BIFIDA AND *KAYSERIA* (BRACHIOPODA) AND THEIR AFFINITY

by PAUL COPPER

ABSTRACT. The internal morphology of the European Middle Devonian brachiopods *Bifida* and *Kayseria* is truly athyridid in every character, especially with regard to the structure of the spiralia. Several previously unknown internal structures and two new species, *Kayseria alvea*, and *K. nohnensis* are described. One species of *Kayseria* is also shown to have an unusual external shell cover consisting of bushy frills located in rib troughs. It is proposed that both genera, as well as other known dayiacean brachiopods, be removed entirely from the order Atrypida and be reassigned to the suborder Athyridina (order Spiriferida).

IT is widespread practice to assign the two spire-bearing brachiopod superfamilies Atrypacea and Dayiacea to a single large group of either subordinal or ordinal rank. This is, for example, the classification followed in the two most recent brachiopod treatises, the Osnovy (Rzhonsnitskaya 1960) and the *Treatise on Invertebrate Paleontology* (Boucot *et al.* 1965). This usage also was followed in the Geological Society of London's symposium on the Fossil Record (Copper 1967). Re-examination of the internal structures of *Bifida* and *Kayseria*, established by Davidson in 1882, showed none of the typical characters of the true *Atrypa*. This paper attempts to show why the dayiaceans, or at least the two genera in question, are more aptly grouped with the athyridid brachiopods, where they were placed by Schuchert as early as 1894. The coiling of the spiral lophophore supports in those dayiaceans where such structures are known (e.g. *Bifida, Kayseria, Dayia, Aulidospira*) shows a ventral or ventro-lateral coiling direction which is the exact opposite or mirror-image to that of the true atrypids, in which the coiling direction is dorsal or dorso-medial. It is nearly impossible to visualize how two groups with such obviously opposed lophophore supports, and hence respiratory habits, can be housed under a single taxonomic roof. There is no evidence at present to indicate that the true spiriferids evolved from atrypids. It should be noted that *Bifida* and *Kayseria* are confined to the Devonian of Eurasia and northern Africa, and that they are absent in eastern North America, where they appear to have been represented ecologically by the vaguely similar probable dayiaceans *Coelospira* and *Leptocoelia*.

Stratigraphic correlations used in this paper are based on the classic work of Struve (1961) in the Eifel region of Germany. The geologic section is summarized in text-fig. 6. House and Selwood (1966) reviewed the stratigraphy of Devon in south-west England, where the type species of *Kayseria* occurs. In supplement it can be said, on the basis of the brachiopod *Kayseria*, that the Hope's Nose Beds are undoubtedly at least in part of Upper Eifelian (Freilingen) age. The Chercombe Bridge Shales, containing *Gruenewaldtia latilinguis* (Schnur), are undoubtedly in part Middle Eifelian (Junkerberg) in age.

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Methods and acknowledgements. The internal structure of the specimens was studied with the use of aceto-butyrate peels (Triafol NB), a technique well suited to calcareous shells with a muddy matrix. The peels were inserted in 35 mm glass slide holders for photography under transmitted light in a standard petrographic microscope. To show the serial development of various structures, the slide-mounted peels were inserted in an ordinary slide projector, focused on a screen to an enlargement of 20 times, and then traced with india ink. A full three-dimensional picture of the internal structure of the shell was reconstructed by transferring peel images to a horizontal grid pattern parallel to the commissural plane. If the peels are aligned according to the plane of bilateral symmetry, then the reconstruction is accurate to within one millimetre at a scale of times 20.

Specimens photographed and sectioned were deposited in the British Museum (Natural History) (BMNH) or the Institute of Geological Sciences Museum, London, England (GSM). The work was mainly carried out during 1965–1967 under a National Research Council of Canada postdoctoral fellowship. Locality references employ the German metric grid system; most material came from the Eifel region of Germany.

The writer is extremely grateful to Drs. D. E. White and D. E. Butler of the Institute of Geological Sciences for assisting in access to type specimens of *Kayseria*, and for supplying photographs of the types, and to Dr. Hermann Jaeger in providing information about types in the Berlin museum.

PALAEOECOLOGY

All dayiaceans are small brachiopods less than 15 mm wide. The small size factor seems to hold generally true also for most athyridids, although exceptional athyridid species may be up to 40 mm wide. Also all dayiaceans apparently lack deltidial plates or pedicle structures of some sort, and all lack a large pedicle opening, delthyrium or interarea. Even *Dayia* apparently has no deltidial plates (see Tucker 1968). So, the dayiaceans were not primarily pedicle-supported brachiopods, or if they were, their pedicle muscle must have been very slender and minute, or must have consisted of thread-like structures along the hinges. The pedicle probably atrophied in most shells during the mature stage. As a result, most adults were in all likelihood loose, sedentary forms positioned on the muddy sea bottom. There are no wide brim-type frills developed on the shell surfaces. The peculiar rib trough-located frills on *Kayseria* may have helped as anchoring devices, or as filtering screens.

Both *Bifida* and *Kayseria* seem to have preferentially lived on a calcareous muddy bottom, and associated with other small brachiopods (especially in the Late Eifelian Ahbach Beds of the Eifel region). There is no evidence that they lived in a biotope of stunted shells. They also occur in the shaly lenses in coral-stromatoporoid-crinoid rich Eifelian Freilingen Beds of the Eifel where the environment shows good evidence of aeration and current sorting. The lithology in which *Bifida* and *Kayseria* are found mainly consists of brownish to dark greyish calcareous shales or argillaceous, thin-bedded limestones. They are not present in clastic rocks such as siltstones or sandstones, or in non-argillaceous biohermal limestones. Their preference is for the normal, muddy, shallow marine Eifel type of facies in zones 5 to 6 as shown in Copper (1966, fig. 2) in relatively quiet to slightly disturbed waters.

There seem to be no specific symbiotic affinities with other invertebrates. In the Eifel region in Middle Devonian time, *Kayseria alvea* sp. nov. is commonly found in association with *Spinatrypa* (*Invertrypa*) *kelusiana* Struve, an atrypid which very probably lived anchored and partially buried in the muddy bottom. The function of fibrous projections of *Kayseria* here is not clear. The fibres are directed towards the hinge area and in such a way that they form a flat shelf-like area. *Kayseria* perhaps lived vertically, with the shell apex near the bottom and the anterior commissure upwards. A short pedicle may have served as an anchor in the mud. No specimens were found in growth position.

Bifida differs from *Kayseria* in its smaller size, unequal, ventribiconvex shell, and lack of distinctive frills or fibres. The beak of *Bifida* is more strongly incurved. This genus may very well have lived attached to other brachiopods by a short pedicle.

Externally other dayiaceans such as *Coelospira* (viz. Boucot and Johnson 1967), *Leptocoelia*, and *Eocoelia* (viz. Ziegler 1966), the first two of which were confined to North America during Devonian time, are very similar to the western European *Bifida* and *Kayseria*. They were probably also very similar in their environmental requirements.

REDESCRIPTION OF THE TYPE SPECIES

Since the main purpose of this paper is to clarify the internal morphology and taxonomy of the two genera treated, the type species of both were re-examined. In addition, the definitions of the suborder Athyrididina, the superfamily Dayiacea, and the families Anoplothecidae and Kayseriidae are modified, since these are not clearly defined in the Brachiopod Treatise.

Suborder ATHYRIDIDINA

The athyridids are identified mainly by their relatively rounded shape, a lack of, or very small interarea and pedicle opening, and internally particularly by their medially directed crura, their unusually elaborate jugum with accessory lamellae, and their laterally-ventrally directed spiralia. The direction of coiling of the spiralia is most critical since it represents the mirror image or exact inside-out replica of atrypid coiling. These characters are also pertinent to *Kayseria* and *Bifida* and may be readily employed as a definition of the whole suborder. The whole superfamily Dayiacea can, in fact, be accommodated in the athyridid group without any alteration in the Treatise definition of the suborder. The only character which makes some Dayiaceans look like atrypids is the superficial one of a radial rib structure, but even a radial rib structure is not unknown in other athyridids such as the genus *Atrythyris* Struve. If the dayiaceans are accepted as true athyridids, as suggested here, then the range of the suborder Athyrididina may be extended downwards to the Middle Ordovician. Investigation of the internal structures of early, ancestral 'spirebearers' such as *Cyclospira*, *Aulidospira*, *Hindella*, and others is being carried out by the author, since there are no reliable data on the structure, orientation, and ontogenetic development of their spiralia.

Superfamily DAYIACEA Waagen 1883

Included in this superfamily are the Dayiidae, Anoplothecidae, Kayseriidae, and Leptocoeliidae, ranging in age from Middle Ordovician to Middle Devonian time. Primitive, Ordovician members of this group are mainly small, smooth shells. This is also true of several early atrypaceans. In fact with present knowledge there may be some confusion in their identification. In Silurian and Devonian time most dayiaceans are ribbed, and many show a prominent median rib-pair on the pedicle valve with corresponding sinus on the brachial valve, or else a sinus on both valves. There are no distinctive long external growth lamellae in dayiaceans; very short fringes are developed in *Bifida* and in *Kayseria* but most others have overlapping growth lamellae which are not freed from the shell surface. An exception is *Leptocoelia flabellites*, a Lower Devonian athyridid common in eastern North America. *Leptocoelia* has growth fringes very much like those of *Kayseria* described in this paper. Growth interruptions may be quite numerous.

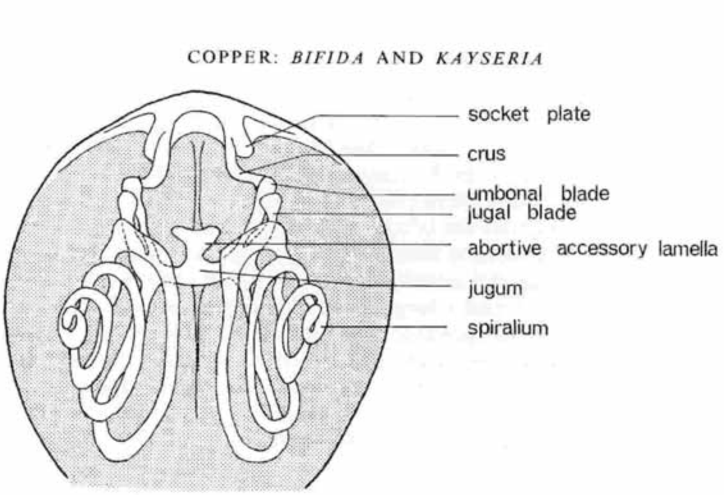
No deltidial plates, pedicle collars, or other pedicle structures are known in dayiaceans, and this is perhaps an important criterion for defining the group.

A simple type of jugum appears to be present in the early representatives of the Dayiacea, like *Dayia* as described by Alexander (1947, p. 305). According to Hall and Clarke (1893, p. 148) the earliest dayiacean *Cyclospira* lacked a jugum, but it was said to have 'two short convergent apophyses which may be construed as discrete elements of a loop'. Hall and Clarke also stated on the same page, 'As for the loop, there is as yet no satisfactory proof of its existence.' There is no recent evidence to substantiate or refute the presence of this type of structure in *Cyclospira*. There is apparently no trend for the jugum to become separated into two unconnected sections, as in Late Silurian and Devonian atrypids. Nearly all dayiaceans show a jugal saddle and accessory lamellae extending posteriorly from the jugal saddle. This feature is identical to that of the true athyridids (see Williams and Rowell 1965, p. H103), and absent in all true atrypids. In *Kayseria* the accessory lamellae lie parallel to the main spiral lamellae up to the tips of the coils. The spiralia are usually ventro-laterally directed; the dayiaceans show more of a ventrally pointed axis than other athyridids.

The crura are more or less parallel to the plane of symmetry and remain very close to the centre of the shell (in atrypids they flare to the sides directly from their point of attachment). The umbonal blades, the beginning portion leading to juga and spiralia, show a distinctive type of attachment to the crura; instead of continuing on smoothly from the crural ends, they geniculate sharply at their point of origin, bend posteriorly and then curve around gently following the contours of the brachial valve. It is not clear why this happens. In the atrypids the crura terminate only at the jugal axis, from which point the jugal processes and spiralia are extended. In the dayiacean family Leptocoeliidae, juga and spiralia are as yet unknown. Perhaps they were never calcified in this group. Nevertheless, external similarities allow the leptocoeliids to be referred to the Dayiacean group.

Family ANOPLOTHECIDAE Schuchert 1894

This group includes small, ribbed dayiaceans with short, abortive accessory lamellae developed from the ventral crest of the jugal saddle. In addition, a *jugal blade* (new term) may be initiated from the dorsal base of the jugum and directed ventro-posteriorly towards the short, abortive accessory lamellae (text-fig. 1). It may be foreseen that in some internally yet undescribed species this jugal blade in fact connects with the first accessory lamellae, to form a kind of looped structure as in



TEXT-FIG. 1. Reconstruction of the brachial valve internal morphology of *Bifida lepida* (Archiac and Verneuil) based on serial sections of specimen shown on Pl. 6, figs. 5–8. Scale × 10.

some meristellids. Spiralia have 3 or more whorls, with the concave side of the spiral lamellae directed outwards. Spiral lamellae may be partly double-edged to form a type of embryonic double lamella (see Pl. 8, fig. 2). Included in the family are *Anoplotheca*, *Bifida*, *Dnestrina*, *Coelospirina*, *Coelospira*, and *Neocoelia*.

Range: Upper Silurian (Ludlovian) to Middle Devonian (Givetian).

Genus BIFIDA Davidson 1882

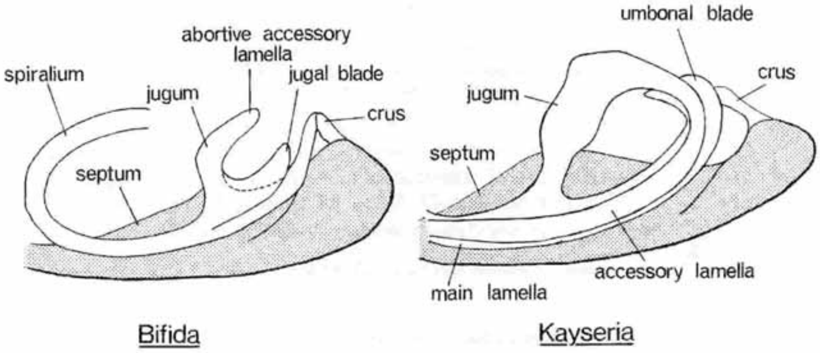
Type species. *Terebratula lepida* Archiac and Verneuil 1842, p. 368, pl. 35, figs. 2, 2a–c.

Range. Mainly known from the Eifelian-Givetian, but apparently also present in Lower Devonian (Emsian). (See LeMaitre 1952, p. 117.)

Distribution. Eurasia, North Africa, Nevada (N. America).

Diagnosis. Small, usually less than 5 mm wide, elongately rounded, ventribiconvex-planoconvex shells with numerous, even, less than 1 mm spaced concentric growth lines. Ribs few in number (commonly less than 6), non-bifurcating, tending to broaden and fade towards the commissure. Strong, elevated, mid-rib pair on ventral valve matched dorsally by a sinus flanked by two or more strong ribs and a depressed thin median rib. One or two weak ribs may appear to the sides of these. Ventral beak adpressed (squeezed against dorsal valve) and interarea and deltidial plates absent. Internally, ventrally, and laterally directed spiralia with 4–5 coils, joined by a 'wishbone' jugum giving off two brief accessory lamellae. An additional jugal blade, projecting from base of jugum in a posterior direction, is present in at least one species. Spiral lamellae are 'embryonically' double, with a thin outer strip turning whorls into 'troughs' which are outwardly pointed.

Comparison. Anoplotheca is undoubtedly closely related to *Bifida*, despite the fact that the type species *Anoplotheca venusta* (Schnur 1853) from Emsian beds of the Prüm syncline (Eifel region, Germany) has not yet been revised or re-examined in detail. The two genera may even be congeneric, as Hall and Clarke (1893, p. 133) believed. Havlíček (1956) and Siehl (1862) have supported this view. Nevertheless, it seems possible to distinguish the two by their shape, size and ribbing, and possibly internal structure. *Anoplotheca* is wider, more rounded and has ribs near the apex only (these are bifurcating and intersected by numerous growth lamellae), and has more coils in the spiralium and a larger cardinal process (after Boucot *et al.* 1964, pl. 125, figs. 20–25). It seems possible that there are also important differences in the structure of the jugum and accessory lamellae. *Anoplotheca* may have had a type of accessory lamellae-jugum structure where the jugal blade is joined to the abortive accessory lamella (see text-fig. 2). *Anoplotheca* is Lower Devonian in age and *Bifida* mainly, if not wholly, Middle Devonian.



TEXT-FIG. 2. Cut-away reconstruction in lateral view of the brachial valves of *Bifida lepida* (Archiac and Verneuil) on the left and *Kayseria dividua* (Schnur) on the right, based on serial sections. Specimens sectioned are shown on Pl. 4, figs. 1–8. Spiralia have been left out to show the connection between the crura, umbonal blades, juga, and spiralia. Note how the dorsal septum functions as a resting site for the jugum in both shells (refer to Pl. 6, fig. 4 and Pl. 5, fig. 2). Scale × 10.

Havlíček (1956, p. 656) determined that his genus *Coelospirina* has spiralia with only a few coils which are ventrally directed (but did not illustrate this). It probably belongs to the Anoplothecidae, but it is very unlike either *Bifida* and *Anoplotheca* externally because it has sharply edged ribs and very few growth lamellae except anteriorly. Its external features seem to indicate a much closer affinity with *Coelospira*, as the name suggests. Until internal illustrations of *Coelospirina* are given, its classification remains doubtful.

The genus *Dnestrina* Nikiforova and Modzalevskaya (1968) from the Upper Silurian of Podolia (Dzvinogorod marls, Skala horizon) is clearly an early anoplothecid perhaps ancestral to *Anoplotheca*. No spiralium, however, is known, but the long median septa of the two valves are virtually identical to those of *Bifida*.

The smooth-shelled specimens referred to *Bifida* by Whidborne (1893, pp. 102-103, pl. 12, figs. 8, 8a-b) are probably not Anoplothecidae.

Coelospira (see Boucot and Johnson 1967, pl. 166, figs. 20-21) is internally similar to *Bifida* but stands less closely externally and in terms of septal structures to *Bifida* than *Dnestrina*.

Species assigned to *Bifida*: *Anoplotheca* (*Bifida*) *dahlia* Havlíček (1956, pp. 590-591, pl. 4, figs. 9-13), *Anoplotheca nitida* Schmidt (1951, pp. 91-93, pl. 1, figs. 5a-c, text-figs. 1-3).

Anoplotheca levigata Wolburg (1933, p. 49, pl. 10, figs. 8a-n) is a doubtful member.

Bifida lepida (Archiac and Verneuil 1842)

Plate 4, figs. 5-8; Plate 5, figs. 3-4; Plate 6, figs. 1-4; Plate 7, figs. 23-24

1842 '*Terebratula lepida* Goldfuss, Bonn Mus', Archiac and Verneuil, p. 368, pl. 35, figs. 2, 2a-c. Though Goldfuss is referred to as the first author, to my knowledge, no description by him of this species exists.

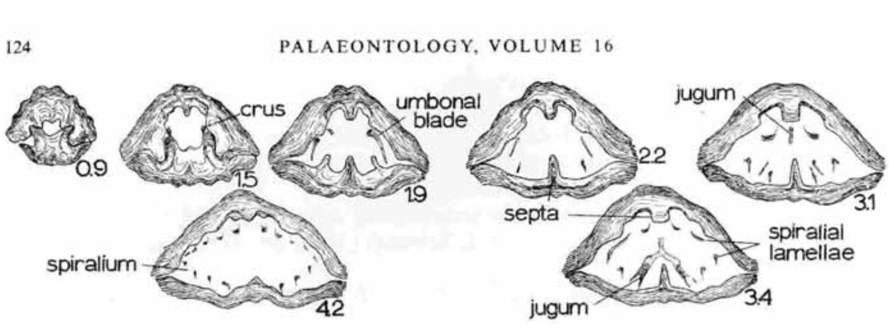
Type specimens. Since only one specimen was figured by Archiac and Verneuil, it automatically becomes the lectotype (see article 74b, ICZN). Syntypes are apparently lost. Hypotype BMNH:BB58557 illustrated in this paper (Pl. 7, figs. 23-26) is similar to Archiac and Verneuil's illustration and since it comes from the source area mentioned (Eifel, Germany), it would serve as a potential neotype if further search for syntypes proves fruitless.

Range. With limited material available there appear to be no major differences between specimens from the Eilenberg horizon and those from higher horizons up to the top of the Ahbach beds, the upper boundary of the Eifelian sequence in the Eifel. The species is not abundant in collections, probably because of its small size.

Distribution. Eifel region, Germany, and Poland. The species probably has a wider geographic spread than this, but other foreign forms need to be verified.

Diagnosis. Small *Bifida* averaging less than 6 mm in width and length and 3 mm in depth with a ventribiconvex-planoconvex shell with a strong median rib pair flanked by 2-3 side ribs on the pedicle valve and a broad median trough lined by strong ribs and weaker lateral ribs on the brachial valve. Internally, septa are present in both valves. Double-sided spiral lamellae number about 4; laterally directed spiralia.

Internal structure. The species lacks deltidial plates. A distinctive median septum is present in the pedicle valve, even in a position very close to the umbo. The septum is 'buried' in a thick layer of calcite tissue (Pl. 5, fig. 3). The crest of the septum flattens out anteriorly to form a broad base against which the forked abortive accessory lamellae of the brachial valve, extending from the dorsal jugum, are pressed. This must have been useful as a stabilizing device to prevent the spiralia and jugum from moving when the shell was closed, and also to separate food currents produced by opposing lophophores (text-fig. 3). The teeth are short, solid (no lateral cavities), nearly vertical in growth and lack crenulated lobes or accessory lobes. On the inner margins of the teeth there are special hollows to accommodate the tips of the brachial valve's socket plates, an unusual feature in most brachiopods (Pl. 6, fig. 1). It is possible that these are the 'crural fossettes' mentioned by Boucot *et al.* (1965, p. 648) but this would be a misnomer here because the crura never rest in these small hollows. The adductor muscle impressions are quite deep posteriorly and are separated by the median septum. Nevertheless the septum here is not so much a muscle separator, i.e. a myophragm, as a base of support for the jugum of the dorsal valve. In fact the term myophragm has been misused in the past and should really be dropped for spire-bearers unless there is definite proof that it served to separate the adductor muscles. The distal disappearance of the septum and broadening of the muscle scars is evident in text-fig. 3.



TEXT-FIG. 3. Serial sections of *Bifida lepida* (Archiac and Verneuil) of specimen illustrated on Pl. 4, figs. 5–8. Observe the critical development of the brachidial apparatus, comparing with photographs on Pls. 5 and 6. Numbers refer to distance in mm from ventral apex. Scale × 5.

In the brachial valve a very weak, small amorphous cardinal process is present only in the most apical portions (Pl. 5, fig. 3). The socket plates are solid, and curved slightly outwards in direction to accommodate the teeth from the opposite valve. The tips of socket plates fit into hollows on the inner margins of the teeth (Pl. 5, figs. 3–4). The crural bases appear less than 1 mm from the apex of the brachial valve, and they are tiny, slender wedge-like plates fixed to the inner and distal margins of the socket plates (Pl. 6, fig. 1). Within 0·5 mm or so of their starting-point on the socket plates, they curve around sharply more than 90° (like walking-cane handles), and they then turn into a rod-like shape (Pl. 5, fig. 4). Instead of continuing directly into spiralial structures, the crura make a very sharp bend to give off what are the beginnings of the spiralia and jugum. This portion of the brachidium, between the end of the crura and the point of junction of the jugum and spiralia, is called the umbonal blade.

The jugum consists of an arched, angularly crested band that connects the spiralia (there is no indication of a break between the opposite sides). It is remarkable that the crest of the jugum splits off into two short prongs about 2 mm long (text-fig. 1). Each jugal prong is directed slightly towards the side, but is also pointed towards the ventral valve and the shell umbo. Then they stop abruptly in squared stubs, which appear to consist of resorbed calcite or carbonate tissue that is poorly defined or preserved. These two little prongs projecting from the jugum have given rise to the name *bifida*. They are very probably an abortive attempt at the growth of complete accessory lamellae, which are present in the genus *Kayseria*. This view is strengthened by the fact that almost identical jugal structures are present in *Kayseria* (compare Pl. 5, fig. 2 with Pl. 6, fig. 4). At the dorsal base of the jugum, where it is attached to the focal point of the umbonal blade and the beginning of the spiralium, each side of the jugum gives off another short, but more distinctly

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EXPLANATION OF PLATE 4

Kayseria dividua (Schnur 1851), Upper Eifelian, Middle Devonian (Freilingen beds, Eilenberg horizon).

Figs. 1–4. Ventral, posterior, dorsal, and lateral views of a typical specimen from the Eifel, MTB Dollendorf r53850:h74689, Germany. Hypotype BMNH:BB59010 (×4).

Figs. 9–12. Photographs of acetate peels of specimen BMNH:BB559010 shown above. 9, shows the hinge mechanism with socket plate (sp), notch for the socket plate in pedicle value (sn), and cardinal process (cp). 10, shows the crus (c), tooth (t), and socket plate. 11, shows the terminus of crus, the umbonal blade attached to it (ub), and the ventral septum. 12, the double spiralial lamellae are separated into a thicker main lamella on the left (ml) and accessory lamellae on the right (al). All peel photographs approx. ×40.

Bifida lepida (Archiac and Verneuil 1842), Upper Eifelian, Middle Devonian (Freilingen beds, Eilenberg horizon).

Figs. 5–8. Posterior, lateral dorsal and ventral views of a typical specimen (see Pls. 5 and 6 for serial peels of same specimen) from the Eifel, MTB Dollendorf r54460:h75550, Germany. Hypotype BMNH: BB58564 (×4).


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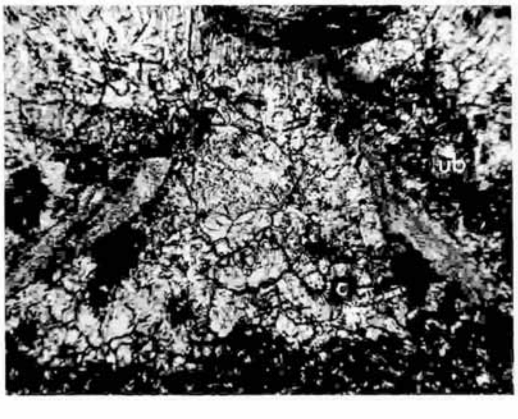

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COPPER, *Keyseria* and *Bifida*

developed blade (here called the *jugal blade*). Each of these jugal blades is directed ventro-posteriorly towards the ends of the jugal prongs described above. But they are not connected to these prongs, stopping short at a point near the crural ends (text-fig. 1). The function of these two structures is unknown but it seems likely that they represent remnants of arrested accessory lamellae which are fused to the spirals instead of continuing freely parallel to the spiralium.

The spiralia contain 3 to 4 whorls. Each spiral lamella is double, with a lateral (or outer) and central (or inner) rim fused on the inner margins of the spiral coils (Pl. 6, fig. 2). The lateral rim of the double spirals is less well developed and occasionally becomes detached or lost completely. In three-dimensional view these spiral coils thus would resemble eavestroughs which had their open sides exposed on the outer parts of the spiral coils (i.e. concave outwards).

The double-sided spiral lamellae are very strong evidence in support of affinity with *Kayseria*. The genus *Bifida* may be visualized as a *Kayseria* in which the accessory lamellae have remained fused or become fused to the primary coils.

The only detailed information previously available on the inner structure of *Bifida* is that published by Siehl (1962, pl. 29, figs. 1–3). Siehl failed to notice the basic structure of the jugum, the jugal blades, the umbonal blades, the jugal prongs, or even the peculiar nature of the spiral lamellae. Biernat (1954, p. 518, fig. 17) illustrated sections of *Bifida* but no details are recognizable, nor were these described. Davidson (1882, p. 28), using preparations made by Glass, illustrated *Bifida* spiralia which show a coiling in exact reverse (!) to that determined in this paper. For example, Davidson's figure (ibid.) shows the right spiralium coiled counterclockwise, whereas it should be clockwise. The error was duplicated by Hall and Clarke (1893, figs. 114–121). In illustrating *Anoplotheca*, which is closely related to *Bifida*, Boucot *et al.* (1964, pl. 125, fig. 20) confirm a normal type of athyridid coiling with the right spiralium clockwise, such as shown in this paper (text-fig. 1).

Comparison. Bifida lepida differs from the Czechoslovakian species *B. dahlia* Havlíček 1956 in its less tubular, less marked ribs which also do not extend clearly to the commissure. Havlíček reports *B. lepida* from the Prokop limestones which lie below the Zlichov beds (Emsian) in which *B. dahlia* are found.

Schmidt (1951, pp. 91–93, pl. 1, figs. 5a–c) distinguishes her *Anoplotheca* (?*Bifida*) *nitida* from *B. lepida* by their larger size, a more rounded pedicle valve, and more distinct as well as different rib structure. No inner structures are mentioned. Schmidt's species was found in Upper Givetian rocks east of the Rhine.

I have not had the opportunity to compare *B. lepida* with *Anoplotheca levigata* Wolburg 1933 mentioned by Schmidt (ibid.).

Specimens labelled as *Bifida lepida* by Davidson (1882, pl. 2, figs. 13a–b) collected at Hope's Nose, Devon, England (probably from Late Eifelian beds), show a much more rounded brachial valve than Eifel *B. lepida* and additional development of

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EXPLANATION OF PLATE 5

Kayseria dividua (Schnur 1851), Upper Eifelian, Middle Devonian.

Figs. 1–2. Photographs of acetate peel, of specimen shown in Pl. 4, figs. 1–4. 1, showing jugum (j) with a finely crystalline dorsal end and coarse ventral end which abuts the ventral septum, but is not fused to it. 2, more anteriorly taken, this view shows the jugum where it gives rise to the main lamella (ml) and accessory lamella (al). When the valves shut the jugum must be immobile. Scale approx. ×40.

Bifida lepida (Archiac and Verneuil 1842), Upper Eifelian, Middle Devonian.

Figs. 3–4. Acetate peels of hypotype BMNH:BB58564 shown on Pl. 4, figs. 5–8. 3, view showing socket plate (sp) fitting into notch in pedicle valve, the cardinal process (cp), and ventral septum buried in calcite tissue. 4, beginning of crus (c) where attached to socket plate, and tooth, dorsal septum. Scale approx. ×40.

PLATE 5

COPPER, *Kayseria* and *Bifida*

more incised side ribs beside the main rib pairs. An earlier Davidson illustration of alleged *B. lepida* (1865, pl. 10, figs. 2, 2a) from near-by Barton is also different from true *lepida* in the same manner.

Material. For 8 specimens measured, average width 5·4 mm, length 5·8 mm, depth 3·0 mm.

Locality C317 (2 specimens), MTB Dollendorf r54460:h75550; C316 (1) r54530:h75590; C364 (1) r53650:h74580; C512 (1) r53850:h74680: all Freilingen beds. Locality C352 (1) r54940:h75890, Junkerberg beds. Locality C279j (1) r55960:h77380, Ahbach beds.

Family KAYSERIIDAE Boucot, Johnson, and Staton 1964

It may be better to regard the family Kayseriidae, with only a single genus *Kayseria*, as a subfamily of the Anoplothecidae to which they are most closely related. The main difference between these two families seems to be that in the Kayseriidae the accessory lamellae are separated from the main spiral lamellae, whereas in the Anoplothecidae they are fused together. Internal structures of members of both families are very similar (see Pls. 4 to 6).

The chief distinction of the Kayseriidae lies in the presence of separated double spiral coils directed latero-ventrally. In the Treatise (Boucot *et al.* 1965, p. 663), the double-spiralled Triassic athyridids which are the only other known brachiopods with double spiralia, are regarded as a subfamily of the single-spiralled Athyrididae. Schuchert (1894, p. 107) grouped Devonian *Kayseria* with the Triassic Diplospirellinae, but these genera are separated widely stratigraphically and it is difficult to demonstrate a genetic link for a time gap of about 150 million years. The development of double spirals may have been independent in unrelated stocks. Moreover, it is possible that the double spirals were developed in an entirely different fashion. The *Diplospirella* type of coil in Triassic forms may have evolved simply by prolonged extension of the accessory lamellae from the jugum right to the spiralium apex (as suggested for *Kayseria* by Boucot *et al.* 1965, p. 649). But *Kayseria*'s double spirals may have arisen from a bifurcated jugal loop such as is known in some Silurian meristellids (Davidson 1882, pl. 5, figs. 13, 13a). Such a double jugal loop, if the dorsal end were extended parallel to the main spiral lamellae (instead of stopping), could have resulted in a new set of accessory lamellae of the *Kayseria* type. This is suggested by the spiral development of *Bifida*, in which the 'double loop' is broken but continues fused to the main spiral coils. A double loop of the meristellid sort is also known in the Devonian-Carboniferous *Camarophorella* group. It is of course feasible that a double jugal loop may also have been the starting-point of the Triassic double-spiralled forms.

Placing the Kayseriidae in the suborder Atrypidina is a completely artificial assignment based only on the presence of surface ribbing. It should be abandoned. The

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EXPLANATION OF PLATE 6

Bifida lepida (Archiac and Verneuil 1842), Upper Eifelian. Middle Devonian.

Figs. 1-4. Acetate peels from BMNH: BB58564 shown on Pl. 4, figs. 5-8. 1, hinge mechanism with traces of crural base (cb) and dental pad (dp). 2, doubly edged spiralial lamellae (l), trace of jugum (j) and ventral septum (s). 3, lateral portions sharing frilly growth lamellae (f) and spiralial lamellae. 4, view of jugum, jugal plate (jp), and dorsal septum (s). Scale approx. × 40.

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COPPER, *Bifida*

ventro-laterally directed spiralia, the typical athyridid jugum, the double spirals, the structure of the crura and socket plates all suggest affinities with the true spiriferids, and the suborder Athyrididina.

Genus KAYSERIA Davidson 1882

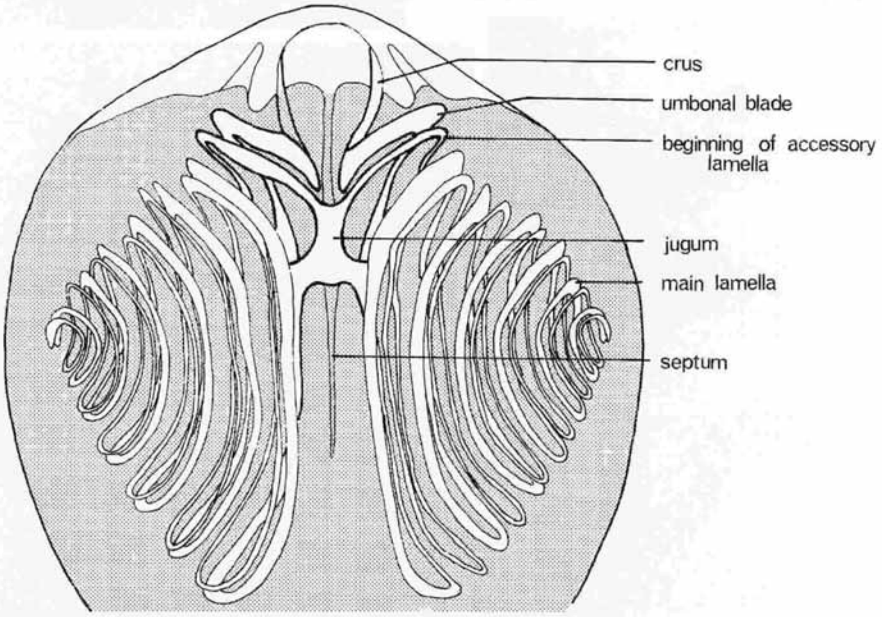
Type species. Orthis lens Phillips 1841, p. 65, pl. 26, figs. 110a-b.

Range. Eifelian.

Distribution. Eurasia.

Diagnosis. Relatively small, weakly biconvex, rather finely ribbed shells which occasionally preserve laterally directed frilly projections in rib troughs. Tiny beaks, minute foramens, no interareas and lack of deltidial plates are typical characters. Sulci present on both valves. Internally teeth massive, with notches for socket plate tips. Median septa occur in both valves, but more prominent in brachial valve. Spiralia begin with umbonal blades which are connected at sharp angle to crura instead of being crural continuations. Accessory lamellae stem from jugal saddle and are maintained separately to ends of spiral coils. Spiralia are latero-ventral, with about 6 double coils (text-fig. 4).

Species included in genus. Orthis lens Phillips 1841, *Terebratula dividua* Schnur 1851, *Kayseria alvea* sp. nov., *K. nohnensis* sp. nov.



TEXT-FIG. 4. Reconstruction of the brachial valve internal morphology of *Kayseria dividua* (Schnur) based on serial sections of specimen shown on Pl. 4, figs. 1-4. Scale × 10.

Kayseria lens (Phillips 1841)

Plate 7, figs. 1–5

1841 *Orthis lens* Phillips, p. 65, pl. 26, figs. 110a, b.
1864 *Atrypa lens* Phillips, Davidson, pp. 51–52, pl. 10, figs. 1, 1a–d.
1882 *Kayseria lens* Phillips, Davidson, p. 21, pl. 2, figs. 11, 11a–c.
1966 *Kayseria lens* Phillips, House and Selwood, pl. 2, fig. 7.

Type locality and stratum. 'Hope, near Torquay' (Phillips, 1841, p. 65). This probably refers to the fossiliferous Eifelian limestones exposed on the seashore at Hope's Nose near Torquay, Devon. These limestones are probably of Freilingen age (Upper Eifelian in German reference section), as confirmed by *Kayseria*, and must overlie the *Gruenewaldtia*-bearing shales of Chercombe Bridge which are Middle Eifelian in age. If the species is rediscovered at Hope's Nose, a more precise type locality should be established (refer to House and Selwood, 1966, p. 55).

Remarks. Dr. D. E. Butler (pers. comm.) informed me that Phillips's syntypes were deposited in the Institute of Geological Sciences in London and supplied the following data. 'The only specimen of *Orthis lens* listed in our catalogues of that period are GSM6914, GSM50871, and GSM50872. GSM6914 has long been marked as figured by Phillips and by Davidson but the specimen is unlikely to have formed the basis of their drawings alone, as it is incomplete. Furthermore, it is probable that GSM50871–2 were included under the number 6914 before it became practice to give each specimen 2 separate numbers, especially as all three specimens were cited, until recent curation, on the same ancient museum tablet. It seems probable, therefore, that Phillips's figure 1102 and Davidson's figures are composite drawings based on all three.'

Lacking evidence to the contrary, it can be accepted that the specimens are originals from the Phillips collection, and are thus the syntypes described. Of the three specimens, all of which are damaged to some extent, GSM50872 is the best preserved and is selected as lectotype.

Kayseria dividua (Schnur 1851)

Plate 4, figs. 1–4, 9–12; Plate 5, figs. 1–2; Plate 7, figs. 9–11; text-figs. 2, 4, 5

1851 *Terebratula dividua* Schnur, p. 6.
1853 *Terebratula dividua* Schnur, pp. 179–180, pl. 24, figs. 2a–e.
1853 *Orthis eifliensis* Steininger, p. 80, pl. 5, figs. 5a–b.

Type locality. 'Schönecken, Prum, Gerolstein und bei Blankenheim' (Schnur 1853, pl. 180) and 'Weinsheim' (ibid., p. 234). It is impossible to establish the exact locality of Schnur's types, which are certainly not present in the Paläontologisches Institute and Museum, Berlin, DDR. (Hermann Jaeger, pers. comm.). A suitable designate type locality would be the north-east slope of Hönselberg, Dollendorf syncline, Eifel region (MTB Dollendorf r53850:h74680).

Type stratum. 'Im kalk . . .' (Schnur, 1853, p. 180). The most likely horizon where Schnur would have collected material would be the 'Crinoiden-Schichten' or crinoidal limestones which seem to have provided specimens for many early monographs. These beds are mainly of Freilingen (Upper Eifelian) age. The designated type locality is exposed on Hönselberg, in the Eifel, Germany (see above); the type stratum the Eilenberg horizon, Freilingen beds.

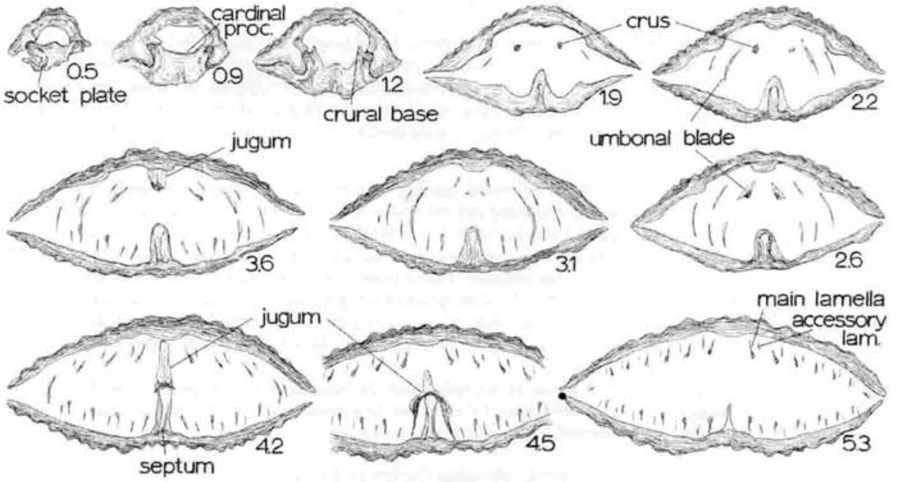
Type material. Holotype or syntypes apparently lost. I have selected two hypotypes for illustration which resemble Schnur's figures and are probably conspecific with them. These are BMNH:BB58558 (Pl. 7, figs. 9–11 which could be chosen as neotype if eventually the syntypes are proved to be destroyed or lost) and BMNH:BB58564.

Diagnosis. Small *Kayseria*, roughly as long as wide, somewhat well rounded in outline, but weakly biconvex in side view. Anterior commissure slightly lobed. Double sulcus weak with poorly defined ribs at sulcal margin. About 20 evenly sized ribs per mature specimen with 3–4 finer ribs located in the sulci. Frilly projections rare.

External. Shells are wider than long in early stages, but become equally long as wide or longer than wider after reaching 10 mm width. Maximum width less than 13 mm (see text-fig. 6).

Internal. Observations depend upon serial sections (text-fig. 5), shown in photographs on Pl. 4, figs. 1–4 and 9–12; Pl. 5, figs. 1–2.

There are no traces of deltidial plates, but a pedicle layer lines the delthyrial cavity. Teeth are short,



TEXT-FIG. 5. Serial sections of *Kayseria dividua* (Schnur) based on specimen shown on Pl. 4, figs. 1–4. Pay special attention to the labelled structures. Proc. refers to process, lam. refers to lamella. Note how the jugum is firmly held in place by the septa in both valves (section 4.2). Numbers refer to distance in mm from ventral apex. Scale × 5.

EXPLANATION OF PLATE 7

All figures × 2, except fig. 22, × 10 and figs. 23–36, × 4.

Figs. 1–5. *Kayseria lens* (Phillips 1841). Three syntypes from the Phillips collection taken from Hope's Nose, Torquay, Devon, and very likely of Upper Eifelian (specifically Freilingen) age. 1–3, Lectotype GSM50872, ventral, dorsal, and lateral views respectively. 4, small specimen GSM6914 showing the sulcus. 5, large specimen GSM50871, ventral view.

Figs. 6–8. *Kayseria nohnensis* sp. nov. Holotype BMNH: BB58563. Lower Eifelian, Nohn beds; Eifel, MTB Dollendorf r56980: h78350. Dorsal, ventral, and lateral views.

Figs. 9–11. *Kayseria dividua* (Schnur 1853). Hypotype BMNH: BB58558. Upper Eifelian, Freilingen beds; Eifel, MTB Dollendorf r53850: h74680. Dorsal, ventral, and lateral views.

Figs. 12–22. *Kayseria alvea* sp. nov. 12–14, Holotype BMNH: BB58559. Upper Eifelian, Ahbach beds; Eifel, MTB Dollendorf r55480: h77390; ventral, dorsal, and lateral views: 22, shows the frills in detail. 15–17, Paratype BMNH: BB58560; Upper Eifelian, Ahbach beds; Eifel, MTB Dollendorf r54550: h75730. Note the asymmetry common to this species; dorsal, ventral, and lateral views. 18–19, Paratype BMNH: BB58561 (same locality, horizon as 58560); this specimen clearly demonstrates the frilly projections covering the valves so that only the middle and posterior portions remain bared. Lateral and dorsal views. 20–22, Paratype BMNH: BB58562 (same locality, horizon as 58560); another specimen showing the external frills, this time clearly directed towards the shell hinge (!).

Figs. 23–26. *Bifida lepida* (Archiac and Verneuil 1842). Hypotype BMNH: BB58557. Upper Eifelian, Freilingen beds; Eifel, MTB Dollendorf r54460: h75550. Posterior, dorsal, ventral, and lateral views.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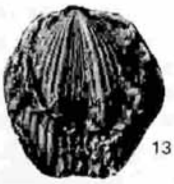
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COPPER, *Kayseria* and *Bifida*

massive, and inwardly directed (no lateral cavities). Inner tooth margins are notched to accommodate tips of socket plates from the opposite valve. A median septum with a broad, flat or even concave crest presses directly against the dorsal jugal saddle when the valves are tightly closed (Pl. 5, fig. 1).

A small, delicate, ragged-edge cardinal process rests on the arch between socket plates. Tiny crura are fastened to the inner, ventral tips of the socket plates (Pl. 4, fig. 10). They project ventrally for 2-3 mm, then gradually bend around to meet the beginning of the spiralium, the umbonal blade (text-fig. 5, 2·6 mm). Crura disappear about 2·7 mm from the ventral apex (Pl. 4, fig. 11). Umbonal blades are first deflected towards the posterior shell margin, then curve back towards the anterior commissure and the dorsal valve floor in a line very close to the plane of symmetry (text-fig. 4). At about 4·5 mm from the pedicle valve apex, the jugum is thrust ventrally up from the umbonal blade, or the first main spiral coil. It projects ventrally until it touches the ventral median septum (Pl. 5, fig. 2), then it extends posteriorly towards the umbo to form the accessory lamellae. Accessory lamellae parallel the main spiral lamellae to the apices of the spiralia, at a constant distance of 0·4 to 0·5 mm (Pl. 4, fig. 12). The main lamellae have a thickened interior rim. The accessory lamellae are extremely thin and stay in a position directly across from the thin flanges of the main lamellae. Maximum coils 6 to 7.

Comparison. K. dividua and *K. lens* are superficially very similar, though adequate material for comparison of the latter is not yet available. The German *K. dividua* differs externally from *K. alvea* sp. nov. in being more rounded, generally smaller, and especially in having a rounded double sulcus which is not as clearly marked. The pedicle valve appears to have a slightly deeper sulcus. Frilly projections appear to be scarce or missing. Internal comparisons are not yet possible.

Material. Total 32 specimens. Freilingen beds, Eilenberg horizon C353 (3) MTB Dollendorf r54340: h75320; C360 (2) r53880:h74660; C512 (3) and C359 (11) r53850:h74680; C316 (6) r54530:h75590; C305 (4) MTB Hillesheim r52830:h73780; C361 (1) r53810:h74630.

Others provisionally assigned: C289 (1), Ahrdorf beds (top), MTB Doll r56930:h78800; C513 (1), Junkerberg beds (middle), MTB Prüm r34660:h64590.

Width–length relationships with increase in size are shown in text-fig. 6. Maximum width 12·6 mm, maximum length 13·7 mm, maximum depth 5·4 mm. Average width 10·6 mm, average length 10·4 mm, average depth 4·4 mm.

Kayseria alvea sp. nov.

Plate 7, figs. 12–22; text-fig. 6

Type locality. Hillesheim syncline, Eifel, Germany, south-west slope of Mühlenberg, MTB Dollendorf r54550:h75730.

Type stratum. Mullert horizon (Upper part?), Ahbach beds, Upper Eifelian.

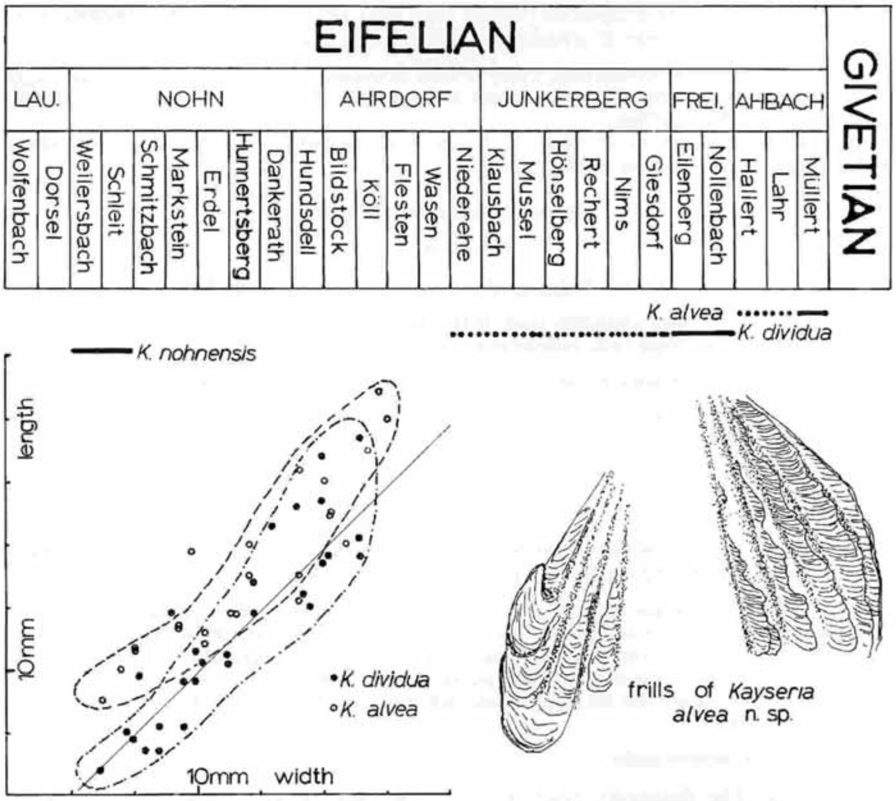
Range. Ahbach beds, Upper Eifelian (stratigraphically above Freilingen with *K. dividua*).

Distribution. Eifel, Germany.

Type material. Holotype BMNH:BB58559; paratypes BMNH:BB58560–58562.

Diagnosis. Shells flat, longer than wide, margins of sulcus on both valves sharply defined by 2 strong ribs, with 4–6 delicate ribs in dorsal sulcus. Very prominent frilly projections on most shells concentrated in rib troughs, especially around commissure.

External. Scatter diagrams (text-fig. 6) show that on average shells are longer than wide in comparison to shells of *K. dividua* (Schnur). Because of the frilly projections, sometimes covering the whole shell rib counts are very difficult to make. On the whole, there is a much greater size difference in ribs located in the sulci and the ribs located lateral to the sulci which are always longer. This difference in rib size is less marked in the stratigraphically older species *K. dividua* and *K. nohnensis*.



TEXT-FIG. 6. Composite diagram showing the stratigraphic ranges of the three *Kayseria* species in the Eifel region, (top) the width/length ratios of *K. alvea* and *K. dividua* (the diagonal line represents the line where width equals length) and to the right sketch diagrams of the frills of two specimens of *K. alvea* (scale × 5 approx.).

Frilly projections of *K. alvea* are extremely unusual and seem to be unknown in any other brachiopods except the Devonian *Leptocoelia* from North America. They are more or less flat-lying, pressed against the shell surface, are usually absent in the postero-central parts of the valves (presumably they are worn down with age) and tend to grow primarily out of the rib troughs (see text-fig. 6; Pl. 7). The crystalline fibres of the frills are directed towards the sides at a greater angle than the direction of the ribs themselves. Towards the hinge area and the postero-lateral margins the tips of these fibres are redirected towards the hinge instead of anteriorly. They could therefore have served as anchoring devices. In *Leptocoelia* (from James Hall's type collection) I have seen specimens which show very similar structures along the hinge line (Hall and Clarke 1893, pl. 53, fig. 47).

Internal. No serial sections were made.

Comparison. The thick rib pair lining the sulci on both valves, the larger ribs at the sides, the delicate ribs inside the sulci, the greater length: width ratio, and the prominent frill development (which may also be a preservational factor), distinguish this species from *K. dividua* (Schnur) and *K. nohnensis* sp. nov.

Material. Müllert horizon, Ahbach beds, Upper Eifelian. 24 specimens (see text-fig. 6 for width and length dimensions). C279i (9). MTB Dollendorf r55480:h77390; C279j (7) r55460:h77380; C321 (7) r54550:h75730; C412 (1) r54900:h77960.

Maximum width 13·0 mm, maximum length 14·5 mm, maximum depth 5·1 mm. Average width 10·9 mm, average length 11·7 mm, average depth 3·7 mm.

Kayseria nohnensis sp. nov.

Plate 7, figs. 6–8

Derivation of name. After the town Nohn, less than 1 km to the west of the type locality, Eifel, Germany.

Type locality. Cut on Nohn–Dankerath road, MTB Dollendorf r56980:h78350, almost at type locality of Weilersbach horizon, Nohn beds, Hillesheim syncline, Eifel, Germany.

Type stratum. Weilersbach horizon, basal Nohn beds, Lower Eifelian, Middle Devonian.

Range. Nohn beds, Lower Eifelian. The genus *Kayseria* is very scarce below the Upper Eifelian and the true range of *K. nohnensis* is uncertain.

Distribution. Eifel, Germany.

Holotype. BMNH:BB58536.

Diagnosis. More globose *Kayseria* with pointed beaks, less squared outline, relatively fine ribs over the whole shell, weaker sulci on both valves.

External. The limited material makes the range of variation unknown. On the holotype there are 26–28 fine ribs on the shell with rib size increasing towards the sulci, but not markedly. Ribs are slightly finer in the troughs and about 4 occur there. The sulci on both valves leave the typical indentation on the anterior commissure. Poorly preserved frills are present on the brachial valve of one specimen. The shell has a pointed beak outline, but the ventral beak itself does not project more than normal for *Kayseria* (i.e. less than 1 mm).

Internal. No serial sections made.

Comparison. The diagnosis describes the difference between other species which mainly concern the more globose shell, a pointed beak, finer ribs, and narrow outline.

Material. Weilersbach horizon, Nohn beds, Lower Eifelian. Two specimens from type locality and also C284 C (2) MTB Dollendorf r56900:h78130. Holotype width 11·2 mm, length 13·3 mm, depth 6·0 mm (thickest of known *Kayseria* in the Eifel region).

CONCLUSIONS

Both *Kayseria* and *Bifida* display distinctive non-atrypid characters (defining true atrypids as spire-bearers with dorsally directed spiralia). These characters are:

1. Wedge-like crural bases instead of ball-like crural bases as in atrypids.
2. Sharp deflection from the ends of the crura to the beginning of the spiralia instead of direct continuation.
3. Fused, ventrally arched jugum, instead of separate jugal processes as present in nearly all Siluro-Devonian atrypids.

4. Posterior extension of the jugum to form accessory spiral lamellae (*Kayseria*), absent in atrypids.
5. Short rudimentary accessory lamellae extending from the dorsal base of the jugum (*Bifida*), absent in atrypids.
6. Ventro-laterally directed spiralia which are mirror image, 'inside-out' opposites of atrypid spiralia.
7. Plane of spiral ribbons convex inwardly, versus outwardly in atrypids.
8. True septal structures with reinforcing rods, instead of simple calcite tissue built on the shell wall as in atrypids.

These are major points of comparison with the athyridid brachiopods and are absent in true atrypids of any age known thus far.

REFERENCES

ALEXANDER, F. E. S. 1947. On *Dayia navicula* (J. de C. Sowerby) and *Whitfieldella canalis* (J. de C. Sowerby) from the English Silurian. *Geol. Mag.* **84,** 304–316.

ARCHIAC, E. J. A. D. D' and VERNEUIL, E. P. P. 1842. On the fossils of the older deposits in the rhenish provinces; preceded by a general survey of the fauna of the Palaeozoic rocks, and followed by a tabular list of the organic remains of the Devonian System in Europe. *Trans. geol. Soc. Lond.* **6,** 304–408, pls. 25–38.

BIERNAT, G. 1954. Brachiopods from the Couvinian of Grzegorzowice. *Acta geol. pol.* **4,** 485–533, pls. 1–6.

BOUCOT, A. J., JOHNSON, J. G., and STATON, R. D. 1964. On some atrypoid, retzioid and athyridoid Brachiopoda. *J. Paleont.* **38,** 805–822, pls. 125–128.

—— —— —— 1965. Spiriferida. *In* MOORE, R. C. (ed.), *Treatise on invertebrate paleontology*, **H(2),** 632–728, figs. 518–593.

—— —— 1967. Species and distribution of *Coelospira* (Brachiopoda). *J. Paleont.* **41,** 1226–1241.

COPPER, P. 1966. Ecological distribution of Devonian atrypid brachiopods. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **2,** 245–266, 7 figs.

—— 1967. Order Atrypida. *In* HARLAND, W. B. *et al.* (eds.), *The fossil record*, Geol. Soc. Lond. 408–409, fig. 12.2A.

DAVIDSON, T. 1864. A monograph of the British Devonian brachiopods. *Palaeontogr. Soc.* (*Monogr.*), **3,** 1–131, 20 pls.

—— 1882. Supplement to the British Silurian Brachiopoda. Ibid. **5,** 1–134, 7 pls.

HALL, J. and CLARKE, J. M. 1893. An introduction to the study of the genera of paleozoic Brachiopoda. *Palaeont., New York*, **8**(2), 1–394, pls. 21–84.

HAVLÍČEK, V. 1956. Brachiopods of the Branik and Hlubocepy limestones in the immediate vicinity of Prague. *Sbor. Ústřed. Úst. geol.* **22,** 535–665, pls. 1–12. (English summary.)

HOUSE, M. R. and SELWOOD, E. B. 1966. Palaeozoic paleontology in Devon and Cornwall. *In* Present views of some aspects of the geology of Cornwall and Devon. *Roy. geol. Soc. Cornwall*, 150th Anniv. Vol. 45–86.

LEMAITRE, D. 1952. La faune Dévonien inférieure et moyen de la Saouara et des abords de l'Erg el Djemel. *Matér. Carte géol. Alger.* **12,** 1–170, 22 pls.

NIKIFOROVA, O. I. and MODZALEVSKAYA, T. L. 1968. The discovery of shells of a new brachiopod genus *Dnestrina* from the Silurian of Moldavia and Podolia. *Ezheg. vses. paleont. Obshch.* **18,** 206–210, 1 pl. (In Russian.)

PHILLIPS, J. 1841. Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon, and West Somerset. *Mem. geol. Surv. U.K.* **1,** 1–123, 60 pls.

RZHONSNITSKAYA, M. A. 1960. Order Atrypida. *Osnovy paleontologii*, Brachiopoda, 257–264, pls. 53–56, figs. 310–335. (In Russian.)

SCHMIDT, H. 1951. Zur Brachiopoden-Fauna des mitteldevonischen Flinzkalks von Iserlohn-Letmathe. *Senckenbergiana*, **32,** 87–94, pl. 1.

SCHNUR, J. 1851. Die Brachiopoden aus dem Uebergangsgebirge der Eifel. *Progr. ver. höh. Bürg. Prov. Gewerbesch. Trier*, 1-16.

—— 1853. Zusammenstellung und beschreibung sämmtlicher im Übergangsgebirge der Eifel vorkommenden Brachiopoden nebst Abbildungen derselben. *Palaeontographica*, **4**, 169-254, 45 pls.

SCHUCHERT, C. 1894. A revised classification of the spire-bearing Brachiopoda. *Am. Geol.* **13**, 102-107.

SIEHL, A. 1962. Der Greifensteinerkalk (Eiflium Rheinisches Schiefergebirge) und seine Brachiopodenfauna, I Geologie; Atrypacea und Rostrospiracea. *Palaeontographica*, **119**, 173-221, pls. 23-40.

STEININGER, J. 1853. *Geognostische Beschreibung der Eifel.* 143 pp., 9 pls., 1 map (Trier).

STRUVE, W. 1961. Zur Stratigraphie der südlichen Eifler Kalkmulden. *Senckenberg. leth.* **42**, 291-345, 3 pls.

TUCKER, E. V. 1968. The atrypidine brachiopod *Dayia navicula* (J. de C. Sowerby). *Palaeontology*, **11**, 612-626, pls. 118-121.

WHIDBORNE, G. F. 1893. A monograph of the Devonian fauna of the south of England. *Palaeontogr. Soc.* (*Monogr.*), 91-160, pls. 11-17.

WILLIAMS, A. and ROWELL, A. J. 1965. *In* MOORE, R. C. (ed.), *Treatise on invertebrate paleontology*, **H.** Brachiopoda, 57-155.

WOLBURG, J. 1933. Das Devon im Gebiet der oberen Lenne. *Abh. preuss. geol. Landesanst.* N.F. **151**, 1-70.

ZIEGLER, A. M. 1966. The Silurian brachiopod *Eocoelia hemisphaerica* (J. de C. Sowerby) and related species. *Palaeontology*, **9**, 523-543, pls. 83-84.

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