventral cardinal area and the presence of a clearly discernable antero-median ridge of the dorsal muscle field (characters 13 and 34). *Schizophoria amanaensis*, *S. sulcata*, *S. ferronenesis* and *S. macfarlanii* further share a deeply impressed sulcus (character 17). The sister relationship of *S. amanaensis* and *S. sulcata* is supported by shared wide dorsal umbonal angle and long ventral muscle scars (characters 9 and 27). *Schizophoria ferronenesis* and *S. macfarlanii* are joined by a shared extension of the dorsal umbo across the hinge line. In the initial analysis (Fig. 2), *S. meeki* and *S. macfarlanii* shared a sister group relationship. Comparison of the character coding for these two forms indicated that they were identical in all but three characters, slope of dorsal lateral flanks, delthyrial angle

and location of the maximal dorsal convexity (characters 14, 19 and 20). Therefore, *S. meeki* is synonymised with *S. macfarlanii* in the systematic palaeontology section below.

Evolutionary and ecological implications

From the preceding section, it is apparent that many of the characters reflecting evolutionary changes and speciation within *Schizophoria* involve aspects of the overall shape and size of species as well as the development of features of the ventral and dorsal muscle fields. The relative muscle development and overall shell size and convexity may be related to the palaeoecology of different species. Species of *Schizophoria* from the Appalachian basin (e.g. *S. impressa*

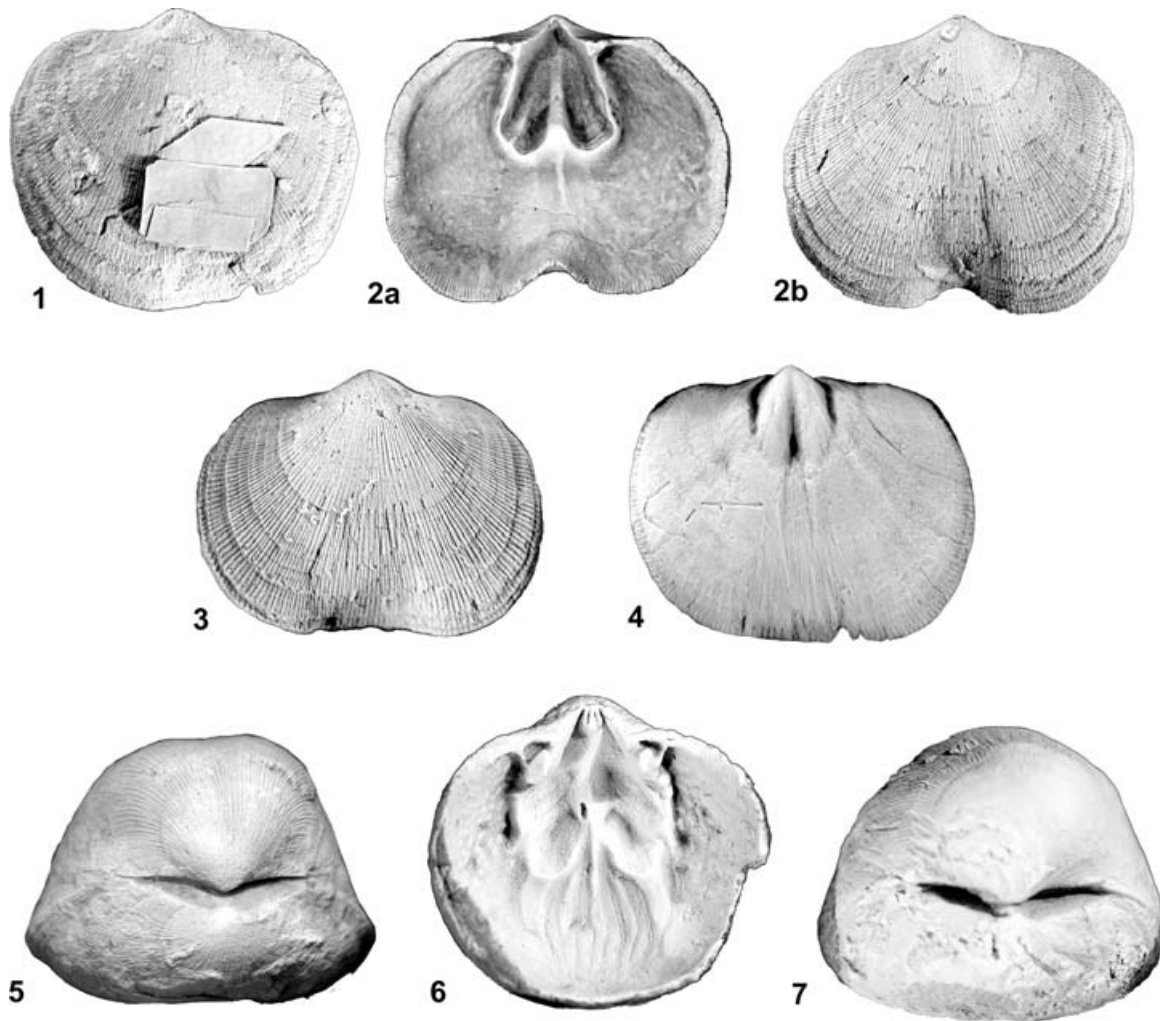


Figure 5 1, *Schizophoria (Schizophoria) magna* Fenton & Fenton, 1924; AMNH 32506, dorsal view, 2.6×. 2, *Schizophoria (Schizophoria) magna* Fenton & Fenton, 1924; FMNH 25246, 1.6×; 2a, ventral valve interior, 2b, ventral valve exterior. 3, *Schizophoria (Schizophoria) iowensis* (Hall, 1858); AMNH 32506 (lectotype), ventral view, 1.8×. 4, *Schizophoria (Schizophoria) impressa* (Hall, 1843); AMNH 30602 (holotype), ventral valve interior, 1.8×. 5, *Schizophoria (Schizophoria) macfarlanii* (Meek, 1868); YPM S1467c, posterior view, 2.1×. 6, *Schizophoria (Schizophoria) macfarlanii* (Meek, 1868); FMNH 25993 (holotype of *S. meeki* Fenton & Fenton, 1928), dorsal valve interior, 1.9×. 7 *Schizophoria (Schizophoria) macfarlanii* (Meek, 1868); FMNH 7465 (paratype of *S. meeki* Fenton & Fenton, 1928), posterior view, 1.9×.

and *S. striatula*) have previously been interpreted as free-resting epibenthic species, with the convex dorsal valve resting partly within the sediment and the commissure projecting above the sediment–water interface (e.g. Bowen *et al.* 1974; Thayer 1974; McGhee & Sutton 1981). This interpretation is based partly on the size of the pedicle foramen, which has been perceived as being too small to accommodate a pedicle of appropriate size to anchor the shell, and partly on the lack of quality pedicle attachments sites on the soft substrates in which these species occur (Bowen *et al.* 1974; Thayer 1974; Rodriguez & Gutschick 1978). The soft sediment resting interpretation is probably most accurate where species occur in platform to offshore settings and possess dorsal valves demonstrably more convex than the ventral valve. This description characterises many of the species present within the *S. (Schizophoria)* clade (i.e. *S. macfarlanii*, *S. iowensis* and *S. multistriatula*) but does not apply to all species within this analysis. Rodriguez & Gutschick (1978) discussed possible alternative palaeoecological interpretations for a shallow

water *Schizophoria* species and suggested that neither the size of the pedicle foramen nor a soft substrate can be used as conclusive evidence for lack of pedicle attachment.

While the Lower Devonian through Frasnian schizophoriids discussed above have been previously interpreted as members of offshore benthic communities, Famennian and later schizophoriids have been interpreted as commonly inhabiting shallow water or nearshore environments (e.g. Weller 1914; Parkinson 1954; Pocock 1968; Rodriguez & Gutschick 1978). This observed ecological shift can be considered within the phylogenetic framework established herein. The Mississippian species included in this analysis, *S. subelliptica*, *S. swallowi*, *S. resupinata* and *S. chouteauensis*, do not form a clade but are connected with long branches to disparate clades consisting of Devonian taxa, many of which have been previously considered offshore taxa. Each of the Mississippian species considered herein was originally interpreted to inhabit shallow water environments, including

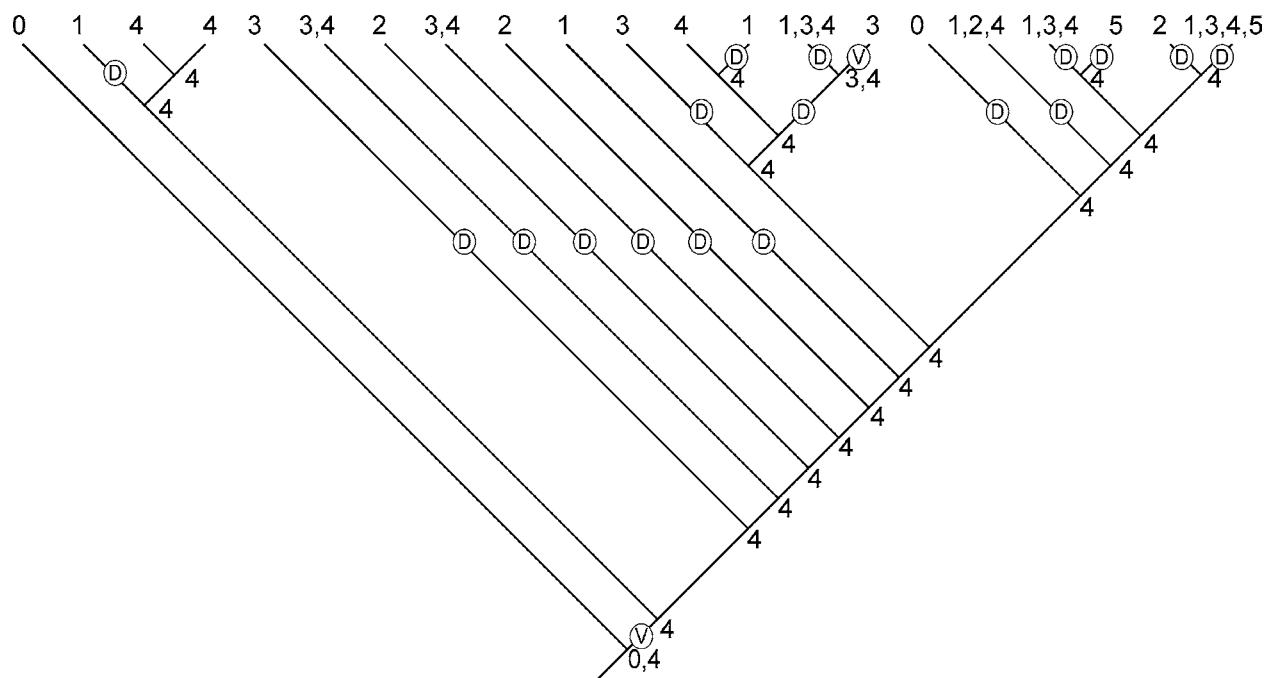


Figure 6 Phylogeny from Fig. 3, with biogeographical states substituted for terminal taxa and mapped onto the ancestral nodes. Inferred episodes of speciation by vicariance (V) and dispersal (D) are indicated. Ancestral nodes calculated using a modified Fitch optimisation (Lieberman & Eldredge 1996; Lieberman 2000). 0, Europe; 1, Appalachian Basin; 2, Michigan Basin; 3, Central United States; 4, Western United States; 5, Western Canada.

reefs and oolite shoals, based on the lithology of the strata in which they occur. This potentially indicates at least four separate invasions of the shallow water environment by species with ancestors that inhabited deeper water. Similar patterns of invasion and speciation within shallow water from offshore stock has been documented in other lineages (Stanley 1979).

The pattern of offshore to onshore colonisation and cladogenesis is interesting both from paleoecological and evolutionary standpoints. The colonisation of shallow water environments and the concomitant morphological changes represent a grade of convergent evolution. The subgenus *S.* (*Schizophoria*) cannot be subdivided into additional subgenera based on these morphological convergences. The timing of this major ecological change coincides with the Late Devonian biodiversity crisis, approximately the boundary between the Frasnian and Famennian stages. Frasnian *Schizophoria* species continue to exhibit offshore environmental preferences, while Mississippian species are clearly adapted to shallow water conditions. The Famennian, therefore, appears to represent a key evolutionary interval. Day & Over (2002) document an offshore Early Famennian post-extinction fauna from the Appalachian basin that includes a single specimen of *Schizophoria*, indicating that some offshore holdovers continued into the Famennian. *Schizophoria williamsi* from the Famennian Leatham Formation of Utah inhabited a shallow algal bank environment (Rodriguez & Gutschick 1978). Although information on additional species would be beneficial, it seems clear that the transition from offshore to deeper water environments was at least partially completed during the Famennian, as species inhabiting both environments have been recorded. During this time, *Schizophoria* began to colonise shallow water environments, probably due to speciation events from offshore ancestral stock.

Biogeographical implications

Biogeographical patterns in *Schizophoria* were evaluated in conjunction with the phylogeny in Fig. 3. The phylogeny was converted to an area cladogram. This involved first substituting species' geographical distributions for species' names. Geographical distributions were assigned to areas of endemism that existed in Laurentia during the Devonian. Large-scale geological features defined the boundaries of these areas of endemism and their existence was established by the presence of large numbers of unique taxa in each of the regions. The areas of endemism considered within this analysis were: Europe; the Appalachian Basin; the Michigan Basin; central North America; western United States; Western Canada. These biogeographical areas have been considered previously in a similar context for other Devonian taxa including phyllocarid crustaceans (Rode & Lieberman 2002, 2005) and bivalves (Rode 2004). Certainly, other areas of endemism existed outside the study region, but Devonian *Schizophoria* were either not present in those regions or were not included within this study for the reasons discussed above. In addition, although some of these regions could potentially be more finely divided biogeographically, this would involve creating several additional regions with only a single taxon present. This was not pursued because areas that have only a single taxon in them can create artificial problems for phylogenetic biogeographical analysis (Fortey & Cocks 1992; Lieberman 1997, 2000). After geographical distributions were placed at the tips of the tree, they were optimised to ancestral nodes using a modified version of the Fitch parsimony algorithm (Fitch 1971) described by Lieberman & Eldredge (1996) and Lieberman (2000). The Fitch algorithm, in this context, assumes unordered transformations between areas. The area cladogram is shown in Fig. 6.

Two types of information can be retrieved from the area cladogram. First, the ranges of ancestral nodes are reconstructed, so the areas inhabited by the ancestors of species or clades can be inferred. Second, the mode of speciation (vicariance versus dispersal) can be ascertained for some cladogenetic events. Only allopatric speciation events can be constrained by this type of analysis and the style of allopatry is the primary type of information retrieved. When a daughter species occupies only a fragment of the ancestral range, speciation can be inferred to have occurred by vicariance (passive allopatry, type I of Wiley (1981)). Conversely, when a daughter species occupies a geographical range that includes biogeographical areas additional to or different from the ancestral range, speciation occurs when a small subset of the population disperses across a previous barrier and establishes a new species (dispersive allopatry, type II of Wiley (1981)).

From examining Fig. 6, it is evident that the *Schizophoria* species included in this analysis were present ancestrally in both Europe and Western North America. Throughout most of the evolutionary history of this group within North America, speciation was related to dispersal events originating from Western North America. Species inhabiting additional basins entered these regions by subsequent range expansions, which may correspond to episodes of traditional dispersal (*sensu* Humphries & Parenti 1986) or geo-dispersal (*sensu* Lieberman & Eldredge 1996). Episodes of range expansion are frequent and can be identified by an expansion or shift in the geographical distribution of a descendant relative to its ancestor (indicated in Fig. 6). By contrast, another prominent biogeographical pattern within this clade is the limited amount of vicariant differentiation, which can be identified by a contraction in the range of a descendant species relative to its ancestor (indicated in Fig. 6). In fact, there is evidence for only two episodes of vicariance in the history of this clade: one of these vicariance events occurred early in the history of the clade, at the first cladogenetic event recorded within the ingroup and the other in the speciation of *S. magna*. Vicariance accounts for only 11% of the cladogenetic events in which there is evidence for speciation mode.

The relative lack of vicariance within North American shizophoriids is atypical and extremely low compared to documented levels of vicariant speciation (passive allopatry) in extant taxa described by Brooks & McLennan (1991) and Wiley & Mayden (1985), where it is the dominant form of speciation (typically accounting for greater than 70% of speciation events). The increased tendency of taxa to disperse (dispersive allopatry) with concomitant reduction in vicariance has been observed in numerous Middle Devonian and Late Devonian taxa including trilobites (Lieberman 1999), phyllocarid crustaceans (Rode & Lieberman 2002) and bivalves (Bailey 1978, Rode 2004). This relative lack of vicariance during the Middle to Late Devonian appears to be a cross-faunal phenomenon.

Systematic palaeontology

Taxa and material examined that do not require detailed discussion or synonymy

The following specimens were examined to determine character states for each species. These specimens belong to either the type series or have been previously illustrated elsewhere. Each of the species included within this list is considered

to be a valid species within the designated subgenus. Since neither taxonomic revision nor lectotype designation is required for these taxa, they are not treated exhaustively in the systematic palaeontology section below. Enhanced diagnoses for these species can be determined by supplementing the original species descriptions cited below with the character coding presented in Table 3.

- Schizophoria* (*Rhenoschizophoria*) *provulvaria* (Maurer, 1886), YPM S1399, S1400, S1400a, S1401a-d;
S. (Schizophoria) amanaensis Stainbrook, 1945, USNM 135272, 200880;
S. (Schizophoria) australis Kindle, 1909, USNM 62005c, 62006, 180935;
S. (Schizophoria) ferronensis Imbrie, 1959, USNM 124322;
S. (Schizophoria) impressa (Hall, 1843), AMNH 30602, 30603, 5980/2, 37143, 37144, 37147, 37149;
S. (Schizophoria) marylandica Clarke & Schwartz, 1913, USNM 177086-177091;
S. (Schizophoria) mesacarina Imbrie, 1959, USNM 124250;
S. (Schizophoria) multistriata (Hall, 1857), AMNH 33281-33286, NYSM 1882, E2076a-b;
S. (Schizophoria) resupinata (Martin, 1809), YPM S1449, S1449a-b;
S. (Schizophoria) subelliptica (White & Whitfield, 1862), YPM S1391, 1391a, FMNH 14227a-b;
S. (Schizophoria) sulcata Johnson & Perry, 1976, GSC 42723-42727;
S. (Schizophoria) traversensis Grabau, 1931, USNM 134335, 134394, 124395;
S. (Schizophoria) tulliensis (Vanuxem, 1842), YPM S1405, S1405a-d; AMNH 36857-36859.

Order **ORTHIDA** Schuchert & Cooper, 1932

Suborder **DALMANELLIDINA** Moore, 1965

Superfamily **ENTELOIDEA** Waagen, 1884

Family **SCHIZOPHORIIDAE** Schuchert & LeVene, 1929

Genus **SCHIZOPHORIA** King, 1850

- 1850 *Schizophoria* King: 106.
 1892 *Schizophoria* Hall & Clarke: 211–213.
 1914 *Schizophoria* Weller: 161–162.
 1932 *Schizophoria* Schuchert & Cooper: 143–144.
 1965 *Schizophoria* Williams & Wright: H332.
 1966 *Schizophoria* Pocock: 381–383.
 1976 *Schizophoria* Lazarev: 100–106.
 2000 *Schizophoria* Harper: H840–842.
 2001 *Schizophoria* Jansen: 104–113.

TYPE SPECIES. *Conchylolithes Anomites resupinatus* Martin, 1809.

DIAGNOSIS. Transversely semioval, weakly uniplicate valves; ventral interior with strong teeth and dental plates extending forward as ridges laterally confining the muscle field; dorsal interarea with prominent, crenulated cardinal process (Harper 2000). For additional characters see Pocock (1966) and Jansen (2001).

REMARKS. *Schizophoria* encompasses a large number of species that exhibit a diverse array of morphologies. All assigned species share the generic characteristics, but vary substantially in external outline, shape and size of both dorsal and ventral muscle fields and hinge characteristics. Pocock (1966, 1968) delineated species groups within Devonian and Carboniferous species of Western Europe in an initial attempt at intrageneric classification. More recent attempts to clarify the relationships of species within the genus have resulted in the erection of subgenera: *Schizophoria* (*Schizophoria*) King, 1850, *S. (Paraschizophoria)* Lazarev, 1976, *S. (Pocockia)* Lazarev, 1976, *S. (Eoschizophoria)* Rong & Yang, 1980, *S. (Pachyschizophoria)* Jansen, 2001 and *S. (Rhenoschizophoria)* Jansen, 2001. Harper (2000) noted that subgenera are of restricted utility since the diagnostic features of the subgenera *S. (Paraschizophoria)* and *S. (Pocockia)* are present in the *S. (Schizophoria)* lineage. Harper (2000) also elevated *S. (Eoschizophoria)* to generic status. Jansen (2001) published a thorough revision of Lower Devonian schizophoriids from Western Europe and Northern Africa, in which he supported the validity of the subgenera *S. (Eoschizophoria)* and *S. (Schizophoria)* and proposed two new subgenera, *S. (Pachyschizophoria)* and *S. (Rhenoschizophoria)*, which are restricted to the Lower Devonian. Jansen (2001) noted that additional subgenera could be present within the *S. (Schizophoria)* lineage, but this was outside the scope of his analysis of Lower Devonian species. The phylogenetic analysis presented herein suggests that further division of subgenera within *S. (Schizophoria)* would result in paraphyletic lineages due to the pectinate nature of the early evolution of that group.

OCCURRENCE. Upper Silurian (Ludlow) to Lower Carboniferous (Viséan); cosmopolitan.

Subgenus **SCHIZOPHORIA (EOSCHIZOPHORIA)**

Rong & Yang, 1980

1980 *Schizophoria (Eoschizophoria)* Rong & Yang: 286.

2000 *Eoschizophoria* Harper: H843.

2001 *Schizophoria (Eoschizophoria)* Jansen: 105–106.

TYPE SPECIES. *Schizophoria hesta* Rong & Yang in Rong *et al.*, 1974.

DIAGNOSIS. Small, biconvex to dorsibiconvex valves; long, thin median ridge bisecting and extending through ventral muscle scar; dorsal interior with delicate cardinalia and narrowly divergent brachiofores (Rong & Yang 1980; Harper 2000).

REMARKS. The taxonomic rank of *S. (Eoschizophoria)* has varied in recent publications. Harper (2000) considered *Eoschizophoria* a genus, while Jansen (2001) retained the original subgeneric rank. Jansen (2001) suggested potential evolutionary pathways between Lower Devonian *Schizophoria* subgenera and he proposed *S. (Eoschizophoria)* was the ancestral stock from which *S. (Schizophoria)* and *S. (Rhenoschizophoria)* may have arisen. Under this evolutionary scenario, retention of *S. (Eoschizophoria)* as a subgenus within *Schizophoria* is preferred to its elevation to generic status because this preserves the monophyly of *Schizophoria*, while its removal would render *Schizophoria* paraphyletic.

Schizophoria (Eoschizophoria) is characterised by its small size, a lightly impressed, narrow, ovate ventral muscle

field, equi-biconvex to slightly dorsi-biconvex shape, poorly developed sulcus and subtriangular, bipartite dorsal adductor field. *Schizophoria (Schizophoria)* can be distinguished from *S. (Eoschizophoria)* by a more prominently developed fold and sulcus, oval to subtriangular ventral muscle field that is more deeply impressed and quadripartite, elongate to subelliptical dorsal muscle field (Jansen 2001). *Schizophoria (Rhenoschizophoria)* differs from *S. (Eoschizophoria)* with its larger size, more deeply impressed, wide, subelliptical to subtriangular ventral muscle field and subrectangular to subelliptical dorsal muscle field (Jansen 2001). *Schizophoria (Pachyschizophoria)* is differentiated from *S. (Eoschizophoria)* by its larger size, clearly dorsi-biconvex profile, long ventral muscle field and quadripartite, oval to subrectangular dorsal adductor field (Jansen 2001).

OCCURRENCE. Upper Silurian (Pragian) to Lower Devonian (Emsian); China, Western Canada, central Asia, Podolia, USA (Harper 2000).

INCLUDED SPECIES. *Schizophoria hesta* Rong & Yang in Rong *et al.*, 1974 (Ludlovian to Pridolian), *Schizophoria oriskania* Schuchert, 1913 (Emsian), *Schizophoria parafragilis* Johnson, 1970 (Pragian), *S. (Eoschizophoria) paraprimita* Johnson *et al.*, 1973 (Pragian). Rong & Yang (1980) include several additional species within *S. (Eoschizophoria)*, but these were not examined herein.

Schizophoria (Eoschizophoria) oriskania

Schuchert, 1913 (Fig. 4.1a, 1b)

1913 *Schizophoria oriskania* Schuchert: 307, pl. 56, figs 9–12.

TYPES. Schuchert's (1913) original description included illustrations of two specimens, but did not specifically designate either as the holotype of the species. Within Schuchert's (1913) discussion, he indicated, however, that he considered the type specimen to possess a fold and sulcus. This feature is only apparent in YPM S1413B, a complete internal mold, while YPM S1413A, an external mold, does not have a well-developed sulcus. YPM S1413B is, therefore, selected here as lectotype.

ADDITIONAL MATERIAL EXAMINED. YPM S1413A (paralectotype).

EMENDED DIAGNOSIS. Medium-sized, biconvex *S. (Eoschizophoria)*; hinge line short; cardinal extremities rounded; poorly developed fold and sulcus, onset distal; shell depth short; moderate to low inflation of brachial and ventral valves; narrow dorsal and ventral umbonal angles; ventral cardinal area high, delthyrium narrow; ventral umbo extends further posteriorly than dorsal umbo, dorsal valve flanks dip steeply away from umbonal region; ventral muscle field bilobate, diductor tracks parallel; dental plates form low-relief ridge on lateral edges of ventral muscle field; ventral muscle field long and narrow; median septum continues beyond ventral muscle field; dorsal muscle field long and narrow.

REMARKS. *Schizophoria oriskania* is transferred into the subgenus *S. (Eoschizophoria)* based on its possession of the diagnostic features of that subgenus. Notably, *S. oriskania* exhibits a ventral median ridge extending beyond the muscle field, small size and dorsibiconvex shape. In addition, its placement within the phylogenetic analysis in a clade with

S. parafragilis, a species previously assigned to *S. (Eoschizophoria)* (Rong & Yang 1980), further supports this placement.

COMPARISONS. *Schizophoria oriskania* can be distinguished from other *S. (Eoschizophoria)* species by its larger size, narrow dorsal umbonal angle, steeply dipping flanks of the dorsal valve and long dorsal muscle field.

OCCURRENCE. Emsian; Oriskany Formation, Ridgely member, Cumberland, Maryland, USA.

Schizophoria (Eoschizophoria) parafragilis
Johnson, 1970

1970 *Schizophoria parafragilis* Johnson: 86–87, pl. 8, figs 1–12.

TYPES. USNM 156820 (holotype), USNM 156817–156819 (paratypes).

EMDENDED DIAGNOSIS. Small *S. (Eoschizophoria)*; hinge line short; cardinal extremities rounded; poorly developed fold and sulcus, onset distal; shell depth short; shell height low; low inflation of brachial valve; highly inflated ventral valve; wide dorsal and narrow ventral umbonal angles; ventral cardinal area low, delthyrium narrow; ventral umbo extends further posteriorly than dorsal umbo, dorsal valve flanks dip gently away from umbonal region; ventral muscle field bilobate, diductor tracks parallel; dental plates form low-relief ridge on lateral edges of ventral muscle field; ventral muscle field long and narrow; dorsal muscle field short and narrow; antero-median ridge divides dorsal muscle field.

REMARKS. *Schizophoria parafragilis* is transferred to the subgenus *Eoschizophoria* on the basis of its small size, biconvex shape, long, narrow ventral muscle scars bounded by parallel dental lamellae and narrowly divergent branchiophore plates. Furthermore, Johnson (1970) noted the internal and external similarity of this species with *S. oriskania* and *S. fragilis*, both of which are also assigned to *S. (Eoschizophoria)*.

COMPARISONS. *Schizophoria parafragilis* most closely resembles *S. paraprimita*. In addition to the subgeneric characters, these species share synapomorphies including small size, low shell height, a wide dorsal umbonal angle, dorsal valve flanks dipping gently away from the umbonal region. *Schizophoria parafragilis* can be distinguished from *S. paraprimita* by its shorter hinge line, greater inflation of the ventral valve, upright instead of inclined delthyrial plates, larger dorsal cardinal area, complete subdivision of ventral muscle field by the median septum (only anteriorly in *S. paraprimita*), longer ventral muscle scars and the presence of an antero-median ridge dividing the dorsal muscle field not present in *S. paraprimita*. *Schizophoria parafragilis* also resembles *S. fragilis*, but can be distinguished by its broader ventral adductor track (Johnson 1970).

OCCURRENCE. Pragian; lower McMonnigal Limestone, Roquima Range, central Nevada, USA.

Schizophoria (Eoschizophoria) paraprimita
Johnson *et al.*, 1973 (Fig. 4.2)

1973 *Schizophoria paraprimita* Johnson *et al.*: 24–25, pl. 10, figs 19–34, pl. 11, figs 1–11.

TYPES. Johnson *et al.* (1973) did not select a holotype among their large collection of specimens. Of the 11 specimens illustrated, Johnson *et al.* (1973) (USNM 171380–171390), USNM 171386 is selected as the lectotype herein. This specimen is an isolated ventral valve that exhibits the distinguishing features of the species: a low broad, ventral myophragm, rectimarginate anterior, transverse outline and narrow ventral muscle field.

EMDENDED DIAGNOSIS. Small, biconvex *S. (Eoschizophoria)*; hinge line long; cardinal extremities rounded; poorly developed fold and sulcus, onset distal; shell depth short; shell height low; low to moderate inflation of ventral valve; highly inflated dorsal valve; wide dorsal and narrow ventral umbonal angles; delthyrium narrow; ventral umbo extends further posteriorly than dorsal umbo, dorsal valve flanks dip gently away from umbonal region; ventral muscle field bilobate, diductor tracks parallel; dental plates form low-relief ridge on lateral edges of ventral muscle field; ventral muscle field short and narrow; dorsal muscle field short and narrow.

REMARKS. *Schizophoria paraprimita* is transferred to the subgenus *Eoschizophoria* on the basis of its small size, biconvex shape, narrow ventral muscle field and subparallel dental lamellae. Johnson *et al.* (1973) remarked on the resemblance of this species with *S. fragilis*, which was assigned to *S. (Eoschuchertella)* in the original description of the subgenus (Rong & Yang, 1980).

COMPARISONS. *Schizophoria paraprimita* closely resembles *S. parafragilis*. The similarities and differences between these species are discussed above. *Schizophoria paraprimita* also resembles *S. fragilis*, but can be readily distinguished by the presence of the broad median septum separating the diductor muscles in *S. paraprimita* that is absent in *S. fragilis* (Johnson *et al.* 1973).

OCCURRENCE. Pragian, Roberts Mountains Formation, central Nevada, USA.

Subgenus *SCHIZOPHORIA (SCHIZOPHORIA)* King, 1850

1850 *Schizophoria* King: 106.

1976 *Schizophoria (Schizophoria)* Lazarev: 106–110.

2000 *Schizophoria (Schizophoria)* Harper: H840–841.

2001 *Schizophoria (Schizophoria)* Jansen: 108–112.

TYPE SPECIES. *Conchylolithes Anomites resupinatus* Martin, 1809.

DIAGNOSIS. Dorsibiconvex *Schizophoria*; delthyrial plates upright; ventral muscle field short, bilobed to widely chordate, confined by divergent dental plates; dorsal diductor scar wide, petaloid and equidimensional.

REMARKS. *Schizophoria (Schizophoria)* has previously been considered to be a potentially paraphyletic taxon that encompassed all *Schizophoria* species not assigned to another more clearly circumscribed subgenus, such as *S. (Pachyschizophoria)*. Williams & Harper (2000) and Jansen (2001) both comment that features diagnostic of each of the other subgenera are present in the *S. (Schizophoria)* lineage. However, these character convergences tend to be at disparate stratigraphical horizons. For example, Lower Devonian *S. (Schizophoria)* tend to be small in size, while Middle and

Upper Devonian species can approach a large size, such as that considered to be characteristic of the Lower Devonian subgenera *S. (Pachyschizophoria)* or *S. (Rhenoschizophoria)* (Jansen 2001). Jansen (2001) suggested that species currently placed within *S. (Schizophoria)* could potentially be split into several new subgenera. The pectinate cladogenetic pattern recovered within this analysis (Fig. 3), however, argues against establishing additional subgenera since removing a subset of the basal portion of *S. (Schizophoria)* would result in paraphyletic subgenera.

Schizophoria (Schizophoria) is characterised by its moderate to well developed fold and sulcus, narrow oval to subtriangular ventral muscle field that is less than half the valve length and quadripartite, elongate to subelliptical dorsal adductor field. *Schizophoria (Eoschizophoria)* can be distinguished from *S. (Schizophoria)* by a poorly developed fold and sulcus, oval, narrow ventral muscle field that is less deeply impressed and a bipartite, subtriangular dorsal muscle field (Jansen 2001). *Schizophoria (Rhenoschizophoria)* differs from *S. (Schizophoria)* with its wide, subelliptical to rhombohedral ventral muscle field and shorter, bipartite to quadripartite, oval to subrectangular, dorsal muscle field (Jansen 2001). *Schizophoria (Pachyschizophoria)* is differentiated from *S. (Schizophoria)* by its consistently larger size, clearly dorsibiconvex profile, ventral muscle field extending beyond half the valve length and oval to subrectangular dorsal adductor field (Jansen 2001).

OCCURRENCE. Lower Devonian (Upper Lockhovian) to Lower Carboniferous (Visean); cosmopolitan.

INCLUDED SPECIES. Most species of *Schizophoria* can be assigned to this subgenus, rendering a complete list of included species cumbersome. Species examined within this analysis that are ascribed to *S. (Schizophoria)* include: *Conchyliolithes Anomites resupinatus* Martin, 1809 (Visean), *Schizophoria amanaensis* Stainbrook, 1945 (Frasnian), *Schizophoria australis* Kindle, 1909 (Frasnian), *Schizophoria chouteauensis* Weller, 1914 (Tournaisian), *Schizophoria feronensis* Imbrie, 1959 (Givetian), *Orthis impressa* Hall, 1843 (Eifelian to Famennian), *Orthis iowensis* Hall, 1858 (Givetian to Frasnian), *Orthis macfarlanii* Meek, 1868 (Givetian to Frasnian), *Schizophoria magna* Fenton & Fenton, 1924 (Givetian to Frasnian), *Schizophoria marylandica* Clarke & Schwartz, 1913 (Givetian), *Schizophoria mesacarina* Imbrie, 1959 (Eifelian to Givetian), *Orthis multistriata* Hall, 1857 (Emsian to Eifelian), *Orthis resupinata* Martin, 1809 (Mississippian), *Orthis subelliptica* White & Whitfield, 1862 (Tournasian), *Schizophoria sulcata* Johnson & Perry, 1976 (Eifelian), *Orthis swallowi* Hall, 1858 (Tournaisian), *Orthis traversensis* Grabau, 1931 (Givetian), *Orthis tulliensis* Vanuxem, 1842 (Eifelian to Givetian).

***Schizophoria (Schizophoria) chouteauensis* Weller, 1914 (Fig. 4.5a–c)**

1914 *Schizophoria chouteauensis* Weller: 163, pl. 23, figs 6–19.

TYPES. Weller (1914) did not designate a holotype specimen in the original description of this species and a lectotype has not subsequently been designated. Therefore, FMNH 9689a is here designated the lectotype. FMNH 9689a is a complete external mold with well preserved ornamentation and details

of the cardinal area. Although other members of the former syntype series preserve internal features, none of these preserve both valves and none of these were illustrated by Weller (1914). Also, since Weller's (1914) original description differentiates this species from similar forms based on external characteristics, FMNH 9689a is the most appropriate choice for lectotype designation. Specimens FMNH 9689b–g and 14226a–b become paralectotypes.

ADDITIONAL MATERIAL EXAMINED. FMNH 9689b–g, 14226a–b (paralectotypes).

EMENDED DIAGNOSIS. Medium-sized, biconvex *S. (Schizophoria)*; shell height low, dorsal valve moderately and ventral valve highly inflated; hinge line short, cardinal extremities truncated; sulcus poorly developed, onset distal; shell depth short; narrow dorsal and wide ventral umbonal angles; ventral cardinal area low; delthyrium wide, delthyrial plates inclined; posterior extension of the ventral valve more pronounced than dorsal valve; dorsal valve flanks dip gently away from umbonal region; diductor muscles parallel; dental plates form high ridge, enclose ventral muscle field; ventral median septum present anteriorly only; ventral muscle scars wide and of variable length; dorsal muscle field long and wide; vascular system with four trunks.

COMPARISONS. *Schizophoria chouteauensis* most closely resembles contemporaneous species *S. swallowi* and the Frasnian species *S. australis*. *Schizophoria (Schizophoria) swallowi* differs from *S. chouteauensis* in its longer hinge line, extended cardinal extremities, increased development of the sulcus and larger size. *Schizophoria australis* closely resembles *S. chouteauensis* but is larger in size, more dorsibiconvex and more sparsely costellate. In addition, a median septum extends beyond the ventral muscle field in *S. australis* but not in *S. chouteauensis*.

OCCURRENCE. Tournasian; Chouteau Limestone, Providence, Green County, and Pettis County, Missouri, USA.

***Schizophoria (Schizophoria) iowensis* (Hall, 1858) (Fig. 5.3)**

1858 *Orthis iowensis* Hall: 488, pl. 2, fig. 4c, d.

1897 *Orthis (Schizophoria) impressa* Calvin: 167.

1892 *Orthis (Schizophoria) iowensis* Hall & Clarke: pl. 6A, fig. 29.

1924 *Schizophoria iowaensis* Fenton & Fenton: 83–85, pl. 19, figs 5–11.

1940 *Schizophoria iowensis* Stainbrook: 483, pl. 1, figs 1–10.

1982 *Schizophoria iowensis* Cooper & Dutro: 37, pl. 3, figs 1–5.

TYPES. Hall's (1858) original paratype series contains specimens referable to *S. iowensis* as well as specimens that should be placed within *S. magna*. This bimodality within the type series has been noted previously by Stainbrook (1940). Within this analysis, paratypes that were transverse with a deep sulcus were referred to as type A (specimens AMNH 5268, 32504, 32506, 32507a, 32507b), and those specimens with a shallow sulcus and length approximately equal to width were referred to as type B (specimens AMNH 32500, 32501, 32502a, 32502b, 32503, 32505). Type B specimens grouped with *S. magna* in the phylogenetic analysis (Fig. 2)

and are transferred to that species herein. Type A specimens are retained within the paratype sequence of *S. iowensis*.

A lectotype, AMNH 32506, is here chosen for *S. iowensis* from the revised former syntype series. This is a complete, articulated specimen in which the external details are well preserved (Fig. 5.3). This specimen has been figured previously in Hall's (1858) original species description.

ADDITIONAL MATERIAL EXAMINED. NYSM 1881, USNM 200955.

EMENDED DIAGNOSIS. Medium-sized, dorsibiconvex *S. (Schizophoria)*; shell height variable, dorsal valve moderately and ventral valve inflation-reduced; hinge line short, cardinal extremities truncated; sulcus moderately to highly developed, onset proximal; shell depth short; narrow dorsal and wide ventral umbonal angles; delthyrium narrow, delthyrial plates upright; dorsal valve flanks dipping gently away from umbonal region; diductor muscles parallel; dental plates form high ridge, enclose ventral muscle field; ventral median septum separated entire muscle field; ventral muscle scars short and narrow; dorsal muscle field short and wide; antero-median ridge of the dorsal muscle field present; vascular system with four trunks.

COMPARISONS. *Schizophoria iowensis* most closely resembles the Givetian *S. traversensis* from the Michigan Basin. *Schizophoria traversensis* can be distinguished by its larger size, less inflated dorsal valve, dorsal valve flanks dipping steeply away from the umbonal region and obchordate ventral muscle field. *Schizophoria magna* has also been associated with this species, but can be differentiated by its longer hinge line, greater shell depth, wider dorsal umbonal angle, lower ventral cardinal area and narrower delthyrium.

OCCURRENCE. Frasnian; Sly Gap Formation, New Mexico; Lime Creek Formation, Iowa, Cedar Valley Limestone, Iowa, USA.

Schizophoria (Schizophoria) macfarlanii (Meek, 1868) (Figs 5.5–5.7)

1868 *Orthis McFarlanei* Meek: 88, pl. 12, fig. 1.

1928 *Schizophoria meeki* Fenton & Fenton: 160, pl. 11, figs 1–8.

1940 *Schizophoria meeki* Stainbrook: 491, pl. 1, figs 11, 15–20.

1944 *Schizophoria macfarlanii* Shimer & Shrock: 357, pl. 140, figs 1–3.

MATERIAL EXAMINED. YPM S1467a–c; FMNH 347, 348, 349 a–b, 350a–d; FMNH 7465, 25993 (*S. meeki* holotype).

EMENDED DIAGNOSIS. Medium-sized, moderate to highly inflated *Schizophoria*; hinge short, cardinal extremities rounded; dorsal valve height greater than ventral; sulcus moderate to high, proximal origination; dorsal umbo extending across hinge line; dorsal muscle scars wide and elongate, antero-median ridge developed; dorsal umbonal region thickened.

REMARKS. *Schizophoria meeki* was erected to include specimens of this species from Iowa, which Fenton & Fenton (1928) considered to be distinct from *S. macfarlanii* due to its shorter hinge line, greater shell length, more rounded lateral margins and finer costae in the Iowa specimens. This analysis, however, found that these specimens assigned to these

two species did not differ in the characters noted by Fenton & Fenton (1928) (see Table 1, characters 4, 8, 18 and 22). Of the characters considered in this study, specimens previously assigned to *S. meeki* and *S. macfarlanii* consistently differed in only three characters: delthyrial angle, location of maximal dorsal convexity and dip of dorsal flanks away from the umbo (characters 14, 19 and 20; Table 1). This amount of character difference is markedly lower than between other species pairs within the analysis and is within the range of intraspecific variation observed within other *Schizophoria* species. Furthermore, Meek's (1868) original collections included specimens from Iowa, which he considered to fall within the range of variation of *S. macfarlanii*. *Schizophoria meeki* is, therefore, synonymised with *S. macfarlanii*.

COMPARISONS. *Schizophoria macfarlanii* is a very distinctive species. The increased thickness of the dorsal umbonal region and the extreme dorsibiconvexity are not shared by any other species of *S. (Schizophoria)*. This species, therefore, can be readily differentiated from all other species.

OCCURRENCE. Givetian; Cedar Valley Group, Iowa and Illinois, USA, Western Canada; Frasnian; Chemung Group, High Point, New York, USA.

Schizophoria (Schizophoria) magna Fenton & Fenton, 1924 (Figs 5.1–2)

1924 *Schizophoria iowensis* var. *magna* Fenton & Fenton: 85–86, pl. 19, figs 12–18.

TYPES. UMMP 7920 (holotype), 7921–7926 (paratypes); FMNH 25246 (paratypes).

ADDITIONAL MATERIAL EXAMINED. AMNH 32500–32503, 32505 (formerly *S. iowensis* syntypes).

EMENDED DIAGNOSIS. Medium sized, low to moderately inflated *S. (Schizophoria)*; hinge short, cardinal extremities rounded; dorsal valve convexity greater than ventral; sulcus moderate to high, proximal origination; dorsal and ventral umbos extension across hinge line limited; ventral muscle field bilobate, surrounded entirely by high dental ridge.

REMARKS. Fenton & Fenton (1924) described *S. magna* as similar to *S. iowensis*, but with a heavier shell and increased convexity. The examination of the paratype series of *S. iowensis* revealed two distinct forms: transversely elongate specimens with deep sulci, and specimens with a shallow sulcus and shell width approximately equal to depth. As discussed above, these groups were analysed separately and the second (more equidimensional specimens with low sulci) grouped with *S. magna*. These specimens (paratypes of *S. iowensis*) consistently differed from paratype specimens of *S. magna* in only three characters: relative inflation of the dorsal valve, shell height and amount of extension of the ventral umbo across the hinge line (characters 2, 6 and 15). This amount of character difference is markedly lower than between other species pairs within the analysis and is within the range of intraspecific variation observed for other *Schizophoria* species. Several specimens that were originally part of the *S. iowensis* type series are, therefore, transferred to *S. magna*, the diagnosis of which is emended above.

COMPARISONS. *Schizophoria magna* most closely resembles *S. impressa* from the Middle to Late Devonian of the

Appalachian Basin. *Schizophoria impressa* differs by having a less inflated dorsal valve, slightly more transverse outline, smaller ventral cardinal area and longer dorsal muscle scars. *Schizophoria magna* has previously been referred to *S. iowensis*; the distinction between these species is discussed above.

OCCURRENCE. Givetian to Frasnian; Cedar Valley Limestone and Lime Creek Formation, Iowa, USA.

Schizophoria (Schizophoria) swallowi (Hall, 1858) (Fig. 4.4)

1858 *Orthis swallowi* Hall: 597, pl. 12, figs 5a–b.

1892 *Orthis Swallowi* Hall & Clarke: pl. 6, figs 23, 24.

1894 *Orthis swallowi* Keyes: 63, pl. 38, fig. 5.

1914 *Schizophoria swallowi* Weller: 167, pl. 22, figs 1–6.

1944 *Schizophoria swallowi* Shimer & Shrock: 357, pl. 140, figs 8–9.

TYPES. Hall (1858) did not choose a holotype specimen and a lectotype has not been subsequently designated. AMNH 32847, a complete dorsal valve embedded within an oolitic limestone matrix is chosen here as the lectotype. This specimen was previously figured in Hall's (1858) original description of the species.

ADDITIONAL MATERIAL EXAMINED. YPM S1248, S1248a, S1248b.

EMENDED DIAGNOSIS. Large, biconvex *S. (Schizophoria)*; shell height low, ventral and dorsal valves inflation-reduced; hinge line long, cardinal extremities elongate; sulcus poorly developed, onset distal; shell depth short; narrow dorsal and wide ventral umbonal angles; ventral area high, delthyrium wide, delthyrial plates upright; dorsal valve flanks dip gently away from umbonal region; ventral muscle field obchordate; dental plates form low ridge, enclose ventral muscle field; ventral median septum separates entire muscle field; ventral muscle scars short and narrow; dorsal muscle field long and narrow; antero-median ridge of the dorsal muscle field present.

COMPARISONS. *Schizophoria swallowi* most closely resembles the contemporaneous species *S. subelliptica*. Both have an extended hinge line, transverse shape and valves with little inflation. *Schizophoria subelliptica* differs from *S. swallowi* in its smaller size, increased ventral valve convexity, narrower ventral umbonal angle and delthyrium, obchordate ventral muscle field and increased elevation of the ridge bounding the ventral muscle field.

OCCURRENCE. Tournaisian; Burlington limestone, Burlington, Iowa; Springfield; and Henderson Co., Sedalia, Missouri, USA.

REVISION OF 'SCHUCHERTELLA'

Background

The genus *Schuchertella* Girty, 1904 was erected to include streptorhynchoid brachiopods previously assigned to *Orthis* but lacking ventral septa, extended dental plates and dorsal socket walls surrounding the dorsal muscle scar (Girty 1904). Placing species within *Schuchertella* has historically been problematical. Dunbar & Condra (1932) noted

that many species referred to *Schuchertella* at that time possessed dental lamellae and should be reassigned to *Schell-wienella*. A generic revision was not undertaken at that time and later authors continued to cite the need for revision of the genus (e.g. Stehli 1954). In the first edition of the brachiopod volume of the 'Treatise on Invertebrate Paleontology,' Williams (1965) clarified the morphological diagnosis of *Schuchertella* and described the genus as impunctate. It was subsequently discovered that the type species, *Streptorhynchus lens* (White, 1862), is extropunctate, while many other species otherwise morphologically assignable to *Schuchertella* were impunctate (Boucot & Johnson 1968; Thomas 1971; Cooper & Dutro 1982). The recognition of this discrepancy led several authors to assign schuchertellid species to open nomenclature as '*Schuchertella*' since a suitable replacement genus was not immediately available (e.g. Boucot & Johnson 1968; Johnson 1970). Recognising the need for a new genus to encompass impunctate species, Gratsianova (1974) erected *Eoschuchertella*. A number of Lower Devonian species from Western North America have been referred to this genus; however, at least one of them, *Eoschuchertella tuktui* Jones & Smith, 1985 has dental lamellae and does not belong within *Eoschuchertella*. Cooper & Dutro (1982) erected *Floweria* for impunctate forms formerly referred to *Schuchertella*. They differentiated their genus from *Eoschuchertella* by its cup-like cardinalia and greater development of the cardinal process (Cooper & Dutro 1982). Williams & Brunton (2000) further differentiated *Eoschuchertella* and *Floweria* on costal bifurcation pattern, which are branching and parvicostellate, respectively.

An overall assessment and revision of Devonian schuchertellids of North America has frequently been suggested (e.g. Dunbar & Condra 1932; Stehli 1954; Cooper & Dutro 1982). Although several schuchertellid species have been reassigned to either *Floweria* or *Eoschuchertella* (e.g. Cooper & Dutro 1982; Norris 1993; Linsley 1994), a thorough revision has not been previously undertaken. The recent revision of the 'Treatise on Invertebrate Paleontology,' places *Schuchertella* into a separate superfamily from *Floweria* and *Eoschuchertella* (Williams & Brunton 2000) based on shell structure (i.e. punctation). Therefore, correctly determining the generic affinities of schuchertellid species has renewed importance.

This analysis considers the generic assignment of Middle and Upper Devonian species previously assigned to *Schuchertella* from North America within a phylogenetic context. The estimated phylogeny is used to determine taxonomic assignments and the evolutionary history of the group. The phylogeny is also used to examine biogeographical changes with North American schuchertellids during the Middle and Late Devonian.

Phylogenetic Analysis

Taxa analysed

Specimens representing 17 species previously regarded as '*Schuchertella*' were analysed phylogenetically. Most species known from the Middle and Upper Devonian and several Lower Devonian species from North America (those for which sufficient morphological information exists) were included within the phylogenetic analysis. Several taxa were excluded due to lack of sufficient morphological data for character analysis. Because this analysis focuses on

determining evolutionary and biogeographical patterns during the Middle and Upper Devonian, some species of '*Schuchertella*' from older and younger strata were excluded. Several Early Devonian and Early Mississippian species were included, however, to help constrain the ages of ancestral speciation events and to allow examination of which lineages persisted through the Late Devonian biodiversity crisis.

As above, whenever possible, type specimens were examined for analysis supplemented when possible by additional non-type specimens and specimens illustrated in the literature. Only specimens interpreted to represent adult individuals were included. Ontogenetic variation, therefore, is not considered within this analysis and all character codings represent the adult condition.

Xystostrophia umbraculum (Schlothheim, 1820) was chosen as the outgroup taxon for character polarisation. This taxon was selected because it is the type species of *Xystostrophia*, a Middle Devonian genus from Europe of the Childiopsinae, a lineage considered to occupy a more basal position within the Orthotetredina than either the Alectorhynchinae or Schuchertellinae, to which *Floweria* and *Schuchertella* respectively belong (Williams & Brunton 1993; Williams & Harper 2000). *Streptorhynchus woolworthana* Hall, 1857 has previously been assigned to both *Schuchertella* (Alexander & Gibson 1993) and *Eoschuchertella* (Linsley 1994); however, the development of dental plates in the paratype specimens requires exclusion from those genera. This species is, therefore, reassigned to *Xystostrophia* in the systematic palaeontology section below and included with *X. umbraculum* in the outgroup.

Specimens were examined from the following collections: American Museum of Natural History (AMNH); Carnegie Museum of Natural History (CM), Field Museum of Natural History (FMNH), New York State Museum (NYSM); Smithsonian Institution (USNM); University of Iowa Paleontology Repository (UIPR); the University of Michigan Museum of Paleontology (UMMP) and Yale Peabody Museum (YPM).

Character and character states

Parsimony analysis was conducted using 36 characters. As in the analysis of *Schizophoria*, internal and external characters were examined because both character sets have been useful in species level taxonomy of this group (Cooper & Dutro 1982; Williams & Brunton 2000). Due to the limited amount of discrete character variation (presence versus absence characters) within '*Schuchertella*,' most schuchertellid species designations include relative differences in size, shape, or expression of features such as ornamentation or muscle scars (e.g. Imbrie 1959; Cooper & Dutro 1982). Consequently, although a number of discrete characters, such as presence or absence of fila in interspaces (character 14), can be coded, many characters represent relative proportions, such as the relative length of the hinge line (character 2). Schuchertellid characters that appear to be quasi-continuous, such as ratios, are treated in the same manner as described within the *Schizophoria* characters and character states section, above. Measured values for each species per morphometric character are shown in Table 4. Character states were separated on the basis of natural breaks, as described above. Data values within each class were compared using ANOVA using Minitab (Minitab Ltd. 1996). The distribution of morphometric data by character state is presented in Table 5. In all

cases, the 95% confidence intervals of the mean values of each character state were non-overlapping suggesting character states are discrete. Character coding for each species is based on the entire distribution of morphometric data in Table 4 and all variation within specimens observed for the other characters. Character coding was accomplished in the same way as for the *Schizophoria* species as described above.

Characters are arranged into general, ventral valve internal and dorsal valve internal groups. (0) represents the presumed primitive state. Morphological terminology follows Williams & Brunton (1997). Where characters are based on measured values or ratios, character states were delimited by natural breaks within the data series. Character codings for analysed taxa are presented in Table 6. The location of external morphological measurements is analogous to that of *Schizophoria* and illustrated in Fig. 1.

General characters

All measurements are in millimetres

1. Size. Determined by measuring the maximum shell width parallel to the hinge line (as in Fig. 1.1a): (0), large (≥ 37.8 mm); (1), small (≤ 28.2 mm).
2. Relative length of the hinge line. The ratio of the length of the hinge divided by the maximum width, measured parallel to the hinge line (as in Fig. 1.1b): (0), long (≥ 0.857); (1), short (≤ 0.787).
3. Termination of the cardinal extremities: (0), angular, corners are sharp (see Fig. 9.1); (1), rounded, corners are truncated (see Fig. 9.5).
4. Location of maximum width. Portion of the valve in which the maximum shell width parallel to the hinge line occurs: (0), posterior of midlength (see Fig. 8.1); (1), midlength.
5. Shape of the lateral profile: (0), resupinate; (1), plano-convex; (2), biconvex.
6. Relative shell height. The ratio of the shell thickness (total height) of the individual and the maximum width, measured parallel to the hinge line (as in Fig. 1.1d): (0), low (≤ 0.296); (1), high (≥ 0.379).
7. Relative inflation of the ventral valve. The ratio of the maximum ventral valve height, measured perpendicular to the commissural plane, divided by the maximum width, measured parallel to the hinge line (as in Fig. 1.1e): (0), low (≤ 0.153); (1), high (≥ 0.200).
8. Outline of the ventral valve: (0), elliptical, evenly round, width greater than depth; (1), subrectangular, anterior corners rounded, lateral edges approximately parallel, width greater than depth (see Fig. 9.3); (2), subtriangular; anterior corners rounded, length nearly equal to width (see Fig. 8.1).
9. Development of cicatrix of attachment: (0), absent; (1), small (see Fig. 9.6); (2), large, cicatrix width at least half the valve width.
10. Extent of deformation of the ventral valve. Relative amount that the ventral valve has grown irregularly due to attachment with the substrate: (0), none (see Fig. 8.4a); (1), moderate, shape asymmetrical, asymmetrical shape of the valve (see Fig. 9.5); (2), extensive, anterior or lateral margins deformed.
11. Costal density. Number of costae per 5 mm at the anterior margin: (0), few (≤ 10); (1), many (≥ 11).

Table 4 Data range of morphometric characters of species in 'Schuchertella' analysis.

	1	2	6	7	20	26	29	30	32	35	36
<i>Xystrotophia umbraculum</i>	30.6– 48.9	0.939– 1.000	0.196– 0.284	0.067– 0.109	0.097– 0.117	0.086	0.590	0.520	0.116	0.320	0.381
<i>Xystrotophia woolworthana</i>	29.1– 41.0	0.793– 1.000	0.120– 0.215	0.073– 0.173	0.073– 0.344	0.061– 0.072	0.401– 0.557	0.388– 0.594	0.142– 0.202	0.351– 0.431	0.335– 0.505
<i>Schuchertella lens</i>	15.7– 20.8	0.850– 1.000	0.308– 0.433	0.159– 0.369	0.147– 0.274	0.042– 0.053	0.351– 0.415	0.216– 0.281	0.147– 0.171	0.399– 0.457	0.293– 0.374
<i>Schuchertella percha</i>	29.6– 42.0	0.856– 0.941	0.212– 0.245	0.088– 0.115	0.088– 0.103	?	?	?	?	?	?
<i>Floweria anomala</i>	31.2– 39.1	0.854– 0.881	>0.247	0.247	<0.284	0.075	0.344	0.256	0.122	0.523	0.372
<i>Floweria arctostrata</i>	14.0– 25.4	0.890– 1.000	>0.271	0.126– 0.271	0.071– 0.271	0.023– 0.600	0.338– 0.448	0.358– 0.488	0.152– 0.230	0.415– 0.478	0.316– 0.444
<i>Floweria becraftensis</i>	11.2– 21.7	0.815– 0.995	0.381	0.266– 0.378	0.272– 0.392	0.086	0.306	0.330	0.117	0.350– 0.439	0.303– 0.327
<i>Floweria chemungensis</i>	31.2– 40.3	0.881– 1.000	>0.345	0.115	0.249	?	0.395– 0.426	0.233– 0.337	0.111– 0.117	0.428	0.412
<i>Floweria cornucopia</i>	37.9	0.712	0.518	0.264	0.390	?	?	?	?	?	?
<i>Floweria crassa</i>	28.0	0.787	0.435	0.252	0.316	?	?	?	?	?	?
<i>Floweria deformis</i>	25.3– 28.3	0.731– 0.742	0.400	0.494	0.224	?	?	?	0.157– 0.200	?	?
<i>Floweria iowensis</i>	28.1– 32.0	0.799– 0.890	0.434	0.244	0.208	0.045	0.272	0.259	?	1	0
<i>Floweria lirella</i>	43.2	0.597	0.456	0.227	0.256	?	?	?	?	?	?
<i>Floweria magnacatrix</i>	23.4	0.944	0.320	0.145	0.154	?	?	?	?	?	?
<i>Floweria pandora</i>	31.5– 41.5	0.833– 0.997	0.222	0.086– 0.169	0.140– 0.162	0.066	0.315– 0.428	0.353– 0.444	0.150	0.490	0.410
<i>Floweria perversa</i>	30.4– 44.1	0.871– 10.210	0.266	0.100	0.100	?	?	?	0.052– 0.064	0.371– 0.493	0.326– 0.389
<i>Floweria prava</i>	16.5– 22.0	0.794– 0.909	0.320– 0.405	0.231– 0.295	0.263– 0.325	0.130	1	1	0.192	0.541	0.415
<i>Floweria transversalis</i>	29.7	0.906	0.404	0.148	0.164	?	?	?	?	?	?

12. Presence of concentric rugae: (0), present (see Fig. 8.4b); (1), absent (see Fig. 9.7).
13. Pattern of costal alternation: (0), costae of alternating size (see Fig. 9.2); (1), costae subequal (see Fig. 8.1); (2), costae with one large and several small, repeating (see Fig. 9.4a).
14. Presence of fila perpendicular to costae in interspaces: (0), present (see Fig. 8.4a); (1), absent (see Fig. 9.5).
15. Abundance of growth lines: (0), few, sparse and uncommon (see Fig. 9.7); (1), many, commonly occurring, especially near the anterior margin (see Fig. 9.5).
16. Spacing of growth lines: (0), growth lines absent; (1), irregular (see Fig. 8.4a); (2), regular.
17. Relative width of costae versus striae: (0), subequal (see Fig. 8.1); (1), costae wider (see Fig. 9.5); (2), striae wider (see Fig. 9.2).
18. Development of fold and sulcus: (0), absent, no noticeable deflection in anterior commissure (see Fig. 9.6); (1), present, noticeable deflection in anterior commissure.
19. Punctuation. Punctuation style is discussed extensively by Williams & Brunton (1993): (0), impunctate; (1), extropunctate.

Characters of the ventral valve

20. Height of the ventral cardinal area. Ratio of the vertical distance from the hinge line to the top of the ventral interarea, measured perpendicular to the hinge line, divided by the ventral valve height, measured as the maximum

vertical height of the ventral valve perpendicular to the commissural plane (as in Fig. 1.1e): (0), low (≤ 0.157); (1), high (≥ 0.244).

21. Angle of the ventral cardinal area. The angle observed between the lateral boundaries of the ventral interarea (as in Fig. 1.1e): (0), high ($\geq 150^\circ$); (1), low ($\leq 140^\circ$).
22. Angle of the delthyridium. The angle observed between the lateral edges of the delthyrial opening (as in Fig. 1.1e): (0), high ($\geq 60^\circ$); (1), low ($\leq 55^\circ$).
23. Extension of umbo over hinge line. Posterior extension of the ventral umbo over the hinge line: (0), present (see Fig. 8.4b); (1), absent.
24. Delthyrium convexity. Extent of curvature of the deltidial plates: (0), weak (see Fig. 8.2); (1), strong (see Fig. 9.2).
25. Presence of dental lamellae, extending from hinge line as raised ridges along the posterior lateral edges of the ventral muscle field: (0), present (see Fig. 8.2); (1), absent (see Fig. 9.1).
26. Relative length of the hinge teeth. Measured as the length of the hinge teeth divided by the total length of the hinge line: (0), long (≥ 0.074); (1), short (≤ 0.068).
27. Presence of a median septum separating the diductor muscle tracks: (0), pronounced (see Fig. 9.1); (1), weak or absent (see Fig. 8.2).
28. Development of the ventral muscle field: (0), deeply impressed and flabellate (see Fig. 8.2); (1), weakly impressed (see Fig. 9.1).

Table 5 Statistical separation of morphometric characters in ‘*Schuchertella*’ analysis are non-overlapping.

Character	Mean	S.D.	Range (mean \pm 1 S.D.)	ANOVA results
1. Maximum width				
(i) small	22.23	5.92	$x \leq 28.15$	$P < 0.001$
(o) large	42.50	4.71	$x \geq 37.79$	
2. Relative hinge length				
(i) short	0.732	0.055	$x \leq 0.787$	$P < 0.001$
(o) long	0.939	0.082	$x \geq 0.857$	
6. Relative total shell height				
(o) low	0.230	0.066	$x \leq 0.296$	$P < 0.001$
(i) high	0.423	0.044	$x \geq 0.379$	
7. Relative ventral valve height				
(o) low	0.115	0.038	$x \leq 0.153$	$P < 0.001$
(i) high	0.291	0.091	$x \geq 0.200$	
20. Height of ventral interarea				
(o) low	0.112	0.045	$x \leq 0.157$	$P < 0.001$
(i) high	0.300	0.056	$x \geq 0.244$	
26. Length of hinge teeth				
(i) short	0.053	0.015	$x \leq 0.068$	$P = 0.001$
(o) long	0.094	0.020	$x \geq 0.074$	
29. Length of ventral muscle scars				
(i) short	0.384	0.055	$x \leq 0.439$	$P < 0.001$
(o) long	0.624	0.082	$x \geq 0.542$	
30. Width of ventral muscle scars				
(i) narrow	0.287	0.054	$x \leq 0.341$	$P < 0.001$
(o) wide	0.508	0.068	$x \geq 0.440$	
32. Cardinal process width				
(o) narrow	0.097	0.027	$x \leq 0.124$	$P < 0.001$
(i) wide	0.180	0.025	$x \geq 0.155$	
35. Length of dorsal muscle scars				
(o) short	0.379	0.060	$x \leq 0.439$	$P < 0.001$
(i) long	0.511	0.037	$x \geq 0.474$	
36. Width of dorsal muscle scars				
(i) narrow	0.304	0.032	$x \leq 0.336$	$P < 0.001$
(o) wide	0.405	0.036	$x \geq 0.369$	

For all classes, the 95% confidence intervals are non-overlapping.
S.D., standard deviation.

Table 6 Character state distribution for taxa in the phylogenetic analysis of Schuchertellids.

	123456789	1111111111 0123456789	2222222222 0123456789	3333333 0123456
<i>Xystostrophia umbraculum</i>	000000000	0000000000	0000000000	0000000
<i>Xystostrophia woolworthana</i>	000000020	0001011000	X000001100	001000X
<i>Schuchertella lens</i>	1000Y1XZ0	0101011101	X000011101	1011001
<i>Schuchertella percha</i>	000000011	1102012201	010001????	?0???0??
<i>Floweria anomala</i>	00X020111	X111011100	1110010111	1101010
<i>Floweria arctostriata</i>	1000YoX11	oX12100000	X100111001	00111XX
<i>Floweria becraftensis</i>	101011100	0011101X00	1111110101	1101101
<i>Floweria chemungensis</i>	000001oX1	101X100100	111001?111	1101000
<i>Floweria cornucopia</i>	011121101	111111100?	111011????	?1?????
<i>Floweria crassa</i>	111101111	211110000?	111111????	?0?????
<i>Floweria deformis</i>	011021121	1X1111110?	11000?????	?11????
<i>Floweria iowensis</i>	101101101	1101011000	1110111111	11?1010
<i>Floweria lirella</i>	011121111	110111110?	101001????	?1?????
<i>Floweria magnacatrix</i>	100000012	101110021?	000011????	?1?????
<i>Floweria pandora</i>	0000000X0	0001000000	0000111001	0011010
<i>Floweria perversa</i>	001000010	0000000000	oX0011????	?101oXX
<i>Floweria prava</i>	10X121101	1101011010	1110110111	1111010
<i>Floweria transversalis</i>	100001012	111111101?	000011????	?1?????

Missing data are indicated by ‘?’.

Character states listed as X, Y and Z are polymorphic, where X = (0 & 1), Y = (1 & 2), and Z = (0 & 2).

Character numbers are listed across the top of the table.

29. Length of the ventral muscle scars. The ratio of the maximum length of the ventral muscle field, measured perpendicular to the hinge line, divided by the maximum shell length, measured perpendicular to the hinge line: (0), long (≥ 0.542); (1), short (≤ 0.439).
30. Width of the ventral muscle scars. The ratio of the maximum width of the ventral muscle field, measured parallel to the hinge line, divided by the maximum valve width, measured parallel to the hinge line: (0), wide (≥ 0.440); (1) narrow (≤ 0.341).

Characters of the dorsal valve

31. Dorsal umbonal angle. The angle observed between the two limbs of the umbo when the dorsal valve is lying on the commissural plane (as in Fig. 1.1a): (0), low ($\leq 130^\circ$); (1), high ($\geq 150^\circ$).
32. Width of the cardinal process. Measured as the width of cardinal process divided by the total length of the hinge line: (0), narrow (≤ 0.124); (1), wide (≥ 0.155).
33. Shape of the dental sockets: (0), linear (see Fig. 8.3); (1), cup-like (following Cooper & Dutro (1982)) (see Fig. 8.5).
34. Development of the dorsal myophore: (0), weak, low relief (see Fig. 8.5); (1), strong, high relief (see Fig. 9.4b).
35. Length of the dorsal muscle scars. The ratio of the maximum length of the dorsal muscle field, measured perpendicular to the hinge line, divided by the maximum shell length, measured perpendicular to the hinge line: (0), short (≤ 0.439); (1), long (≥ 0.474).
36. Width of the dorsal muscle scars. The ratio of the maximum width of the dorsal muscle field, measured parallel to the hinge line, divided by the maximum valve width, measured parallel to the hinge line: (0), wide (≥ 0.369); (1), narrow (≤ 0.336).

Parsimony analysis

Phylogenetic analysis used PAUP* 4.0b10 (Swofford 2002). A heuristic search was performed using a random addition sequence of 1000 replications with tree-bisection-reconnection used as the branch-swapping algorithm. All characters were unordered and assigned equal weight and taxa coded as having multiple states for a character were treated as polymorphic for that state. Characters were optimised using the accelerated transformation (ACCTRAN) option.

A single most parsimonious tree with a length of 106 steps was recovered and is presented in Fig. 7. The consistency index (CI) is 0.42, and the retention index (RI) is 0.61. This CI significantly ($P < 0.05$) exceeds those derived from sets of similarly sized matrices constructed from random data (CI = 0.20; Klassen *et al.* 1991). The g_1 statistic, a measure of the skewness of tree length distributions and phylogenetic signal, obtained from a distribution of 10000 random trees constructed from this data set is -0.419 , significantly stronger than in random data ($P = 0.01$; Hillis & Huelsenbeck 1992). The amount of support for the recovered cladogram was further characterised by bootstrap and jackknife analyses. The bootstrap analysis was performed using a 'fast' stepwise-addition search with 10000 replicates; groups compatible with the 50% majority rule consensus tree were retained. Confidence values

for nodes duplicated in the bootstrap analysis are presented in Fig. 7. Jackknife analysis was accomplished using the 'fast' stepwise addition search with 10000 replicates and 5 percent deletion of characters (equivalent to 3 characters). As in the bootstrap analysis, groups compatible with the single most parsimonious tree were retained and confidence values for nodes duplicated in the jackknife analysis are presented in Fig. 7. Bremer support for specific branches was also determined by computing the strict consensus trees of lengths 107 to 108 steps. Bremer support values indicate how many additional steps are required to collapse support for a specific clade and are shown in Fig. 7 (Bremer 1994).

Results and taxonomic implications

Recognition of clades within the genus

Several patterns are apparent from inspection of the single most parsimonious cladogram in Fig. 7. First, *Schuchertella lens* (White 1862), the type species of *Schuchertella*, and *S. percha*, which is known to be extropunctate, group together in a distinct clade (Fig. 7). All other species included within this analysis group into a primarily pectinate clade that includes *Floweria prava* (Hall 1858), the type species of *Floweria* (Fig. 7).

Each branch of the reconstructed cladogram is supported by one or more synapomorphies. The sister group relationship of *Schuchertella lens* and *S. percha* (Stainbrook 1947), is supported by the development of numerous fine costae and extropunctuation (characters 11 and 19). The presence or absence of extropunctuation has been considered to be of great evolutionary importance (Williams & Brunton 1993) and is considered to be the basic difference between *Schuchertella* and *Floweria* (Dutro pers. com., 2003). All other species in the ingroup form a clade that includes *Floweria prava* and are united by strong convexity of the delthyrium (character 24).

Schuchertella and *Floweria* are assigned to different superfamilies within the current brachiopod taxonomy (Williams & Brunton 2000), and the apparent sister group placement of these genera within this analysis is not intended to suggest taxonomic revision of super-generic relationships. Several additional genera and a greater temporal span of taxonomic information would be required for such an analysis. The phylogenetic analysis of the orthotetridines by Williams & Brunton (1993) firmly establishes the subfamilial relationships and renders this unnecessary. Instead, the inclusion of both *Schuchertella* and *Floweria* in this analysis was intended to clarify the correct placement of the Middle and Upper Devonian 'schuchertellid' species within two genera known to be evolutionarily distant but with extensive homeomorphy that has previously impeded species placement. The reconstructed species relationships indicates that only *Schuchertella percha* should be retained within *Schuchertella*, as all other species share a closer relationship with the type species of *Floweria* than the type species of *Schuchertella*. These other species, formerly referred to as *Schuchertella* or 'Schuchertella,' therefore, are transferred to *Floweria* herein. The pectinate branching pattern within the *Floweria* clade does not support further subdivision of these species into additional genera or subgenera.

Within the *Floweria* clade, most cladogenetic events occur in a pectinate pattern (Fig. 7). Each branch is supported

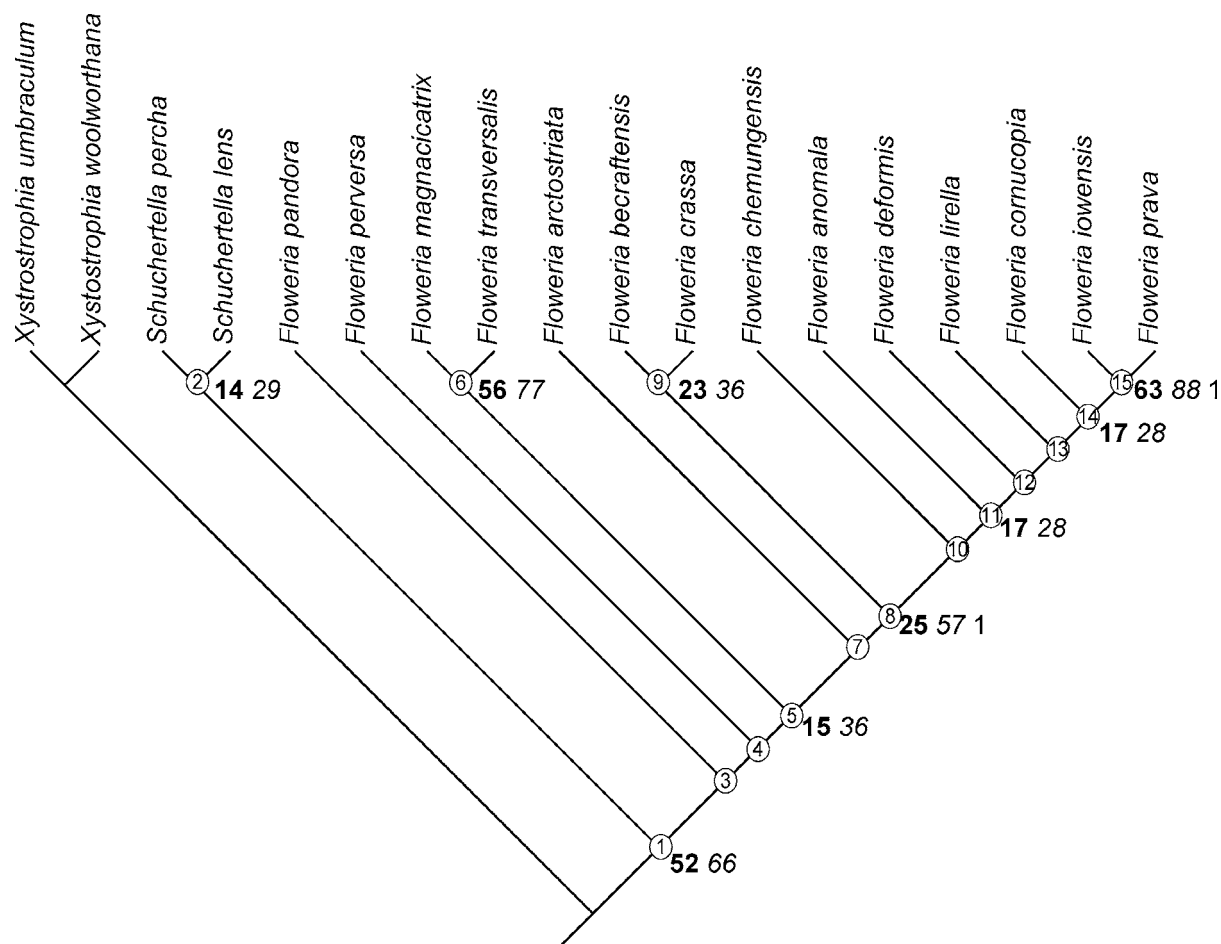


Figure 7 Single most parsimonious tree produced from analysis of character data given in Table 6 using PAUP* 4.0b10 (Swofford 2002). Tree length is 106 steps. The consistency index is 0.42 and the retention index is 0.61. The g_i statistic for the tree is -0.419 . Bootstrap and jackknife values are indicated next to the nodes that they support, in bold and italic numerals, respectively. Bremer support is indicated in regular font. Character states were placed at the nodes using MacClade 3.04 (Maddison & Maddison 1992) under ACCTRAN optimisation. Node numbers are circled on the cladogram. Apomorphic characters that change unambiguously below nodes are listed in parentheses. Node 1, 25(1), 29(1), 33(1); Node 2, 11(1), 19(1); Node 3, 24(1); Node 4, 31(1); Node 5, 1(1), 12(1), 14(1); Node 6, 10(1), 18(1); Node 7, 21(1); Node 8, 6(1), 7(1), 20(1), 22(1), 26(0), 30(1); Node 9, 23(1); Node 10, 1(0), 10(1), 17(1), 24(0), 28(1); Node 11, 5(2), 11(1), 15(1), 16(1), 35(1); Node 12, 2(1), 32(1); Node 13, 4(1); Node 14, 8(0), 17(0), 24(1); Node 15, 2(0), 14(0).

by specific character evidence. The monophyly of all species exclusive of *F. pandora* (Billings 1860) is supported by a high dorsal umbonal angle (character 31). All species exclusive of *F. pandora* and *F. perversa* (Hall 1857) share a derived large size, absence of costal rugae and loss of intercostal filae (characters 1, 12 and 14). The sister relationship of *F. magnacatrix* Cooper & Dutro, 1982 and *F. transversalis* Cooper & Dutro, 1982 is supported by shared moderate deformation of the ventral valve and development of a fold and sulcus (characters 10 and 18). The monophyly of the remaining *Floweria* species exclusive of these is supported by a derived low angle of the pedicle area (character 21). The relationship of all species crownward of *F. arctostriata* (Hall 1867) is supported by high shell height, high ventral valve, high ventral interarea, narrow delthyrial angle, long hinge teeth and narrow ventral muscles (characters 6, 7, 20, 22, 26 and 30). The sister group relationship of *F. becraftensis* (Clarke 1900) and *F. crassa* (Imbrie 1959) is supported by shared reduction of the ventral umbo so that it does not extend over the hinge line (character 23). The

monophyly of the clade consisting of *F. chemungensis* (Conrad 1842) and species up the tree is supported by their shared small size, moderate deformation of the ventral valve, costae wider than striae, weak convexity of the delthyrial plate and weak impression of the ventral muscle scars (characters 1, 10, 17, 24 and 28). The clade of *F. anomala* (Winchell 1866), *F. deformis* (Hall 1857), *F. lirella* (Imbrie 1959), *F. cornucopia* (Imbrie 1959), *F. iowensis* (Stainbrook 1943) and *F. prava* (Hall 1858) is supported by the development of a biconvex shape, increased number of costae, presence of many, uneven growth lines and long dorsal muscles (characters 5, 11, 15, 16 and 35). The clade including *F. deformis* and species crownward is supported by shared extended length of the hinge line and wide cardinal process (characters 2 and 32). The relationship of *F. lirella*, *F. cornucopia*, *F. iowensis* and *F. prava* is supported by the maximum valve width located at midlength (character 4), while the monophyly of those species exclusive of *F. lirella* is supported by an elliptical ventral valve, subequal costae and striae widths and strongly convex delthyrium (characters 8, 17 and 24). The sister

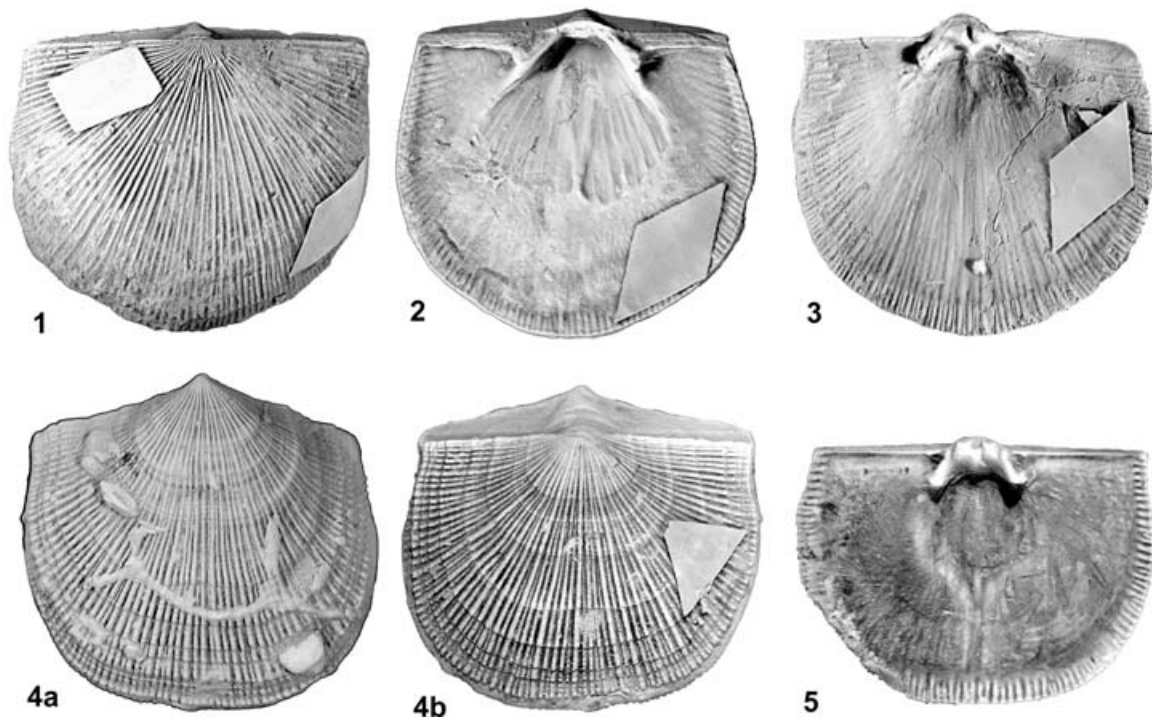


Figure 8 1, *Xystostrophia woolworthana* (Hall, 1857); AMNH 33145 (lectotype), dorsal view, 1.7 \times . 2, *Xystostrophia woolworthana* (Hall, 1857); AMNH 33147, ventral valve interior, 1.8 \times . 3, *Xystostrophia woolworthana* (Hall, 1857); AMNH 33143, dorsal valve interior, 1.9 \times . 4, *Schuchertella lens* (White, 1862); YPM S2155A, 3.1 \times ; 4a, ventral view, 4b, dorsal view. 5, *Schuchertella lens* (White 1862); FMNH 6693, dorsal valve interior, 3.4 \times .

relationship of *F. iowensis* and *F. prava* is supported by hinge lines of reduced length and the presence of fila (characters 2 and 14).

Evolutionary and ecological implications

The reconstructed phylogenetic relationships in Fig. 7 provide insight into evolutionary and ecological patterns within Devonian schuchertellids. A prominent pattern is the absence of any species of *Schuchertella* before the Famennian. Although all Devonian species of *Schuchertella* were considered, all species of Early, Middle, to early Late (i.e. Frasnian) age grouped within the *Floweria* clade in the phylogenetic analysis (Fig. 7). This indicates that *Schuchertella* had either not evolved or were simply not present in North America prior to the Frasnian–Famennian extinction. Famennian *Schuchertella* species, however, span a wide geographical range including New Mexico, Missouri and Pennsylvania (White 1862; Cooper & Dutro 1982; Carter & Kammer 1990) and must have dispersed rapidly during the Famennian. Additionally, all representative Mississippian species examined, although not included in the phylogenetic analysis (*S. macensis* Carter & Kammer, 1990 and *S. hardinensis* Carter, 1988), were demonstrably members of *Schuchertella*, but no known *Floweria* species ranges into the Famennian or Carboniferous. *Floweria*, thus, appears to have become extinct while *Schuchertella* appears to have evolved during the Frasnian–Famennian crisis. The extensive amount of homeomorphy between these two genera, therefore, may represent similar solutions to common environmental stresses before and after a time of great ecological overturn (Droser *et al.* 2000).

Within the *Floweria* clade, phylogenetic relationships are supported by a broad array of characters including features of both external shape and internal musculature. One of the key morphological changes within this group is the variation in the extent of ventral valve attachment. More basal *Floweria* species exhibit a resupinate shape, ventral valve with low inflation and no deformation and no appreciable cicatrix of attachment. More advanced members of the genus, however, are biconvex with a highly inflated ventral valve, distinguishable cicatrix and moderate deformation of the ventral valve. This morphological trend is also reflected stratigraphically as the species exhibiting greater areas of attachment and extent of deformation are Givetian and Frasnian in age, while less deformed, resupinate forms tend to occur from the Early Devonian to the Eifelian. Internal morphological changes also follow this pattern. The more crownward species, especially *F. becraftensis* up the tree, have relatively longer hinge teeth, a weakly impressed ventral muscle field with narrower muscle scars, a weak to absent median septum and longer dorsal muscles. These internal changes may suggest a lack of dependence on well-developed musculature as pedicle attachment by cementation became more prominent. Interestingly, *Schuchertella* appears to follow a similar trend with increased cementation and reduction of internal musculature when Famennian and Carboniferous species are compared.

The morphological changes impacted the paleoecology of *Floweria* species. Early and Middle Devonian resupinate species have been interpreted as free-lying animals resting on the ventral valve (Brower *et al.* 1978; Alexander & Gibson 1993) and were members of community assemblages

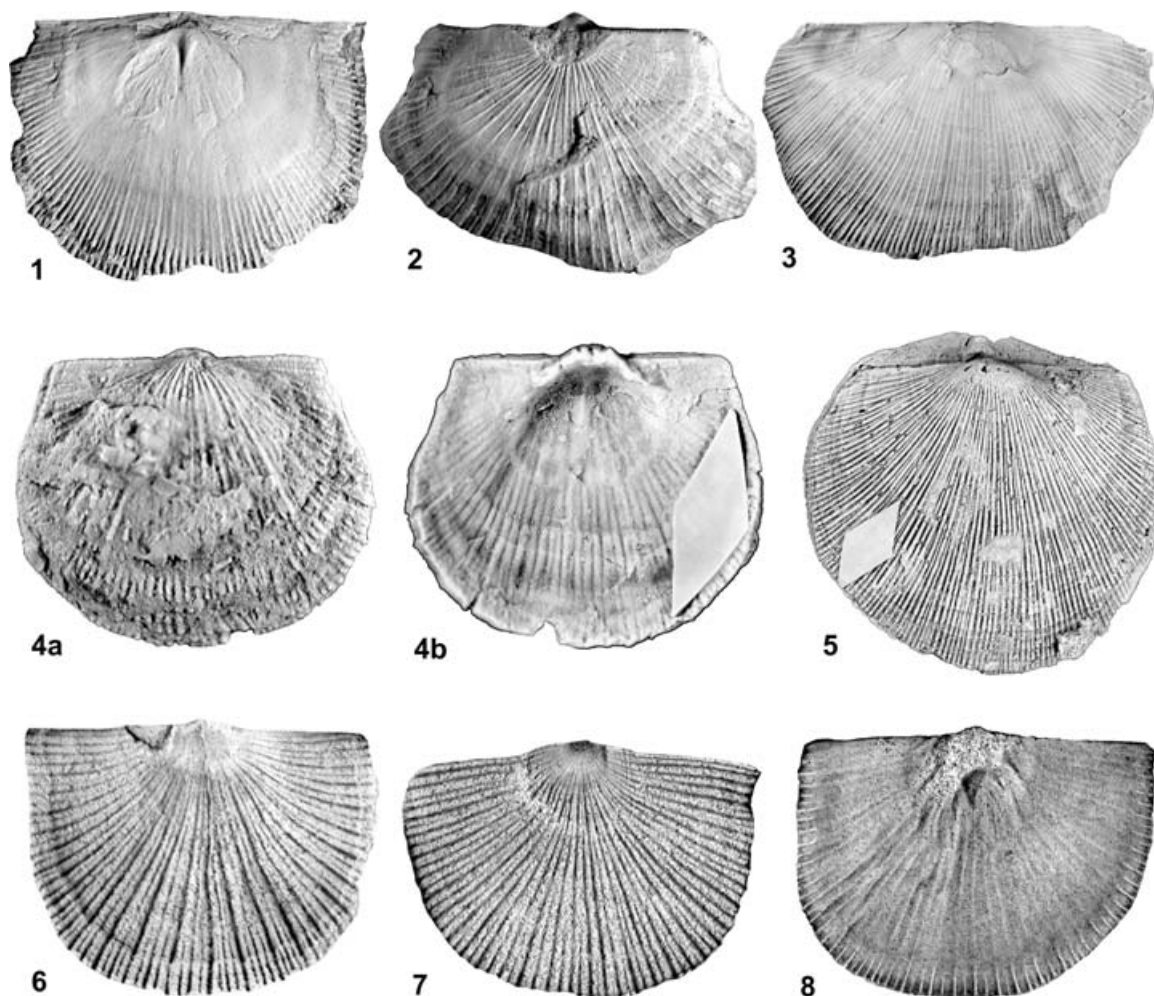


Figure 9 1, *Floweria pandora* (Billings 1860); AMNH 37173, ventral view, 1.9×. 2, *Floweria perversa* (Hall, 1857); AMNH 37271, ventral view, 2.3×. 3, *Floweria perversa* (Hall, 1857); AMNH 37177, dorsal view, 1.3×. 4, *Floweria arctostriata* (Hall, 1843); AMNH 32847, 3.5×; 4a, dorsal view, 4b, dorsal valve interior. 5, *Floweria deformis* (Hall, 1857); AMNH 33297, dorsal view, 1.2×. 6, *Floweria chemungensis* (Conrad, 1842); AMNH 37157c, 2.3×. 7, *Floweria chemungensis* (Conrad, 1842); AMNH 37157b, ventral view, 2.3×. 8, *Floweria chemungensis* (Conrad, 1842); AMNH 37157a, ventral view, 2.8×.

found in low energy, shelf margin settings (Feldman 1980; Koch 1981). Frasnian species, such as *Floweria chemungensis*, were members of inner platform and nearshore environments that exhibit adaptations for attachment (McGhee 1976; McGhee & Sutton 1981, 1983). The transition to a cementing lifestyle, therefore, resulted in a habitat shift to higher energy environments closer to the palaeoshoreline.

Biogeographical implications

Biogeographical patterns were evaluated in conjunction with the phylogeny in Fig. 7. This phylogeny was converted to an area cladogram and nodes were optimised as described in the discussion of *Schizophoria* biogeography, above. The areas of endemism considered in schuchertellid biogeography were: Europe; the northern Appalachian Basin; the southern Appalachian Basin; the Michigan Basin; the Iowa–Illinois basin; the Missouri basin; the western United States. The area cladogram is shown in Fig. 10. The type of information present and rationale for interpretation of area cladograms is discussed above under *Schizophoria* biogeography.

The biogeographical patterns illustrated in Fig. 10 suggest that ancestral members of both the *Schuchertella* and *Floweria* lineages were present in North America, particularly within northern Eastern North America (ENA) and central North America. The establishment of the genus *Schuchertella* involved dispersal events into western North America and the Iowa Basin, while subsequent speciation events within the genus involved range reduction and vicariance. Conversely, the establishment of the *Floweria* lineage involved a vicariance event limiting the *Floweria* stock to northern ENA. Further speciation events within *Floweria* involved both dispersal and vicariance events. Dispersal events typically occurred from an eastern into a more westerly basin, such as from northern ENA to the Michigan Basin (as in *F. crassa*) or the Iowa basin to the Western United States (as in *F. prava*). Vicariance events usually resulted in widespread ancestral ranges covering two or three areas reduced to a single biogeographical range in descendants. Overall, the North American *Floweria* lineage included eight episodes of vicariance and seven of dispersal. The nearly equivalent distribution of vicariance and dispersal events contrasts with

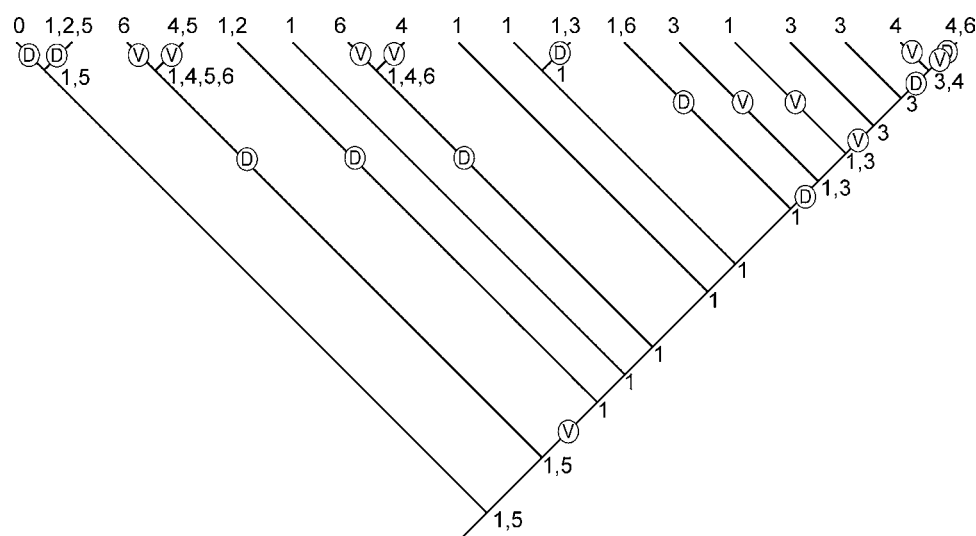


Figure 10 Phylogeny from Fig. 7, with biogeographical states substituted for terminal taxa and mapped onto the ancestral nodes. Inferred episodes of speciation by vicariance (V) and dispersal (D) are indicated. Ancestral nodes calculated using modified Fitch optimisation (Lieberman & Eldredge 1996; Lieberman 2000). 0, Europe; 1, Northern Appalachian Basin; 2, Southern Appalachian Basin; 3, Michigan Basin; 4, Iowa/Illinois Basin; 5, Missouri; 6, Western United states.

the relative absence of vicariance observed in *Schizophoria*, above. The level of vicariance observed in *Floweria*, however, is below the level observed within the modern biota.

Systematic Palaeontology

Taxa and material examined that do not require detailed discussion or synonymy

The following specimens were examined to determine character states for each species. These specimens belong to either the type series or have been previously illustrated elsewhere. Each of the species included within this list is considered to be a valid species within the designated subgenus. Since neither lectotype designation nor taxonomic revision within these species is required for these taxa, they are not treated exhaustively in the systematic palaeontology section below. Enhanced diagnoses for these species can be determined by supplementing the original species descriptions cited below with the character coding presented in Table 6.

Fardenia subplana (Conrad, 1842) NYSM 1705, E1915, E1883, AMNH 40758-40761

Floweria anomala (Winchell, 1866) YPM S3184, S3184a-c, USNM 124377, 124270

Floweria? bellula (Clarke, 1894b) NYSM 1670, 1671 (syntypes)

Floweria cornucopia (Imbrie 1959) USNM 124373 (holotype)

Floweria crassa (Imbrie, 1959) USNM 142316 (holotype)

F. iowensis (Stainbrook, 1943) UIPR 6-323A (holotype), 6-323

Floweria lirella (Imbrie, 1959) USNM 124393 (holotype)

Floweria magnacatrix Cooper & Dutro, 1982 USNM 200855 (holotype)

Floweria prava (Hall, 1858) USNM 200854, 200874, 135266, UMMP 7948-7950

Floweria transversalis Cooper & Dutro, 1982 USNM 200873

Schuchertella bowdenensis Carter & Kammer, 1990 CM 34821 (paratype), 34822 (holotype), 34823-34825 (paratypes)

'Schuchertella' coloradensis Kindle, 1909 USNM 62008a-b

'Schuchertella' elliptica Clarke & Schwartz, 1913 USNM 177286 (holotype)

'Schuchertella' woolworthana var. *gaspensis* (Clarke, 1907) NYSM 8541 (syntype), 8542-8545

Schuchertella hardinensis Carter, 1988 CM 34628 (holotype), 34629-34634 (paratypes)

Schuchertella lens (White, 1862) YPM S2155a, FMNH 6693

Schuchertella macensis Carter & Kammer, 1990 CM 34816 (holotype), 34817-34820 (paratypes)

Schuchertella percha (Stainbrook, 1947) USNM 135252a-d

'Schuchertella' sylvani (Morris & Sharpe, 1846) NYSM 8538-8540

Xystostrophia umbraculum (Schlotheim, 1820) YPM 202589-202591, 19280

Order ORTHOTETIDA Schuchert & Cooper, 1932

Suborder ORTHOTETIDINA Waagen, 1884

Superfamily ORTHOTETOIDEA Waagen, 1884

Family SCHUCHERTELLIDAE Williams, 1953

Genus **SCHUCHERTELLA** Girty, 1904

1904 *Schuchertella* Girty: 734.

1932 *Schuchertella* Dunbar & Condra: 70-71, 117.

1944 *Schuchertella* Shimer & Shrock: 343.

1954 *Schuchertella* Stehli: 298.

1965 *Schuchertella* Williams: 408.

2000 *Schuchertella* Williams & Brunton: 665.

TYPE SPECIES. *Streptorhynchus lens* White, 1862.

DIAGNOSIS. Variable size and shape; typically subrectangular and rectimarginate, amount of inflation and deformation of ventral and dorsal valves variable; ventral interarea high and linear with convex chilidium; ventral muscle scars flabellate; dorsal muscle scars divided by low myophragm; shell extropunctate (after Williams & Brunton (2000)).

REMARKS. Girty (1904) defined *Schuchertella* to encompass orthotetid species lacking ventral septa, dental plates and ridges bounding the dorsal muscle field. These species were previously included within *Orthotetes* Fischer de Waldheim, 1830, but Girty determined that *Orthotetes* was a distinct taxon and erected *Schuchertella* for these species. The original diagnosis of *Schuchertella* is neither very specific nor informative. This vagueness resulted in continued taxonomic confusion such as that noted by Dunbar & Condra (1932) and Stehli (1954). The realisation that species assigned to *Schuchertella* include both impunctate and extropunctate forms has resulted in a reassessment of the generic placement of some species and revision of the generic diagnosis (e.g. Boucot & Johnson 1968; Gratsianova 1974; Cooper & Dutro 1982; Williams & Brunton 2000).

Examination of Middle and Upper Devonian species previously assigned to *Schuchertella* from North America by light microscopy indicated that none of the pre-Famennian species examined could be conclusively shown to be extropunctate (Table 2, character 19). These species, therefore, cannot be retained within *Schuchertella*. Additionally, the other character states used in the phylogenetic analysis also support the exclusion of the pre-Famennian species from *Schuchertella* as they are more closely related to the type species of *Floweria* than to *Schuchertella lens* (Fig. 7). The lower stratigraphic limit of *Schuchertella* within North America, therefore, is Famennian. *Schuchertella* develops maximal species diversity and geographical range (cosmopolitan) during the Carboniferous. The upper stratigraphic limit of *Schuchertella* is unclear. Cooper & Grant (1974) hesitated to assign Permian species to *Schuchertella* since they doubted the ability of a brachiopod genus to persist for such an extensive amount of time. Other authors, including Girty (1904) and Grant (1995), however, consider species from the Permian to belong within *Schuchertella*.

OCCURRENCE. Upper Devonian (Famennian) to Upper Permian; cosmopolitan.

INCLUDED SPECIES. *Streptorhynchus lens* White, 1862 (Famennian to Tournaisian), *Schellwienella percha* Stainbrook, 1947 (Famennian), *Schuchertella bowdenensis* Carter & Kammer, 1990 (Famennian to Tournaisian), *Schuchertella hardinensis* Carter, 1988 (Tournaisian), *Schuchertella macensis* Carter & Kammer, 1990 (Tournaisian). Other species Famennian and younger may also be attributed to *Schuchertella*, but these were not examined herein.

Superfamily CHILIDIOPSOIDEA Boucot, 1959

Family CHILIDIOPSOIDAE Boucot, 1959

Genus *XYSTOSTROPHIA* Havlíček, 1965

1965 *Xystostrophia* Havlíček: 292.

1967 *Xystostrophia* Havlíček: 196–197.

2000 *Xystostrophia* Williams & Brunton: 675.

TYPE SPECIES. *Terebratulites umbraculum* Schlotheim, 1820.

DIAGNOSIS. Subquadrate to mucronate; resupinate; interarea high with convex pseudodeltidium and low chilidium; dental plates short, widely divergent; ventral muscle flabellate, bounded by peripheral ridges; dorsal muscle scar divided by myophragm; short cardinal process; fila well developed, often extend across costellae as short spines; shell impunctate (after Havlíček (1967) and Williams & Brunton (2000)).

REMARKS. *Xystostrophia* is distinguishable from other orthotetids by its distinct ornamentation pattern in which fila extend across costae, resupinate shape, flabellate muscle field, short dental plates and impunctate shell. This suite of characters readily separates species of this genus from other 'schuchertellids' in this analysis.

OCCURRENCE. Lower to Middle Devonian; Western and Central Europe, Eastern North America.

INCLUDED SPECIES. *Terebratulites umbraculum* Schlotheim, 1820, *Strophomena woolworthana* Hall, 1857. Additional species were included by Havlíček (1965), but were not examined herein.

Xystostrophia woolworthana (Hall, 1857) (Figs 8.1–8.3)

1857 *Strophomena woolworthana* Hall: 8.

1859 *Strophomena woolworthana* Hall: 192–193, pl. 17, figs 1a–r, 2a–c.

1892 *Orthotetes woolworthana* Hall & Clarke: 255, pl. 9, figs 25–31.

1944 *Schuchertella woolworthana* Shimer & Shrock: 343, pl. 132, figs 49–51.

1993 *Schuchertella woolworthana* Alexander & Gibson: 27, fig. 3j.

1994 *Eoschuchertella woolworthana* Linsley: pl. 15, figs 1–21.

TYPES. Hall (1857) did not designate a holotype in the original description and a lectotype has not subsequently been designated. Therefore, AMNH 33145 is herein designated as the lectotype. AMNH 33145 is a complete external mold (Fig. 8.1) and features of the cardinal area, overall shell shape and ornamentation are well preserved. This specimen was figured previously by Hall (1859: pl. 17, fig. 1b–d; 1892: pl. 9, figs 25, 26). The remaining members of the syntype series (AMNH 33142–33144, 33146–33151) are transferred to paralectotype status.

ADDITIONAL MATERIAL EXAMINED. YPM 57466, 202594–202597, 109108, 108100, NYSM 1708, E1407, E2903, E2912, E2856.

DIAGNOSIS. Shell semielliptical, mucronate; ventral valve gently concave, brachial valve convex; dorsal and ventral interareas developed, apsacline; short dental ridges widely divergent; cardinal process bifid, two deep grooves per side, node developed at base; ventral muscle field flabellate with central myophore and bounding ridges posteriorly; parvicostellate with faint fila; shell impunctate.

REMARKS. This species has recently been included within both *Schuchertella* and *Eoschuchertella* (Alexander & Gibson 1993; Linsley 1994), but the presence of dental lamellae excludes this species from either genus. The combination of short dental plates and an impunctate shell places this species within the Chilidiopsoidae. The configuration of the

muscle scars and overall shell shape and structure suggests that this species should be referred to *Xystostrophia*. This species exhibits significant differences from *Hipparionix* and *Iridistrophia*, the other Devonian chilidiopid genera. *Hipparionix* is characterised by a semioval outline and short hinge line, while *X. woolworthana* has an extended hinge line and semielliptical outline. The muscle scars of *Iridistrophia* are indistinct, while the ventral muscle field is well developed in *X. woolworthana*.

COMPARISONS. *Xystostrophia woolworthana* is a distinctive species in the Lower Devonian of eastern and central North America. It superficially resembles *Fardenia subplana* (Conrad, 1842) in external form, however the well-developed dental ridges and flabellate muscle field distinguish *X. woolworthana*.

OCCURRENCE. Lower Devonian; eastern and central North America including Lower Helderberg Group, eastern New York, Quebec; Ross Formation, Birdsong Shale, western Tennessee; Hunton Group, Haragan Limestone, central Oklahoma.

Family AREOSTROPHIIDAE Manankov, 1979

Genus *FLOWERIA* Cooper & Dutro, 1982

1959 *Schuchertella* Imbrie: 390.

1982 *Floweria* Cooper & Dutro: 53.

1993 *Floweria* Norris: 27–28.

2000 *Floweria* Williams & Brunton: 681.

TYPE SPECIES. *Orthis prava* Hall, 1858.

EMENDED DIAGNOSIS. Medium sized, ventral valve more convex than nearly flat dorsal valve; cicatrix variably developed; ventral interarea higher than dorsal; convex delthyrium; cardinal processes low, grooved, with median node at base; muscle scars normally impressed; dorsal myophore present; finely costellate by intercalation; brachiphores contained in cuplike sockets; shell impunctate (after Cooper & Dutro (1982) and Williams & Brunton (2000)).

REMARKS. Cooper & Dutro (1982) erected *Floweria* to include species externally similar to *Schuchertella lens* but which were impunctate and had a reduced dorsal interarea. *Floweria* is distinguished from *Eoschuchertella* Gratsianova 1974 by a more distinct cardinal process, recurved rather than divergent cardinalia and costae increasing by intercalation instead of bifurcation.

Cooper & Dutro (1982) transferred two other species previously assigned to *Schuchertella* and assigned two new species to *Floweria*, but did not comment on which other species should be included within this genus. Cooper (pers. com. in Johnson (1970)) noted the lack of punctuation in pre-Famennian 'schuchertellids,' suggesting that perhaps most of the Devonian species referred to *Schuchertella* were incorrectly assigned. Williams & Brunton (2000: 665) and Dutro (pers. comm., 2003) also noted that many schuchertelloid species might require reclassification following careful examination of their shell structure.

Of the species examined within this analysis, only *Schuchertella lens* and *S. percha* exhibited extropunctation; all other species were impunctate. The impunctate shell structure and other character data for these taxa produces a cladogram that suggests all Early Devonian to Frasnian

'*Schuchertellas*' of North America should be transferred to *Floweria* (Fig. 7). The inclusion of these species within *Floweria* expands both the morphological and stratigraphic definition of this genus. *Floweria* species now range from the Early Devonian through the early Late Devonian (Frasnian) throughout North America and include forms of variable external shape and size.

Linsley (1994) reevaluated the generic placement of several schuchertelloid species from New York. Although he provided no discussion to explain the taxonomic changes, he transferred all Early and Middle Devonian schuchertelloid species to *Eoschuchertella*, while Late Devonian species were retained within *Schuchertella*. Each of the species he discussed was examined within this analysis (Table 2). None of the species (even the Late Devonian species) were extropunctate and thus cannot be retained within *Schuchertella*. Additionally, all species exhibited the characteristics of *Floweria* rather than *Eoschuchertella*. These species are, therefore, transferred to *Floweria* herein.

OCCURRENCE. Lower to Upper Devonian; North America.

INCLUDED SPECIES. *Crania (Pseudocrania) anomala* Winchell, 1866 (Givetian), *Orthotheses becraftensis* Clarke, 1900 (Emsian), *Orthotheses bellulus* Clarke, 1894a (Givetian), *Orthotheses deformis* Hall, 1857 (Emsian), *Floweria magnacatrix* Cooper & Dutro, 1982 (Frasnian), *Floweria transversalis* Cooper & Dutro, 1982 (Frasnian), *Orthis perversa* Hall, 1857 (Emsian to Givetian), *Orthis prava* Hall, 1858 (Frasnian), *Schuchertella cornucopia* Imbrie, 1959 (Givetian), *Schuchertella crassa* Imbrie, 1959 (Givetian), *Schuchertella iowensis* Stainbrook, 1943 (Frasnian), *Schuchertella lirella* Imbrie, 1959 (Givetian), *Strophomena arctostriata* Hall, 1843 (Givetian), *Strophomena chemungensis* Conrad, 1842 (Frasnian), *Streptorhynchus pandora* Billings, 1860 (Emsian). Other species may be included within this genus, but were not examined herein.

Floweria arctostriata (Hall, 1843) (Fig. 9.4)

1843 *Strophomena arctostriata* Hall: 266.

1843 *Orthisina arctostriata* Hall: 81.

1867 *Streptorhynchus chemungensis* var. *arctostriata* Hall: 71–72, pl. 9, figs 1–12.

1892 *Orthotheses chemungensis* var. *arctostriata* Hall & Clarke: pl. 10, fig. 8.

1994 *Eoschuchertella arctostriata* Linsley: 75, pl. 74, figs 1–11.

TYPES. AMNH 30605 (holotype by monotypy).

ADDITIONAL MATERIAL EXAMINED. AMNH 37150–37152, 36819, NYSM 1682–1685.

EMENDED DIAGNOSIS. Small biconvex to planoconvex *Floweria*; cicatrix small; one large and several small costae alternating; hinge teeth short; ventral muscle scars short and broad; well developed myophore separating long dorsal muscle field.

REMARKS. This species exhibits the diagnostic recurved cardinalia, reduced dorsal interarea and parvicostellate ornamentation of *Floweria* and is, therefore, transferred to that genus. *Floweria arctostriata* exhibits a unique combination of characters that differentiate it from *F. chemungensis*

(Table 2, Fig. 7), consequently, its status as a distinct species is supported.

COMPARISONS. *Floweria arctostriata* is distinctive for its small size and costal pattern of alternating groups of one large and several small costae. *Floweria arctostriata* most closely resembles *F. becraftensis*. *Floweria becraftensis* can be distinguished by its rounded cardinal extremities, more highly inflated valves and more elliptical outline. *Floweria arctostriata* is differentiated from *F. chemungensis* by its smaller size, reduced valve inflation and deformation, more open deltidium, more convex deltidial plates and its deeply impressed, flabellate, and wide ventral muscle field.

OCCURRENCE. Givetian; Hamilton Group, New York, USA.

***Floweria becraftensis* (Clarke, 1900)**

1900 *Orthothetes becraftensis* Clarke: 51–52, pl. 7, figs 15–28.

1908 *Orthothetes* (*Schuchertella*) *becraftensis* Clarke: pl. 41, figs 1–8.

1994 *Eoschuchertella becraftensis* Linsley: 121, pl. 16, figs 1–14.

TYPES. NYSM 1659-1666 (syntypes).

ADDITIONAL MATERIAL EXAMINED. NYSM E2847, E2904.

EMENDED DIAGNOSIS. Small planoconvex *Floweria*, cardinal extremities rounded, high ventral valve inflation; numerous subequal costae; ventral interarea high, but not extending across hinge; ventral muscle scar short and narrow; well-developed myophore separating short and narrow dorsal muscle field.

REMARKS. This species exhibits the diagnostic features of *Floweria* (recurved cardinalia, reduced dorsal interarea and parvicostellate ornamentation), not *Eoschuchertella*, so it is transferred to that genus.

COMPARISONS. *Floweria becraftensis* is most closely related to *F. crassa*. The two species can be distinguished by a shorter hinge, resupinate shape and moderate cicatrix development in *F. crassa*. *Floweria becraftensis* also resembles *F. arctostriata*, as discussed above.

OCCURRENCE. Emsian; Oriskany, Glenerie and Port Ewen Limestones, New York, USA; Grand Greve Limestone, Quebec, Canada.

***Floweria chemungensis* (Conrad, 1842) (Figs 9.6–9.8)**

1842 *Strophomena chemungensis* Conrad: 357, pl. 14, fig. 12.

1843 *Strophomena bifurcata* Hall: 266, fig. 2.

1843 *Strophomena pectinacea* Hall: 266, tf. 120.4, fig. 4.

1867 *Streptorhynchus chemungensis* var. *pectinacea* Hall: 67, pl. 10, figs 1–24.

1892 *Orthothetes chemungensis* Hall & Clarke: 255, pl. 10, fig. 9

1994 *Schuchertella chemungensis* Linsley: 78, pl. 118, figs 4–21.

MATERIAL EXAMINED. AMNH 30604a (*S. pectinacea* holotype), 37153-37156, 37157a-d, NYSM 1672-1681.

EMENDED DIAGNOSIS. Large, resupinate *Floweria*, ventral valve elliptical to subrectangular with high relief, moderately deformed, cicatrix small; costae wider than interspaces, occasionally of alternating size; ventral interarea high; ventral muscle scars short and narrow, weakly impressed; dorsal muscle scars short and wide with weak myophore.

REMARKS. Hall (1867) considered *Streptorhynchus pandora* Billings, *Orthosina arctostriata* Hall, *Orthis perversa* Hall and *Strophomena pectinacea* Hall to be variations of *F. chemungensis*. The first three of these species are typified by suites of characters that consistently differentiate them as distinct species of *Floweria* (Table 2). Phylogenetic reconstruction also supports the separation of these species (Fig. 7). The type specimen of *Strophomena pectinacea* Hall (AMNH 30604a), however, cannot be readily distinguished from other specimens attributable to *F. chemungensis* and this species is herein synonymised with *F. chemungensis*. The elevation of *F. pandora*, *F. arctostriata* and *F. perversa* to full species rank restricts the stratigraphic range of *F. chemungensis* to the Frasnian.

COMPARISONS. *Floweria chemungensis* resembles *F. pandora* and *F. perversa* in general outline, but can be distinguished from these species by increased shell height, moderately developed cicatrix and deformation and absence of rugae or fila. *Floweria chemungensis* can be distinguished from *F. anomala* by its moderate rather than extensive amount of deformation.

OCCURRENCE. Frasnian; Chemung Group, New York; Contadero Formation, New Mexico, USA.

***Floweria pandora* (Billings, 1860) (Fig. 9.1)**

1860 *Streptorhynchus pandora* Billings: 226.

1863 *Streptorhynchus pandora* Billings: 369.

1867 *Streptorhynchus chemungensis* var. *pandora* Hall: 68–70, pl. 4, figs 11–19, pl. 9, figs 18–25, 27.

1892 *Orthothetes chemungensis* var. *pandora* Hall & Clarke: pl. 9, fig. 30, pl. 10, figs 1–6.

1994 *Eoschuchertella pandora* Linsley: 75, pl. 74, figs 17–24.

MATERIAL EXAMINED. AMNH 37173, 37175, NYSM 1695-1700, YPM 59685.

EMENDED DIAGNOSIS. Large resupinate *Floweria*, ventral valve inflation low, deformation lacking, cicatrix poorly developed; costae subequal; ventral interarea low; ventral muscle field flabellate with well-developed medial myophragm; dorsal muscle field wide and elongate with low myophragm.

REMARKS. This species exhibits a unique character suite from *F. chemungensis* and is thus afforded independent specific status. Additionally, *F. pandora* exhibits the diagnostic features of *Floweria* (recurved cardinalia, reduced dorsal interarea and parvicostellate ornamentation), not *Eoschuchertella*, so it is transferred to that genus.

COMPARISONS. *Floweria pandora* has previously been allied with *F. chemungensis*; characters distinguishing the two species are described above. *Floweria pandora* most closely resembles *F. perversa* in ornament and overall appearance.

Floweria perversa can be distinguished by its rounded cardinal extremities, costae of alternating size, higher dorsal umbonal angle and narrower cardinal process.

OCCURRENCE. Emsian; Schoharie Grit and Upper Helderberg Group, New York; Camden Chert, Tennessee, USA; Western Canada.

***Floweria perversa* (Hall, 1857) (Figs 9.2–9.3)**

1857 *Orthis perversa* Hall: 137.

1860 *Orthosina alternata* Hall: 81.

1867 *Streptorhynchus chemungensis* var. *perversa* Hall: 72–73, pl. 9, figs 13–17, 26.

1944 *Schuchertella perversa* Shimer & Shrock: 343, pl. 132, figs 43–45.

1994 *Eoschuchertella perversa* Linsley: 85, pl. 74, figs 12–16.

TYPES. Hall's (1857) original description did not include a holotype designation. AMNH 37277 is designated as the lectotype as it is the most complete valve of the former syn-type series (Fig. 9.3). AMNH 37271 becomes a paralectotype.

ADDITIONAL MATERIAL EXAMINED. AMNH 37271 (paralectotype), 37276, NYSM 1702, 1702, E2212.

EMENDED DIAGNOSIS. Large *Floweria*; cardinal extremities rounded; costae large and subequal, fila present in interspaces; ventral valve subrectangular, interarea low; cardinal process wide.

REMARKS. This species exhibits recurved cardinalia, reduced dorsal interarea and parvicostellate ornamentation, features diagnostic of *Floweria* (not *Eoschuchertella*) so *F. perversa* is transferred to that genus.

COMPARISONS. *Floweria perversa* most closely resembles *F. pandora*; differences between these species are discussed above. *Floweria perversa* has also previously been compared with *F. chemungensis*. These species differ in numerous characters including by increased shell height, moderately developed cicatrix and deformation and absence of rugae or fila in *F. chemungensis*.

OCCURRENCE. Emsian to Givetian; Onondaga Limestone, Upper Helderberg Group and Hamilton Group, New York; Indiana, USA; Ontario, Canada.

SYNTHESIS AND SUMMARY

Biogeographical patterns

Biogeographical analysis of North American *Schizophoria* (*Schizophoria*) and *Floweria* revealed low amounts of vicariant speciation (11 and 50%, respectively) compared with rates of vicariance among extant species (70% or higher). Reduced amounts of speciation by vicariance compared to dispersal have also been documented in Devonian bivalves (Bailey 1978; Rode 2004), phyllocarids (Rode & Lieberman 2002) and trilobites (Lieberman 1999). Lack of vicariance and increased dispersal rate thus appear to be a common pattern during the Late Devonian. Episodes of dispersal between

tectonic basins were abundant. *Schizophoria* species disperse from basins in western North America to basins in central and eastern North America. Episodes of dispersal within the *Floweria* clade, however, tend to progress from eastern North American basins to basins further west. These opposing directions of dispersal reflect species migration away from the ancestral range of each genus, the western United States for *S. (Schizophoria)* and the Appalachian basin for *Floweria*. The frequency of range expansion both within and between tectonic basins may have resulted in the reduction in vicariance since population isolation (the mechanism by which vicariance occurs) cannot be sustained against a backdrop of expanding species ranges.

Evolutionary implications

Schizophoria (Schizophoria) exhibited rapid evolution during the Early to Middle Devonian, but many lineages were terminated during the Frasnian–Famennian crisis. Species from the Early Devonian through the Frasnian inhabited the offshore environment, while Famennian and later schizophoriids inhabited shallow water environments. The lineages that persisted into the Famennian and Carboniferous were not closely related phylogenetically. Each of these lineages represented a separate invasion from offshore ancestors. Each lineage, however, converged morphologically on a large, low-lying body, possibly as an adaptation to shallow water, high-energy habitats.

Unlike *Schizophoria*, neither *Floweria* nor *Schuchertella* crossed the Frasnian–Famennian boundary. All *Floweria* lineages became extinct by the end of the Frasnian and the oldest substantiated *Schuchertella* species are Famennian in age. *Floweria* and *Schuchertella* exhibit high morphological similarity and may have occupied similar ecological niches. Both lineages include basal species that are biconvex and relatively free-lying while more derived species develop pedicle attachment structures. Associated with the increased reliance of attachment structures is a shift from shelf edge to inner platform and nearshore depositional settings. This shift in environment, however, is not tied to the Frasnian–Famennian boundary as in *Schizophoria*.

Late Devonian biodiversity crisis

Comparing the evolutionary and biogeographical patterns of these genera during the Late Devonian interval suggests that speciation mode, biogeography and ecology may have been important factors controlling the faunal dynamics of the biodiversity crisis. The decline in vicariant speciation and associated increase in interbasinal invasions may have resulted in an overall decline in effective speciation rate (Rode & Lieberman 2004). The shared environmental shift between outer platform to inner platform and nearshore environments is also an interesting commonality. Other analyses including a wider range of brachiopod and bivalve taxa have indicated increased extinction rates in nearshore and inner platform settings compared to the outer platform (Rode & Lieberman 2004). This relationship could partly explain the persistence of *Schizophoria* but not *Floweria* through the crisis interval, since *Floweria* had already shifted to a strictly nearshore habitat, while *Schizophoria* retained several deep-water lineages.

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