

ZYGOSPIRA AND SOME RELATED ORDOVICIAN AND SILURIAN ATRYPOID BRACHIOPODS

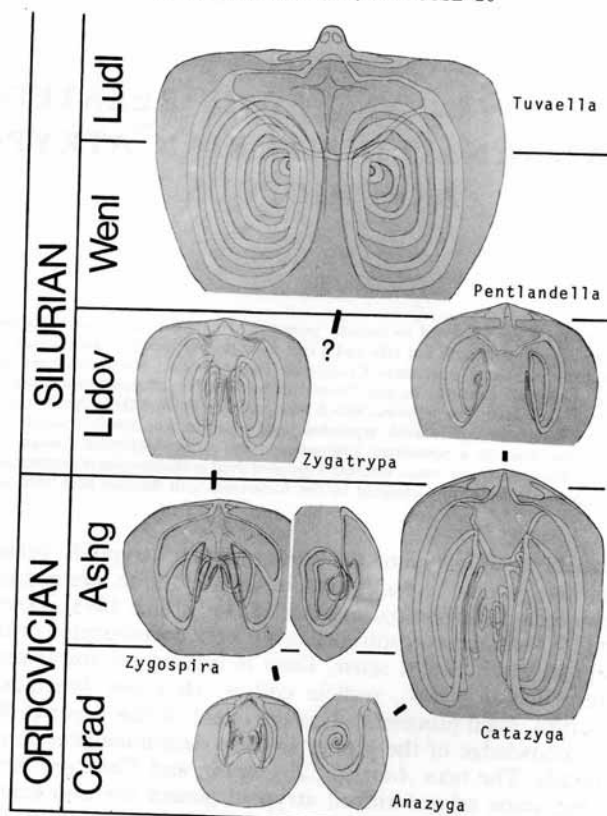
by PAUL COPPER

ABSTRACT. The Zygospiridae are redefined to include 'primitive' atrypod brachiopods with dorsally to dorso-medially directed spiralia, normally with fine ribs and a one-piece jugum dorsal to the spiralia. The Ordovician-Silurian family is divided into three: Zygospirinae, Catazyginae (new sub-fam.), and Tuvaellinae. Internal structures of *Zygospira*, *Anazyga*, *Catazyga*, *Pentlandella*, and *Tuvaella* are evaluated in terms of their evolutionary significance. A new genus *Zygatrypa* is erected. *Eospirigerina*, which was probably derived from zygospirid stock in the late Ordovician, differs in having ventrally located, separated jugal processes and trends towards 'frilly' shells: this represented a major jump towards a postulated *Zygospiraella*-*Protatrypa*-*Gotatrypa* lineage. In late Caradoc-Ashgill times *Catazyga* inhabited deeper water, whereas *Zygospira* lived in shallow-water communities. The Clintonellinae, including *Alispira*, are tentatively assigned to the Atrypidae, with Silurian taxa such as *Nalivkinia* and *Anabaria*.

INTERNAL structures of many of the earlier ribbed atrypoids belonging to the family Zygospiridae, which first appeared in Caradoc time, are not generally well known. The pioneering morphological work of Hall (1862, 1893), Davidson (1882), and Schuchert (1893) on the zygospirids has not been corroborated or used in classifications, except in the broadest sense. Data is lacking on apical shell structures (deltoidal plates, 'dental plates', pedicle collars, etc.) and brachidial structures (socket plates, crura, jugal processes). It is the intent of this paper to fill in some of the gaps in our knowledge of the group, so as to determine generic variation and evolutionary trends. The taxa *Anazyga*, *Zygospira*, and *Catazyga* form the centre of this study, but some related ribbed atrypod genera are also examined. Serial sections demonstrate the affinities of *Pentlandella*, *Tuvaella*, *Alispira*, 'Clintonella', *Nalivkinia*, and *Anabaria*. The first two are retained within the zygospirids, but the others are removed. *Zygospiraella* is interpreted as an ancestor of the *Protatrypa*-*Gotatrypa*-*Atrypa* lineage: this will be described in a subsequent paper. Smooth Ordovician spire-bearing genera, such as *Protozyga*, *Idiospira*, and *Cyclospira*, are not within the scope of this paper, but are also under revision.

EVOLUTION

The main bloom of the group took place during the late Caradoc and Ashgill, but by latest Ordovician time the zygospirids in eastern North America and western Europe had been replaced by *Eospirigerina*. During this interval, and in the early Llandovery in this region, there appears to be no trace of any zygospirids. Nevertheless, by Upper Llandovery (Telychian) time, two zygospirids reappear, *Pentlandella* in Britain and Estonia, and *Zygatrypa*, described herein from Anticosti Island. *Tuvaella*, from the Tuva region of Asian U.S.S.R. and Mongolia, also appeared in



TEXT-FIG. 1. The most important evolutionary trends in the Zygospiridae lie with the disposition and nature of the spiralia and the jugum. The spiralia tend to produce increased numbers of whorls, a change from medially to dorsally directed coils, and the jugum shifts in position from an anterior to a posterior location with an eventual position near the pedicle valve. These trends probably reflect more efficient suspension feeding and changes in the location of the digestive tract.

late Llandovery or early Wenlock time, but was endemic to that area. *Tuvaella* ranged into late Silurian time (Pridoli?), and appears to have been the last-surviving zygospirid.

The origin of the earliest atrypoids is unclear. If *Protozyga* is the common ancestor, a smooth impunctate prototype form is indicated, possibly a camerellid or smooth rhynchonellid. However, if *Protozyga* represents an offshoot from *Anazyga*, a ribbed rhynchonellid, or even an orthid, may be the root-stock. We are no closer to an answer than at the time of Cooper's monograph on the Chazyan brachiopods (1956).

The geological succession in Ontario is for *Protozyga* to appear first, followed by *Anazyga*, then *Zygospira* and *Catazyga*.

A general trend in the Zygospiridae is towards increasing size in all three sub-families, for example, *Zygospira* itself reached maximum width in Ashgill time and the largest catazyginids are late Ordovician *Catazyga*. However, *Zygatrypa* and *Pentlandella*, offshoots of Ordovician genera, are very small by comparison and appear to show a reversed late trend towards decreasing size and finer ribbing. The origin of *Tuvaella* lies in the Zygospiridae, but perhaps not with *Zygatrypa*. *Tuvaella* is the largest known zygospirid, reaching widths of some 60 mm with *T. gigantea* Chernyshev in late Silurian time (Vladimirskaia 1972). Even 'large' late Ordovician zygospirids such as *Catazyga* and *Zygospira* rarely exceed 15 mm. Another trend is rib coarsening in the zygospiridids, leading from *Anazyga* to early *Zygospira* and late *Zygospira* in the Ordovician, and also in the *Catazyga* group. However, in Silurian time, the zygospirids tend to be very fine ribbed, except for *Tuvaella*. A reverse trend, towards loss of ribs, may have occurred in some catazyginids. Ulrich (1888, pp. 196–197) described a late Ordovician species of catazyginid, which he called *Glassia schuchertana*, because ribs were barely, if at all, visible on many well-preserved specimens. Foerste (1910) assigned it to *Catazyga*, as did Meek (1873) who identified it as the same as the type species of *Catazyga*, *C. headi* (Billings 1862). Silurian *Pentlandella* from Estonia also possess such fine ribs that these are frequently not visible on parts of the anterior shell. It is possible that the loss of ribs resulted in the appearance of *Glassia* in Llandovery time, since the spiralia in *Glassia* are medially directed, as in *Catazyga*.

Internal trends differ in individual sub-families but are probably more significant. *Anazyga* has a fused jugum located antero-dorsally to the cone axes, and the spiralia are medially directed (cone axes parallel or near parallel to the commissural plane). Its descendant *Zygospira* has a dorsal jugum located at the cone axes, or posterior to the cone axes, and spiralia directed dorso-medially (cone axes some 45° from the commissural plane). If the two taxa form a continuous lineage from Caradoc through Ashgill time, then the jugum migrated from an anterior position to a posterior position and the cone axes rotated some 45° from the commissural plane in a dorsal direction. In addition, the same lineage shows an increasing trend from only one or two spiralia whorls in *Anazyga* to three to five in *Zygospira*. It is perhaps significant that in the Atrypidae of the Siluro-Devonian, thirty or more spiral whorls are known and the separated jugal processes are located antero-ventrally. *Eospirigerina* in the late Ordovician Ellis Bay Formation of Anticosti Island has eight to nine spiral whorls and unconnected jugal processes located antero-ventrally. This clearly separates *Eospirigerina* from the Zygospiridae, from which it must have evolved. The dorso-medial turning of the cone axes culminated in almost full dorsal directions in the latest Ordovician (text-fig. 1). It is significant that the location of the jugum in the Zygospiridae is dorsal: the jugum is derived from the initial whorl of the spiralia but is directed dorsally and lies very close to the median septum of the brachial valve, frequently arching over it. This implies that the jugum may have rested or been suspended over the brachial valve floor. The jugal processes in the Atrypidae and Palaeferellidae are ventral, i.e. the jugal process is located ventrally and posterior to the spiralia and thus lies closest to the pedicle valve. Thus not only

do these other families differ in having a divided jugum, or jugal processes (Copper 1967), but the implication is that if the jugum-jugal processes held mouth parts, their feeding processes would be quite different.

In the Catazyginae there are different internal trends. *Catazyga* probably evolved from *Anazyga* in the late Caradoc. It is uncertain whether to assign *Anazyga* to the *Catazyga* group or to the *Zygospira* group. Externally *Anazyga* is closer to *Zygospira* in its wider shell, fold-sulcus, and beak structure. Internally it could belong to either, except that *Anazyga* has dental cavities, like *Zygospira*, and *Catazyga* has none. If *Catazyga* evolved from *Anazyga*, as seems most likely, then this involved a loss of dental cavities and great thickening of the pedicle valve anteriorly. *Catazyga*, and its Silurian descent *Pentlandella*, both retain spiralia which are strongly directed towards the centre of the shell. The cone axes show a lesser rotation from the commissural plane than in the zygospirinids. *Catazyga* has about seven spiral whorls. Rubel (1970) recorded four whorls for Estonian *Pentlandella*, but an adult specimen sectioned for this paper, from the same Estonian locality, revealed only two (text-fig. 7). Since Silurian *Pentlandella* are about half the size of Ordovician *Catazyga* this does not necessarily reflect an independent evolutionary reduction in spiralia, but is probably a size-related factor.

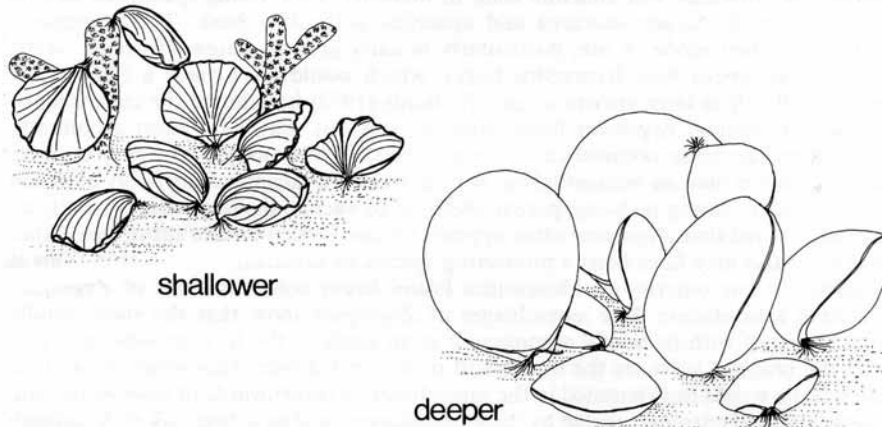
The structure of the jugum and spiralia in Silurian *Zygotrypa* is similar to that of *Zygospira*, except in the location of the jugum. In *Tuvaella rackoviskii* from the Tuva region and Mongolia (text-fig. 14) no dental cavities are present, but the jugum is located dorsally and its central point lies close to the cone apices. This is like other zygospirinids. Functionally this suggests that the central part of the jugum held a mouth organ to which food currents were canalized. The cone axes are directed as in *Zygospira*, and five to eight whorls were present. In later *T. gigantea*, Vladimirskaia (1972) recorded up to ten whorls, which seems to be a maximum figure for any Zygospiridae. It is possible that the family gave way to the Atrypidae and other groups because these had the ability to use larger numbers of spiral whorls and were thus more efficient filter feeders.

THE ORDOVICIAN-SILURIAN BOUNDARY

Atrypoid brachiopods of the transitional period from Ordovician to Silurian time are not well known. In the Anticosti section in eastern Canada, which holds a richly fossiliferous suite of rocks straddling the 'boundary', the zygospirids were halted in the Vaureal Formation and do not continue into the Ellis Bay Formation, most of which (on the basis of brachiopods, rugose and tabulate corals, and stromatoporoids) is still in the Ordovician. I agree with Bolton (1972) that the base of the Becscie Formation with *Zygospiraella* (Atrypidae) corresponds very closely to the boundary. The zygospirids, therefore, are not of great value in eastern North America in determining the boundary. They were in decline some time before the close of the Ordovician, with only two conservative lines maintained as rare elements in the Llandovery (*Pentlandella* and *Zygotrypa*).

Amsden (1971) described a transitional fauna from the Edgewood Formation of Illinois and Missouri including '*Eospirigerina putilla*' (Hall and Clarke, 1893), which is said to be present in the latest Ordovician as well as early Llandovery.

This species may be a true *Zygospira*, as described by the original authors, and needs redescription. *Eospirigerina* is so abundant in the Ellis Bay Formation of Anticosti Island that it forms distinctive shelly horizons; several species are present. The species group of '*Plectatrypa*', is readily confused with *Eospirigerina* in the late Ordovician (but not in the Silurian of Western Europe). '*Eospirigerina*' *hibernica* Reed (1932) from Northern Ireland is a late Ordovician form first figured by Portlock (1843, pl. 37, fig. 4). '*Plectatrypa*' *partita* (Sowerby, 1839) from Goleuoged Hill (Lower Llandovery) in Wales is a similar early Silurian form. The *Eospirigerina*-'*Plectatrypa*' group is complex but could perhaps shed light on the boundary problem. *Zygospiraella* at present is the most useful atrypoid indicator of early Llandovery age.



TEXT-FIG. 2. During Ashgill time, zygospirids were dominant in two assemblages; a shallower-water *Zygospira* assemblage with bryozoans, tabulates, and colonial rugose corals, and a deeper, quiet water assemblage of *Catazyga* and sowerbyellids (examples drawn from *Z. modesta* and *C. headi*; no ribs drawn on latter). Scale $5/3 \times$.

PALAEOECOLOGICAL DISTRIBUTION

The earlier zygospirids *Protozyga* and *Anazyga* were probably moderately deep-water benthos. Their common occurrence is in dark-grey to black calcareous shales or muddy limestones. Common associates of *Anazyga* are other small brachiopods, small hemispherical colonies of *Prasopora* and ostracodes. *Anazyga* does not occur abundantly with bioherms or biostromes with stromatoporoids, tabulate or rugose corals, or with digitate bryozoans in higher energy, shallow-water zones. By later Ordovician time, zygospirids were ecologically sorted into two communities or habitats: *Zygospira* with coarser ribs, well-defined fold-sulcus, and planoconvex-ventribiconvex shells, lived in a shallow-water community with bryozoans (Bretsky 1969; Richards 1972), and *Catazyga* in a deeper-water, muddy environment, frequently nearly barren of anything but crowded catazygid nests (text-fig. 2). The

two genera rarely occur together except in ratios of 100:1 or more. In the Vaureal Formation on Anticosti Island *Zygospira* is apparently absent and *Catazyga* is abundant. Towards Manitoulin Island, some 400 miles westwards, *Zygospira* is locally extremely abundant but *Catazyga* occurs only in isolated patches. A similar presence-absence occurrence is described from Indiana and Ohio by Richards (1972, p. 402). The two taxa seem to be reliable relative depth indicators, but at present actual depths are problematical. It is possible that *Zygospira* represented the depth equivalent in the Silurian of the *Pentamerus-Eocoelia* community and *Catazyga* the equivalent of the *Clorinda* community (Ziegler 1965).

The mode of life of many zygospirids is hypothetical. *Zygospira* has a small, but distinctive, interarea and anacline beak in maturity, with young specimens having a proportionally larger interarea and apsacline-orthocline beak. This suggests a pedicle-attached mode of life, particularly in early growth stages. However, some gerontic specimens have hypercline beaks, which would have made a functioning pedicle difficult in later growth stages. Richards (1972) has shown the clustering of zygospirids around bryozoan finger-colonies and this may have been a common association. In mass occurrences of zygospirids, bryozoans are too rare to have served as more than an occasional anchoring site: the zygospirids probably attached to each other, young to living parent shells or to vacant shells on the sea bottom. Richards noted that *Zygospira* often appears to have settled on live substrates (other benthos), and may have been a pioneering species in substrate colonization. This is possible; in one outcrop on Manitoulin Island heavy concentrations of *Zygospira* preceded a biostrome. Life assemblages of *Zygospira* show that the shell usually attached itself with its lateral commissure at an angle to the host or substrate, and with the brachial valve on the downward or host-ward side. This would mean that the spiralia would be orientated in the same direction (downwards or host-wards and inwards). Food currents created by the lophophore would have been taken in through the sides of the shell and released anteriorly.

Catazyga, with a hypercline beak in maturity, biconvex-ventri-biconvex shell and weak fold-sulcus, is rather different in its usual lack of associates of any kind other than some strophomenids. Cluster accumulations, presumably nests, show that in dense clusters most shells are orientated at a relatively high angle to the substrate with the pedicle valve uppermost and the plane of symmetry tilted away from the vertical. Thus the anterior commissure, and presumably the exhalent current were further away from the substrate than with *Zygospira*. Shell elongation would accentuate this (*Zygospira* is wider: *Catazyga* longer). However, in more moderate densities of 40-60 per 100 square cm, with non-touching shells on the substrate, the *Catazyga* generally lie flat on the substrate and with the pedicle valve uppermost. What this means is not clear. Possibly with decreased densities, waste clearance away from the substrate was not such a problem, or with shells no longer touching and therefore supporting each other upright, the pedicle was too weak to maintain a near vertical or angled position. Since beak incurvature was severe in maturity, suggesting less-functional pedicles, the latter explanation may be more correct.

A reconstruction (text-fig. 2) demonstrates the postulated modes of life of the two dominant late Ordovician taxa. The catazyginids and zygospiridids in the Silurian seem to have maintained essentially the same ecological polarity. *Pentlandella*

normally occurs in shales or mudstones with few other organisms and rarely with coralline skeletons. *Zygatrypa* (known only from the Silurian of Anticosti Island) is an inhabitant of the *Stricklandia* community, and occurs with *Atrypopsis*, common *Gotatrypa* and clintonellinids.

SYSTEMATIC DESCRIPTIONS

Order ATRYPIDA Rzhonsnitskaya, 1960

Family ZYGOSPIRIDAE Waagen, 1883 (emend.)

[= Anazygidae Davidson, 1883]

Primitive, smaller, planoconvex-biconvex, non-lamellose, usually tubular-ribbed atrypoids with minute pedicle openings, beaks orthocline to hypercline, no deltidial plates, or small plates. Internally the family is characterized by a fused jugum, located dorsal to the spiralia and moving in position anteriorly to posteriorly during evolution in the Ordovician. Age: Ordovician (Caradoc) to Silurian (Ludlow).

Subfamily ZYGOSPIRINAE Waagen, 1883

Here emended to include *Protozyga* Hall and Clarke, 1893, *Anazyga* Davidson, 1882, *Zygospira* Hall, 1862, *Hallina* Winchell and Schuchert, 1892, and *Zygatrypa* gen. nov.

The internal structure of *Protozyga* and *Hallina* was described, with some doubts, by Hall and Clarke (1893, pp. 149-151). *Protozyga* was figured with an anteriorly located jugum and short, one coil spiralia (ibid., p. 149) which seems correct in view of the internal morphology of *Anazyga*. *Hallina* was figured with only an anterior jugum and no spiralia (ibid., p. 151). Cooper (1956, pp. 689-690) did not define the latter genus nor find any species with spiralia. The type species of *Hallina*, from the Lebanon Formation of Tennessee, indicates a vertical distribution which in part coincides with that of *Anazyga*. *Hallina* may be a junior synonym of *Anazyga*. Externally they are not possible to differentiate; internally they both have well-defined cavities. Internals of *Hallina* need revision, but topotypic material is invariably badly preserved (G. A. Cooper, pers. comm.). The common features of the Zygospirinae seem to lie in the possession of finely ribbed planoconvex-ventribiconvex shells with a modest to sharp ventral fold-dorsal sulcus, orthocline-anacline beaks, small but visible pedicle openings, dental cavities or nuclei, thin shell walls, an anterior to posterior jugum, and medially to dorso-medially directed spiralia.

Range: Caradoc to Llandovery.

Genus ZYGOSPIRA Hall, 1862

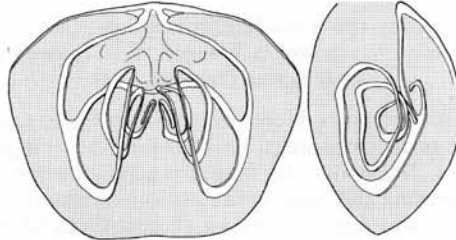
Type species. *Atrypa modesta* (Say in Hall 1847). Say apparently identified this in collections of the Academy of Natural Sciences, Philadelphia as *Producta modesta* (ibid., p. 141).

Range. Late Caradoc (Maysvillian) to Ashgill (Richmondian).

Distribution. North America, western Europe, ?Siberian Platform, Kazakhstan. Not yet reported from South America, but should occur in Australia, in view of great similarities in associated benthic corals with North America.

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Diagnosis. Moderately sized, relatively coarsely ribbed, carinate zygospirids with ventri-carinate, planoconvex shells, small interarea, orthocline-anacline beaks. Internally, dorso-medially directed spiralia with five to eight whorls and dorsal jugum located at or posterior to spiralia apices; dental cavities, small deltidial plates present. For spiralia refer to text-fig. 3.



TEXT-FIG. 3. Reconstruction of the spiralia in the type species *Zygospira modesta* based on serial sections shown in text-fig. 4. Note the nature of the jugum. Scale approx. $\times 7$.

Species assigned.

Zygospira cincinnatiensis James, in Meek 1873 (p. 126, pl. 11, fig. 5a-c), basal Maysville Formation (Foerste 1910), Cincinnati, Ohio, U.S.A.

Zygospira richmondensis Caley, 1936 (p. 78, pl. 1, figs. 4, 6). Kagawong Formation, High Falls, Manitoulin Island, Ontario, Canada (Pl. 37, figs. 9-10).

Zygospira modesta kagawongensis Caley, 1936 (p. 58), Unit 8. Meaford Formation, Section no. 16, Kagawong Falls, Manitoulin Island, Ontario, Canada. Species becomes a *nomen nudum*, unless it is described and figured.

Zygospira putilla Hall and Clarke, 1893 (p. 157, fig. 150; pl. 54, figs. 35-37). Hudson River Group, Edgewood, Missouri, U.S.A. Amsden (1974) relegates this species to *Eospirigerina*.

Zygospira parva Rukavishnikova, 1956 (pp. 162-163, pl. 5, figs. 14-16). Otarsk and Dulankarin Horizons, southern Kazakhstan, U.S.S.R. Very weakly carinate.

Zygospira kentuckiensis Nettleroth, 1889 (pp. 138-139, pl. 34, figs. 21-25). 'Hudson River or Cincinnati Group', Taylor's Station, Kentucky, U.S.A. One of the largest known *Zygospira*.

Zygospira meafordensis Foerste, 1924 (p. 128, pl. 15, fig. 3a-c). 'Queenston Member, Richmond.' North-west Meaford, Ontario.

Zygospira raymondi Foerste, 1924 (p. 128), figured in Raymond (1921, p. 28, pl. 8, figs. 1-5). Collingwood Shale, Craigeleath, Ontario, Canada.

Zygospira meldalensis Reed, 1932 (p. 144, pl. 22, figs. 12, 12a). Kalstad Limestone, Meldalen, Norway.

Zygospira resupinata multicostata Howe, 1965 (pp. 653-655, pl. 81, figs. 1-8). Aleman Limestone, Trans-Pecos, Texas, U.S.A.

Zygospira sulcata Howe, 1965 (pp. 655-656, pl. 81, figs. 9-12). Uppermost Upham Limestone, Lone Mountain, New Mexico, U.S.A. Finely ribbed form.

Zygospira concentrica Ulrich, 1888 (pp. 14-15, pl. 7, figs. 10, 10a, b). Lower part of the Hudson River Group, 300-350 ft above low water, Cincinnati, Ohio, U.S.A.

Eocoelia hemispherica crassa Rozman, 1970 (pp. 123-125, pl. 15, figs. 5-8). Upper Ordovician, lower beds of Taskansk Suite, Sette-Daban range, North-east U.S.S.R.

Zygospira resupinata Wang, 1949 (pp. 18-19, pl. 10A, figs. 1-12). *Cornulites* Zone, Brainard Member, Maquoketa Formation (Ashgill), Fairfield, Iowa, U.S.A.

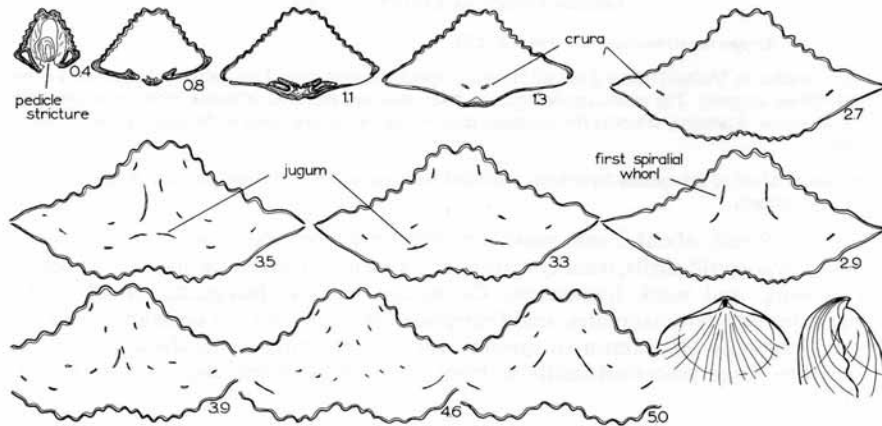
Comparisons. *Zygospira* is distinguished from *Anazyga*, its forerunner, by generally more coarsely ribbed, more strongly carinate shell, differentiated mid and lateral ribs and more planoconvex-ventribiconvex shells. Internally there are more whorls in the adult spiralia and the jugum is located postero-dorsally. Hall and Clarke (1893, p. 154) note an absence of 'dental lamellae', but this is clearly incorrect; dental cavities are prominent in both genera.

Zygospira modesta (Say in Hall, 1847)

Plate 37, figs. 1-8; text-figs. 3-4

1847 *Atrypa modesta* Say in Hall, pp. 141-142, pl. 33, fig. 15.

Type. Lectotype AMNH 1356A (selected by Foerste 1910), Plate 37, figs. 1-4, American Museum Nat. Hist., New York. In the original description Hall noted (1847, p. 142) that the species was rare in New York, where late Ordovician sediments are more sparsely fossiliferous, but abundant in Ohio, Indiana, and Kentucky. He selected no type locality except to state 'It is quite abundant at numerous western localities, particularly Oxford and Cincinnati (Ohio), Madison (Indiana), Frankfort and Maysville (Kentucky)'. When he established the genus in 1862, and also in commenting on the species *modesta* in 1857, Hall cited no source localities. The type specimen is labelled 'Cincinnati'. Foerste (1910, pp. 29-30) examined the type specimen, and stated that although it was labelled 'Cincinnati', this could have meant derivation of the specimen from some Cincinnati collection. The type specimen was labelled 'Hudson River Group'. Foerste (1910) observed that specimens similar to the type came from the Fairmount Bed of the Maysville Formation (late Caradoc) and selected that as the type horizon. Since *Z. kentuckiensis* (Meek) occurs in the Upper Fairmount (according to Foerste), *modesta* may belong to the lower, unless the two taxa were synchronous and allopatric. There is no new data on this, particularly since *Z. modesta* has been very broadly interpreted in the literature and seems to have been ubiquitous in the shallower platform carbonate sequence. Richards (1972) reported *Z. modesta* from the Richmondian Tanner's Creek Formation, well above the typical horizon, but these specimens are not similar to the type material. I have not collected toptype or conspecific material from the Cincinnati region, but judging from other



TEXT-FIG. 4. Serial sections of *Zygospira modesta* (Say in Hall 1847) based on acetate peels. GS 45391 'Cincinnati, Ohio' (material provided by Dr. G. A. Cooper, U.S. National Museum). Scale $\times 5$.

Zygospira in Ontario, abundant in the Georgian Bay Formation, the typical association of *Z. modesta* is with shallow-water benthos, especially digitate bryozoans. Sediments ranged from clayey shales in sub- or peri-biostromal occurrences to finely comminuted bioclastic substrates.

Diagnosis. Moderately sized, wider than long, planoconvex-weakly biconvex zygospirids with 15-18 ribs over all, 4 strong mid-ribs on the pedicle valve, and 3 corresponding mid-ribs on the brachial valve and the remaining lateral ribs decreasing in size posteriorly. Average width 8.1 mm, length 7.2 mm, depth 3.9 mm (based on 15 syntypes in the AMNH Hall Collection). Internally, shell thin; weak, irregular pedicle collar structures line pedicle cavity; dental cavities distinct; teeth near-'horizontal' in sockets (text-fig. 4). Small nodular crural bases on inner socket ridges, crura diverge widely to sides, jugum arising at or near position of cone axes, initially curving postero-medially dorsal to the spiralia, then straightening medially and curving dorso-anteriorly to fuse. Spiralia D-shaped with straight sides forming a weak V (open anteriorly); three to five whorls seen (text-fig. 3). No cardinal process observed; dorsal septum strong. Muscle scars weakly impressed, poorly known.

Remarks. It is premature, without mass collecting, to differentiate clearly between the described species of *Zygospira*, and to delineate an evolutionary succession, but the species group could become a useful tool in zoning late Caradoc-early Ashgill shallow marine sediments. The coarser-ribbed, larger specimens appear to be youngest, but this is not an invariable rule. Some species, such as *Z. kentuckiensis*, show confusing and greater infra-specific variability than do most atrypoids in younger rocks. Most of the described species are from the marine platform carbonate succession of Ontario, Michigan, Ohio, Indiana, and Kentucky. On the Appalachian side and in Quebec, *Zygospira* is rare, and where reported is usually not *Zygospira* but *Anazyga* or *Catazyga*.

Genus ANAZYGA Davidson, 1882

Type species. *Atrypa recurvirostra* Hall, 1847, p. 140.

Range. Caradoc to ?Ashgill. Most if not all 'Trenton' species belong here. This genus is the earliest known wholly ribbed atrypoid. The oldest species appears to be *Anazyga matutina* (Cooper 1956) from the Little Oak Formation, Alabama, whereas the youngest may overlap with *Zygospira* in the late Caradoc to early Ashgill.

Distribution. Most of the species have been identified from eastern North America; also Britain, Scandinavia, and Estonia.

Diagnosis. Small, about 5 mm wide, ventribiconvex-biconvex, equidimensional to elongate zygospirid shells, usually with strongly incurved, anacline-hypercline beaks, fine ribbing, and weak fold-sulcus. Carination lacking. Internally, small dental cavities, minute deltidial plates, undifferentiated teeth. Crura not strongly diverging, jugum branching off anterior to spiralia apices, frequently at the distal side of the crura, then fused postero-dorsally in front of spiralia apices; one to three whorls (text-fig. 5).

Comparisons. *Anazyga* is a widespread genus present in 'Chazyan' rocks (Cooper 1956) of Caradoc age in North America (the oldest is in 'Porterfield' equivalents). The most comparable genus is *Hallina* Winchell and Schuchert 1892 whose vertical

range is almost the same. It is possible that *Hallina* is a junior synonym: its type species must be recollected and internal structures clarified. Winchell and Schuchert (1892, 1893) described and figured the brachidia as consisting of a single fused loop, which looks very much like the jugum, but no spiral whorls were noted. If this is typical of all *Hallina*, then possibly the genus is distinct from *Anazyga*. Hall and Clarke (1893, p. 151, figs. 139–141) appear to confirm the lack of a spirulum and presence of a loop, and believed that the internal structure of their genus *Protozyga* (ibid., p. 151) was nearly identical, except that *Protozyga* had the beginnings of the first spiral whorl (ibid., p. 149). If *Hallina* is distinctive in its primitive non-coiled brachidia, then externally it is a near homoeomorph of *Anazyga*, according to Boucot *et al.* (1965). This would create severe taxonomic difficulties in classifying poorly preserved material and would mean that some taxa may be erroneously attributed. Cooper (1956, pl. 143) illustrated *H. saffordi*, *H. lirata*, and *H. globularis*, which indicate that externally *Hallina* may be distinct in having the posterior shell umbones smooth, as already pointed out by Winchell and Schuchert (1893, p. 473). It is possible that the Clintonellinae (Poulsen 1943) may have arisen independently from the *Hallina* group. *Hallina* cannot be distinguished from *Anazyga* by its 'dental plates', which are present in both genera.

Davidson (1883, p. 136) established the family Anazygidae, including *Anazyga*, *Dayia*, and *Hindella*, to include brachiopods with 'loops arising from bottom of spirals'. This was published in the same year as Waagen (1883), who erected the Zygospiridae: thus seniority is not clear. The Anazygidae are left as a junior synonym of the Zygospiridae. Davidson's view was based on a misinterpretation of the coiling direction of the spiralia; the last two named genera have athyroidoid spiralia directed at mirror-image position compared to the atrypoids.

Species tentatively assigned.

Atrypa deflecta Hall, 1847 (p. 140, pl. 33, fig. 4a, b). 'Central part of the Trenton Limestone near Martinsburgh.'

Zygospira recurvirostris noquettensis Hussey, 1926 (pp. 162–163, pl. 11, figs. 1–3). Stonington Beds, Ogontz member, Stratton's Farm, northern Michigan, U.S.A. Possibly an unusual *Zygospira*.

Zygospira recurvirostris turgida Foerste, 1917 (p. 103, pl. 5, fig. 15a–c). 'Upper part of the argillaceous Richmond', Little Bay de Noquette, northern Michigan. This may not be true *Anazyga*.

Zygospira orbis Reed, 1917 (pp. 944–945, pl. 24, figs. 24–27). Stinchar Limestone Group, Craighead, Girvan, Scotland (Lower–Middle Caradoc). Possibly a rhynchonellid.

Zygospira variabilis Fenton and Fenton, 1924 (pp. 75–76, pl. 2, figs. 7–9). No single locality cited in literature: Plattin–South Becket Hill, Kentucky; Black River–Frankfort and Paris, Kentucky, U.S.A.

Zygospira variabilis fountainensis Fenton and Fenton, 1924 (p. 76, pl. 2, figs. 1–3). Decorah Shale, Fountain, Minnesota, U.S.A.

Zygospira calhounensis Fenton and Fenton, 1924 (pp. 76–77, pl. 2, figs. 4–6). No locality and horizon in literature.

Zygospira tantilla Bradley, 1921 (p. 525, no figs. but see Pl. 38, fig. 4). Lower Maquoketa, Clermont, Iowa, U.S.A. This is one of the last *Anazyga*, unless a diminutive, unusual *Zygospira* (the type specimens from Harvard University show an orthocline beak, Pl. 37, figs. 16–20).

Zygospira gutta Oraspyld, 1956 (pp. 64–65, pl. 4, figs. 14–15). Vazalemmask Horizon (D_m), Saku, Estonia, U.S.S.R.

Zygospira circularis Cooper, 1956 (p. 670, pl. 141C, figs. 18–21; pl. 142B, figs. 6–10; pl. 142D, fig. 16). Upper Carters Formation, Franklin, Tennessee, U.S.A.

Zygospira elongata Cooper, 1956 (pp. 670–671, pl. 268G, figs. 29–32). Lebanon Formation, Readyville, Tennessee, U.S.A.

Zygospira lebanonensis Cooper, 1956 (pp. 671–672, pl. 142C, figs. 11–15). Lebanon Formation, Shelbyville, Tennessee, U.S.A.

Zygospira matutina Cooper, 1956 (p. 672, pl. 141B, figs. 13–17). Little Oak Formation, Alabama, U.S.A.

Zygospira mediocostellata Cooper, 1956 (pp. 672–673, pl. 143D, figs. 13–18). Sevier Formation, Bulls Gap, Tennessee, U.S.A.

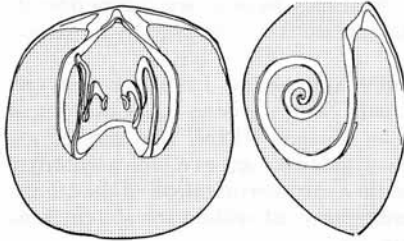
Zygospira recurvirostris aequivalvis Twenhofel, 1928 (p. 214, pl. 19, figs. 10–12). English Head Formation, Zone 4, Anticosti Island, Quebec, Canada. Needs confirmation; possibly related to *noquettensis* Hussey, 1926 and *tantilla* Bradley, 1921.

Anazyga recurvirostra (Hall, 1847)

Plate 37, figs. 11–15; text-figs. 5–6

1847 *Atrypa recurvirostra* Hall, p. 140, pl. 33, fig. 5a–d.

Holotype. AMNH 705.3 (by monotypy), Plate 37, figs. 11–15. American Museum Nat. Hist., New York, from 'near Martinsburgh', New York (Hall 1847, p. 140). The species is abundant in thin-bedded, dark-grey argillaceous limestones (micrites), at outcrops just south of the bridge over Roaring Brook, 1.3 miles east of Martinsburg. This seems suitable as a restricted type locality. The type horizon is a 'Compact greyish blue bed of limestone near the centre of the Trenton Limestone' (ibid.: note that this is almost exactly the middle of the Trenton Group on geological maps, e.g. Miller 1910). This horizon is suspected to be the Shoreham Member of the Sherman Falls Formation, or in other terminology, the Sugar River Limestone (Kay 1938), the zone of *Cryptolithus tessellatus* in New York. The Ontario lithic equivalent is the basal Verulam Formation. Clarke (1919), who described the Martinsburg section, listed '*Zygospira recurvirostris*' at the 100, 165–180, 270–280, and 390 ft levels in the Trenton Limestone. It is not known where the type locality of *recurvirostra* mentioned above fits into this sequence. Possibly it is the member 6 of Miller (1910, p. 29) in the Trenton Limestone, said to be 475 ft thick at Roaring Brook, or the 165–180 ft level of Clarke (1919, p. 7). The associated fauna is common hemispherical *Prasopora* colonies, some 2–4 cm in diameter. *Prasopora* tends to be more abundant in the lower middle part of the old Trenton and stops at 280 ft above the base according to Clarke (1919). Other fossils are rare.

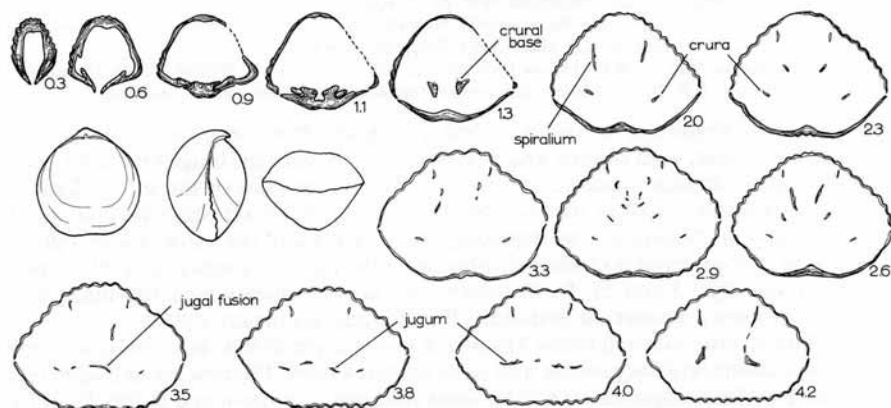


TEXT-FIG. 5. Reconstruction of the spiralia and jugum in *Anazyga recurvirostra*, based on serial sections shown in text-fig. 6. Scale approx. $\times 7$.

the Trenton Limestone, said to be 475 ft thick at Roaring Brook, or the 165–180 ft level of Clarke (1919, p. 7). The associated fauna is common hemispherical *Prasopora* colonies, some 2–4 cm in diameter. *Prasopora* tends to be more abundant in the lower middle part of the old Trenton and stops at 280 ft above the base according to Clarke (1919). Other fossils are rare.

Description. Small, 5–7 mm wide, longer than wide, strongly biconvex–ventribiconvex shells with hypercline beaks. Ribs fine, evenly sized throughout, though slightly larger flanking by sulcus, averaging about twenty-four in number. Brachial valve somewhat flattened anteriorly and very faintly sulcate, pedicle valve more arched; weak anterior fold. Internally, pedicle valve thickened apically with faint median septum, no pedicle constrictions, deltidial plates minute, solid, pointed dorsally, dental cavities elongate, teeth simple, dorso-median projections supported terminally by dorsal wall (text-fig. 6). Brachial valve with sturdy, short socket plates separated medially by pit without cardinal process. Crura extended from small round bases located on inner side of socket plates, diverging laterally at about a 45° angle to the mid-shell, then curving inwardly, with spiral whorls beginning at anterior-most portion. Jugum in broad V-shaped band joined anterior to spiralia apex; two to three spiral whorls with axes directed medially (text-fig. 5).

Comparisons. It is difficult to compare *A. recurvirostra* adequately with the many other species described later (see list). With its rotund, longer-than-wide shell it seems distinct from other species, but the latter still need revision to determine variation. At the type locality *recurvirostra* is quite consistent in shape and small size, but Hall described the species *deflecta* from what may be the same locality. The type specimens of *deflecta* are lost. Many authors have confused *Z. modesta* with *A. recurvirostra*—the former occurs in much higher strata. In general, *Protozyga* characterizes Blackriveran or older Caradoc beds, *Anazyga* the Trentonian, and *Zygospira* the post-Trentonian. Bretsky (1970) suggested that *recurvirostra* had a



TEXT-FIG. 6. Serial sections of *Anazyga recurvirostra* (Hall, 1847), based on acetate peels. GS 45383, Shoreham Member, Sherman Falls Formation (Trenton Lst.), Roaring Brook, 1.3 miles east of Martinsburgh. Inset are umbonal views. Scale $\times 5$.

functional pedicle, but this seems unlikely in adult stages, which have hypercline beaks developed. He also suggested that the species, which he interpreted more broadly than here, was most common in Virginia and north-west Tennessee. However, it is locally abundant in New York and Ontario (Manitoulin Island area). In Ontario similar species occur in the Bobcaygeon, Verulam, and Lindsay Formations. A statistical comparison of rich material may reveal useful horizon indicators or possibly other geographical or ecological species or sub-species.

Genus ZYGATRYPA gen. nov.

Type species. *Zygospira paupera* Billings, 1866, p. 46 (first illustrations, Twenhofel 1928, pl. 21, figs. 21–22).

Range. Llandovery (especially late Llandovery). It must occur in earlier Llandovery strata if derived from *Zygospira*. Upper limit possibly Wenlock.

Distribution. Eastern North America.

Diagnosis. Small, carinate, ventribiconvex–planoconvex zygospirid shells. Fine, usually consistently sized ribs, postero-lateral shell flanks smooth. Minute pedicle

opening, anacline-hypercline beaks, small interarea, and deltidial plates. Commis-
sure sulcate. Internally, valves thick-shelled near hinge and under muscle scars,
pedicle constrictures, minute posterior dental cavity or dental nucleus expanded
anteriorly to strong teeth. Sockets in brachial valve firm, crural bases elongate,
ventro-vertically directed, then sharply laterally turned. Spiralia three to four whorls,
dorso-medially directed. Jugum simple, U-shaped, arising posteriorly and joining
posterior to spiral apices (text-fig. 7).

Species assigned.

Rhynchonella mica Billings, 1866 (p. 445, no figs.). Jupiter Formation, Zone 9 (Upper Llandovery),
Anticosti Island, Quebec, Canada (Twenhofel 1928, pl. 21, figs. 21-22). Plate 37, fig. 30.

?*Atrypa plicatula* Hall, 1843 (p. 71, fig. 4, see also Hall 1852, p. 74, pl. 23, fig. 9a-h). 'Calcareous Shale
at Reynale's basin, New York', U.S.A. (Hall *ibid.*). Requires revision.

?*Zygospira minima* Hall, 1879 (p. 14, see Hall 1882, p. 305, pl. 27, fig. 7). Waldron Shale (Wenlock),
Waldron, Indiana, U.S.A. If the assignment is correct, this would be the youngest *Zygatrypa*.

Comparisons. *Zygatrypa* is distinguished externally from *Zygospira*, its closest
relative, by its finer, even ribbing and its absence of ribs near the hinge line. Internally
it is distinct by its more massive teeth, smaller dental cavities or nuclei, thickening
sub-muscle field shell wall, crura emergent from the tips of socket plates (as compared
with medially in *Zygospira*), but especially by the nature of the spiralia and jugum.
The jugum of *Zygatrypa* is U-shaped, whereas in the older *Zygospira*, it is W-shaped
(compare text-figs. 3 and 5). In *Zygatrypa* the jugum appears near the hinge line
and in *Zygospira* it appears at mid-shell (Beecher and Schuchert 1893).

The Asiatic, later Silurian genus *Tuvaella* is much larger in size, has a long, straight
hinge, prominent cardinal process, and lacks dental cavities. The new genus *Zygatrypa*
spans part of the stratigraphical gap between youngest *Zygospira* and oldest *Tuvaella*

EXPLANATION OF PLATE 37

All figures $\times 2$, except fig. 21, $\times 4$.

Figs. 1-8. *Zygospira modesta* (Say in Hall 1847). 1-4, AMNH 1356a lectotype, ventral, dorsal, lateral,
and posterior views. 5-8, AMNH 1356c paralectotype, ventral, dorsal, lateral, posterior views. 'Hudson
River Group, Cincinnati, Ohio', U.S.A. (data on labels of fifteen syntypes). Ashgill.

Figs. 9-10. *Zygospira richmondensis* Caley, 1936. ROM 12448, holotype, ventral and dorsal views. 'Kaga-
wong Fm. Richmond[ian], High Falls, Manitoulin I.', Canada. Ashgill.

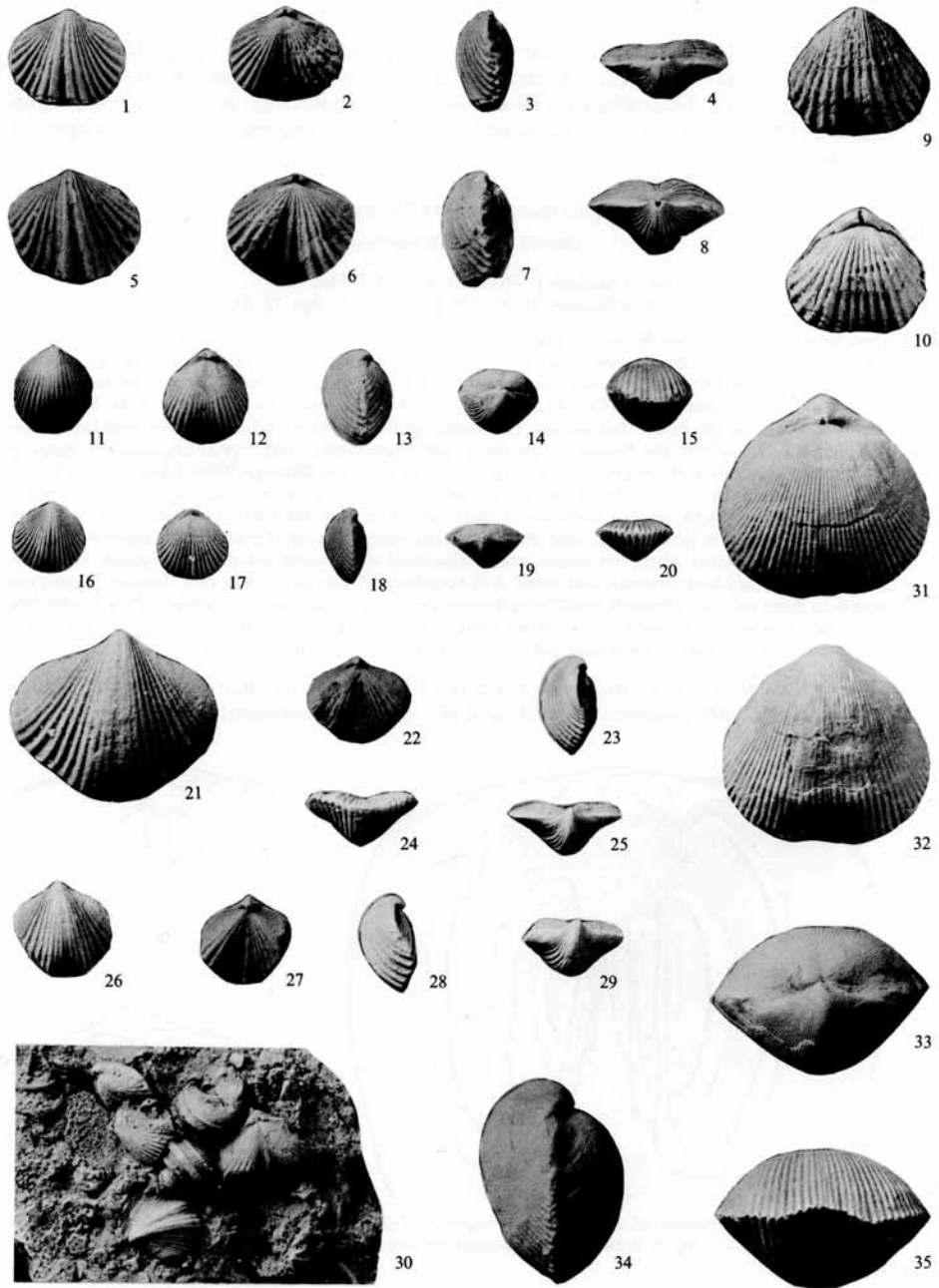
Figs. 11-15. *Anazyga recurvirostra* (Hall, 1847). AMNH 705.3 holotype, ventral, dorsal, lateral, posterior,
and anterior views. 'Trenton Lst., Martinsburgh, New York', U.S.A. Caradoc.

Figs. 16-20. ?*Anazyga tantilla* (Bradley, 1921). MCZ8547a lectotype (one of twelve syntypes), ventral,
dorsal, lateral, posterior, and anterior views. 'Lower Maquoketa, Clermont, Iowa', U.S.A. Ashgill.

Figs. 21-29. *Zygatrypa paupera* (Billings, 1866). 21-25, GS 2454a lectotype, ventral (enlarged $\times 4$),
dorsal, lateral, anterior, and posterior views. Note carination and rib absence postero-laterally. 26-29,
GB 2454b paralectotype, ventral, dorsal, lateral, and posterior views. Jupiter Formation (zones 6-7,
Twenhofel 1928), Anticosti Island, Canada. Llandovery (top).

Fig. 30. *Zygatrypa mica* (Billings, 1866). GS 2517a, lectotype (largest specimen) and three other syntypes
on small slab. Jupiter Formation (Zone 9, topmost), Anticosti Island. Llandovery. Distinguished from
older *Z. paupera* by double fold in brachial valve sulcus.

Figs. 31-35. *Catazyga headi headi* (Billings, 1862). Lectotype from Whiteaves Collection, RM 801a,
dorsal, ventral, posterior, lateral, and anterior views of the best preserved of four syntypes. 'Trois
Rivières, Quebec' (probably Pontgravé River Formation. Ashgill).



COPPER, Ordovician and Silurian Zygospiridae

and was possibly a transitional species group. In particular the jugum of *Zygatrypa* is more like that of *Tuvaella*. Boucot and Johnson (1967) suggested that *Zygospira paupera* may have been ancestral to *Coelospira* (a dayiacean), but this was based on material from California, not Anticosti, and is clearly incorrect. Dayiacean spiralia are like those of the athyridids.

Zygatrypa paupera (Billings, 1866)

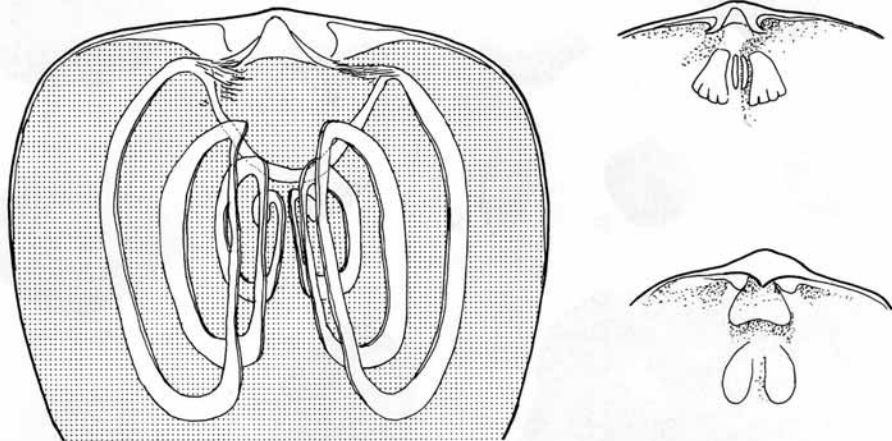
Plate 37, figs. 21-29; text-figs. 7-8

1866 *Zygospira paupera* Billings, p. 46 (Lectotype GS 2454a).

1928 *Zygospira paupera* Billings; Twenhofel, p. 214, pl. 21, figs. 18-20.

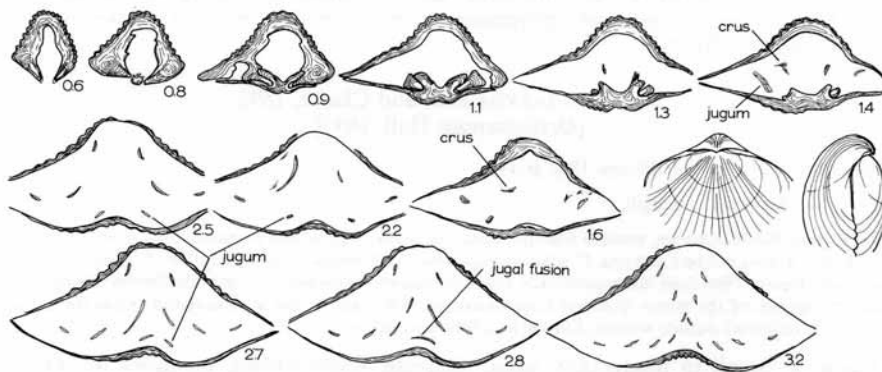
Type locality. 'Near Jupiter River' (Billings 1866), Anticosti Island, Quebec, Canada. From this it seems that the Richardson Collection, on which Billings founded the species, was not actually on the river but close to it. I have been unable to find it in outcrops along the Jupiter, but it was common on the road east of the Jupiter, at firetower no. 5 (NTS 12E/11W, 75180: 87940). The type horizon is 'Div. 3, A. G. J. Richardson' (ibid.). This is the Jupiter Formation. Twenhofel (1928, p. 214) remarked that he found the species in Zones 1, 6, 7, and 9 of the Jupiter Formation (Upper Llandovery), but it probably does not occur in the uppermost zones (8-9), where it is replaced by *Zygatrypa mica* (Billings 1866). I have not seen it in the basal zones of the Jupiter Formation. This leaves zones 6 and 7 as the restricted type strata. The lectotype is one of two syntypes in the Geological Survey (Canada) collections, selected by Twenhofel. GB2454a is the larger and better preserved of these two. The genus occurs in what is probably the equivalent of the *Stricklandia* community, since this pentamerid is abundant in the same few metres of strata. However, *Stricklandia* occurs here in nests, and where it is abundant, *Zygatrypa* is very rare. Instead, *Zygatrypa* occurs in more muddy, yellowish weathering horizons together with other atrypoids such as '*Gotatrypa*' sp. (most abundant), '*Clintonella anticostiana*' (next), and *Atrypopsis julia* (least common). Trilobites and ostracods are very common but stromatoporoids, corals, and bryozoans are absent.

Description. Small, 6-10 mm wide (average 7.0 mm), wider than long, nearly plano-convex shells with anacline-hypercline beaks, foramen commonly penetrating umbo.



TEXT-FIG. 7. Reconstruction of the spiralia and jugum in *Zygatrypa paupera* (Billings, 1866) based on text-fig. 8. Small cardinal process not shown. Scale approx. $\times 7$.

Apical angle 105° – 120° , interarea narrow, pedicle valve angular convex to almost carinate, brachial valve with deep sulcus dividing two convex halves. Ribs 20–24 in number, absent postero-laterally, especially on the brachial valve; rib pattern in general reveals thick, rarely bifurcating ventral mid-rib, flanked by 3–4 fine ribs, then 3–4 thick ribs, and 3 very faint ribs fading into smooth shell surface. Muscle scars not deeply incised, but raised above valve floor; triangular ventral adductor pad matched anteriorly by two obscure elongated diductor scars divided by a weak septum. The large brachial lateral adductors are shaped like footprints and flank two narrow, central adductors raised on the median septum (text-fig. 7). In serial sections, the pedicle valve shows small, round dental cavities forming the nucleus of simple, inwardly directed teeth. A small cardinal process caps the hinge plate. Diagonal crura fit into notches on the teeth and feather out to a solid U-shaped jugum and spirallium with about three whorls (text-fig. 8).



TEXT-FIG. 8. Serial sections of *Zygatrypa paupera* (Billings, 1866) based on acetate peels. GS 45374, Zones 6–7, Jupiter Formation, Anticosti Island, Canada (Upper Llandovery); NTS Jupiter River 75140:87850. Inset are umbonal views. Scale $\times 5$.

Remarks. The species can be distinguished from younger *Z. mica*, also described by Billings (1866) from Anticosti Island, by the single, angular crest on the pedicle valve in *paupera* against a double crest in *mica*. *Z. mica* appears to be a very scarce element in the uppermost part of the Jupiter Formation on Anticosti Island. Bolton (1972, pl. 8, figs. 15–17, 20) figured a '*Zygospira*' *jupiterensis* from the underlying Gun River Formation. This species can now be assigned to *Atrypina*, and is not a zygospirid. *Zygatrypa* has not been found in the earlier Llandovery strata on Anticosti Island (Gun River, Becscie Formations).

Subfamily CATAZYGINAE subfam. nov.

The *Catazyga* group of Ordovician–Silurian atrypoids include two genera with first appearances in late Ordovician time (late Caradoc), and a decline in post-Ordovician time to eventual extinction by the close of the Llandovery. Included in

the group are the type genus *Catazyga* and also *Pentlandella*. Excluded are *Alispira* Nikiforova, 1961, *Clintonella* Hall and Clarke, 1893, *Nalivkinia* Bublichenko, 1928, and *Anabaria* Lopushinskaya, 1965. The Catazyginae are defined as small to moderately sized atrypoids with uninterrupted tubular ribs, lack of carination, and weak anterior folds and generally biconvex-ventribiconvex shells with small interareas hidden by incurved swollen beaks. Internally they possess a posteriorly located single jugum, and have a modest set of spiral whorls directed dorso-medially. Crura tend to be solidly supported on thick socket plates. Dental cavities are normally absent, but a hidden or weak ventral septum is present; the catazyginids are unusual in their relatively massive deposits along the pedicle cavity and hinge plate.

Nikiforova (in press) has discovered a large late Ordovician atrypoid in Central Asia (Shakhriomon area) which she believes may be a coarsely ribbed catazyginid. The internal structures are as yet undescribed but material available to me shows an atrypoid with distinctive wide interarea, large foramen, and weak carination that may be a large *Zygospira* or spirigerininid; it is not one of the *Catazyga* group (see Pl. 39, figs. 20-23).

Genus CATAZYGA Hall and Clarke, 1893
[*Orthonomaea* Hall, 1893]

Type species. *Athyris headi* Billings, 1862, p. 147.

Range. Late Caradoc to Ashgill.

Distribution. North America, western Europe; *Catazyga salairica jacutensis* Rozman, 1968 from the north-east U.S.S.R. may not be *Catazyga*. *C. salairica* Severgina, 1960 needs to be investigated. *C. homeospiroides* Ross and Dutro, 1966 does not superficially resemble known catazygids. *C. rara* Nikiforova has become the type species of the genus *Arabaria* Lopushinskaya, 1965, and is not a catazyginid. Thus the genus is not yet confirmed outside western Europe and North America.

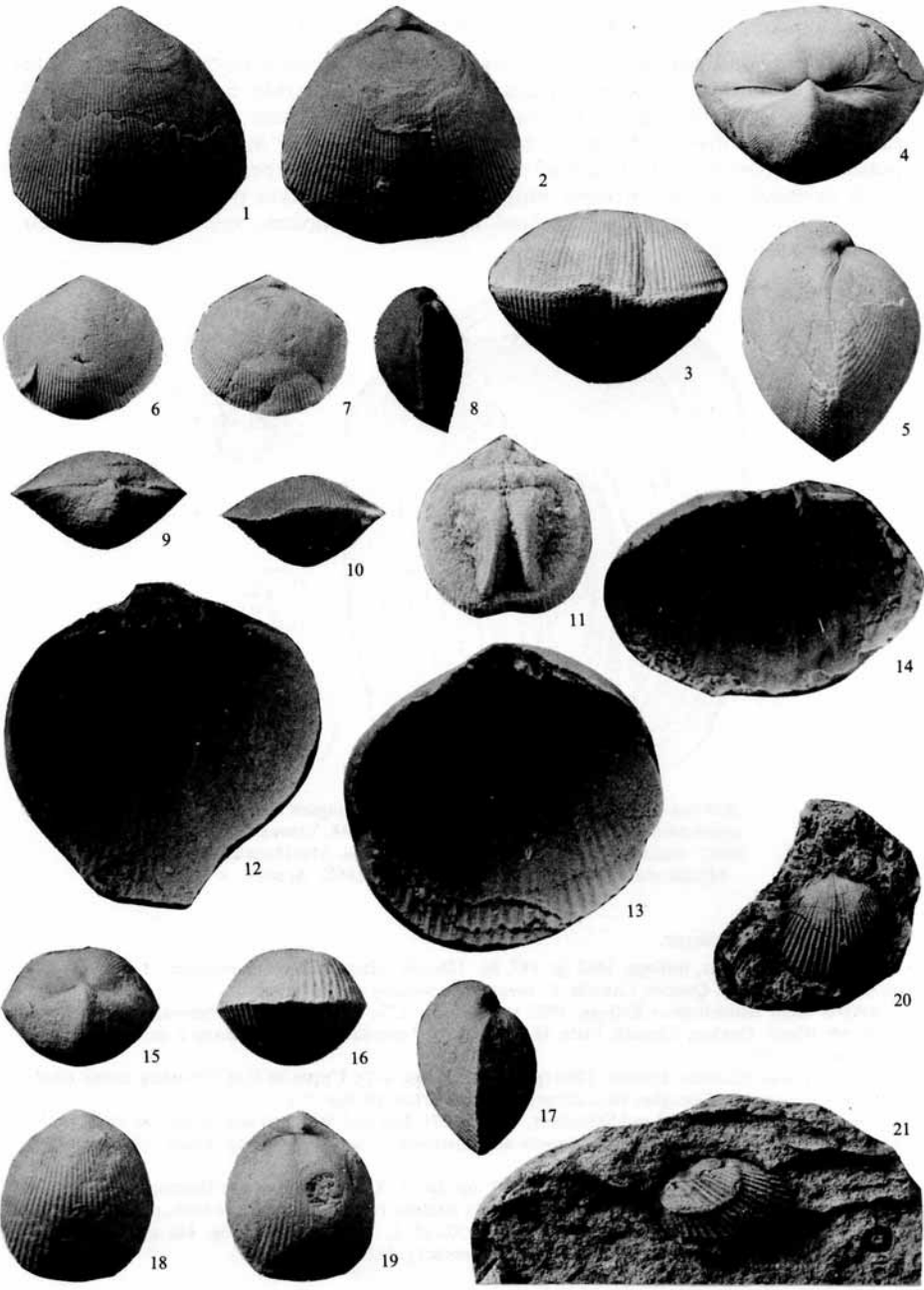
Diagnosis. Small to moderately sized, elongate, finely ribbed, biconvex to ventribiconvex, weakly folded zygospirids with anacline-hypercline beaks covering a minute pedicle opening and deltidial plates (normally not visible). Internally, the

EXPLANATION OF PLATE 38

All figures $\times 2$, except figs. 12-14, $\times 4$.

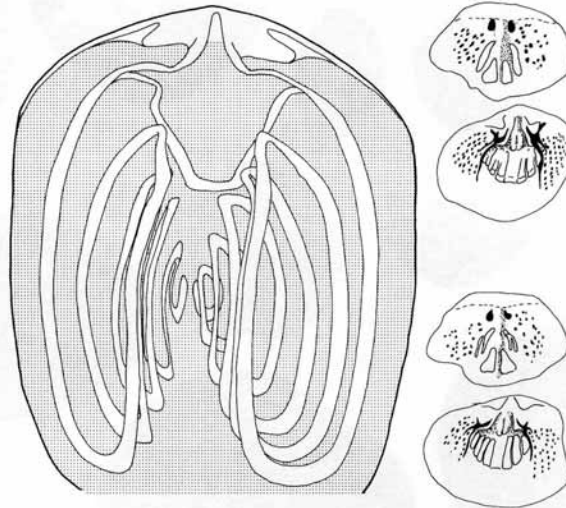
Figs. 1-14. *Catazyga headi headi* (Billings, 1862). 1-5, GS 45385 hypotype, ventral, dorsal, anterior, posterior, and lateral views of large adult specimen with minor growth deformity along sulcus. 6-10, GS 45392 hypotype, ventral, dorsal, lateral, posterior, and anterior views of immature specimen. 11, GS 45401 hypotype, calcined, decorticated mature specimen to show ventral view of the inner spirallial whorls. 12, GS 45393, latex mould of brachial valve interior showing muscle field. 13, GS 45391, latex mould of pedicle valve interior. 14, GS 45384, latex mould of pedicle valve interior showing irregularly emplaced muscle field. All material Pontgravé River Formation, Bécancour (restricted type loc.), Quebec, Canada. Ashgill.

Figs. 15-19. *Catazyga anticostiensis* (Billings, 1862). GS 2038j, lectotype (one of fifteen syntypes) from Billings's Collection. Probably from 'Hudson River Fm., English Head, Anticosti I.', and mislabelled in present collection. This material is very similar to other Anticosti material from the Vaureal Formation. Figs. 20-21. *Catazyga hicksi* (Reed, 1905). 20, A30861 paralectotype, internal mould of brachial valve. 21, A30862 lectotype, internal mould of pedicle valve. Cuckoo Grove Lane, Haverfordwest, Wales. Slade and Redhill Formation (Ashgill).



COPPER, Ordovician and Silurian Zygospiridae

pedicle cavity and muscle field is deeply incised and contains thick irregular calcite deposits; small teeth in socket cavities have a massive centrally directed base, dental cavities absent or elongated horizontally. Ventral adductor muscle field broad, subrectangular, divided by weak median ridge; diductor area narrow, tapering posteriorly, poorly defined; dorsal adductors elongate, narrow. Dorsal valve with small cardinal process on thick hinge plates, strong socket plates support small crura. Posteriorly located jugum bent towards cone apices; spiralia three to ten whorls (text-fig. 9).



TEXT-FIG. 9. Reconstruction of the spiralia and jugum in *Catazyga anticostiensis* (Billings, 1862) based on GS 45394, Vaureal Formation; Anticosti Island, Canada, Loc. BF254 MacDonald Rd. Muscle-scar drawings of *C. headi* (Billings, 1862). Approx. $\times 7$.

Species assigned to Catazyga.

Athyris headi borealis, Billings, 1862 (p. 147, fig. 126a-b). 'Hudson River Formation', Lake St. John, on the river Saguenay, Quebec, Canada. *C. borealis* is probably a valid species.

Athyris headi anticostiensis Billings, 1862 (p. 147, fig. 127a-b). Vaureal Formation, English Head, Anticosti Island, Quebec, Canada, Plate 38, figs. 15-19. I consider *C. anticostiensis* a valid species (see Pl. 38, figs. 15-19).

Catazyga headi filistriata Sproule, 1936 (p. 108, pl. 7, figs. 4-7). Upper 30 ft of 'Cobourg strata' (ibid., Lindsay Formation?), Georgian Bay, Ontario, Canada, Plate 39, figs. 1-2.

Zygospira uphami Winchell and Schuchert, 1892 (p. 291, first figs. Winchell and Schuchert, 1895, pl. 34, figs. 45-48). 'Middle of the Galena horizon at Weisbach's Dam near Spring Valley' (ibid., p. 469), Minnesota, U.S.A.

Orthis erratica Hall, 1847 (pp. 288-289, pl. 79, fig. 5a-f). 'Central part of the Hudson River Group' (ibid.), Washingtonville, New York, U.S.A. (Pulaski member of Lorraine, Foerste 1916, p. 37.)

Catazyga uphami australis Foerste, 1909 (pp. 31-32, pl. 2, fig. 19a-b; pl. 3, fig. 14a-c). High Bridge Formation, Camp Nelson member, High Bridge, Kentucky, U.S.A.

Glassia schuchertana Ulrich, 1888 (pp. 186–187, for figs. see Foerste 1909, pp. 32–35, pl. 2, fig. 3; pl. 3, fig. 11a–c). Waynesville Bed (upper part), Hitz Road, Madison, Indiana, U.S.A.

Catazyga cartieri Cooper and Kindle, 1936 (pp. 359–361, pl. 52, figs. 8–13, 18). Whitehead Formation, north-west Percé, Gaspé Peninsula, Quebec, Canada.

Catazyga arcana Williams, 1962 (pp. 247–248, pl. 25, figs. 20–23, 27–28). Kiln Mudstones, Craighead, Girvan, Scotland.

Atrypa headi var. *anglica* Davidson, 1867 (pl. 22, figs. 1–7). Caradoc. Grangegeeth, Ireland.

Species requiring confirmation.

Catazyga homeospiroides Ross and Dutro, 1966 (pp. 8–9, pl. 1, figs. 7, 9–10, 15, 17–20). Thin bedded, shelly limestone unit, Jones Ridge, Charley River, Alaska, U.S.A. Authors state possibility of a distinct genus.

Orthis? sectostriata Ulrich, 1879 (p. 15, pl. 7, figs. 11, 11a–b). Hudson River Group, 300–375 ft above low-water mark in the Ohio River, Cincinnati, Ohio, U.S.A.

Catazyga salairica jacutensis Rozman, 1968 (p. 73, pl. 62, figs. 6–8). Nalchanskaya Suite (late Ordovician), Sakyndani River basin, north-east U.S.S.R.

Catazyga salairica Severgina, 1960. I have been unable to see the original reference.

Zygospira hicksi Reed, 1905 (p. 452, pl. 23, figs. 17–19). Cuckoo Grove Lane, Haverfordwest, Wales, Slade Beds, Ashgillian (A30861–30862, Sedgwick Museum). Plate 38, figs. 20–21.

Comparisons. *Catazyga* is distinguished from Silurian *Pentlandella* externally by its elongate shape, narrower apical angle, and usually larger shells and internally by its muscle field in both valves (raised, arrow-shaped ventral platform in *Pentlandella*), and bulbous socket plates. Some *Catazyga*, but not all, have dental cavities (e.g. the type species has cavities but *C. borealis* (Billings, 1862) does not. The broad-crested, narrow-troughed ribs of *Catazyga* may be a distinct generic feature. For internal distinctions compare text-figs. 9 and 12, 10–11, and 13.

Catazyga headi (Billings, 1862)

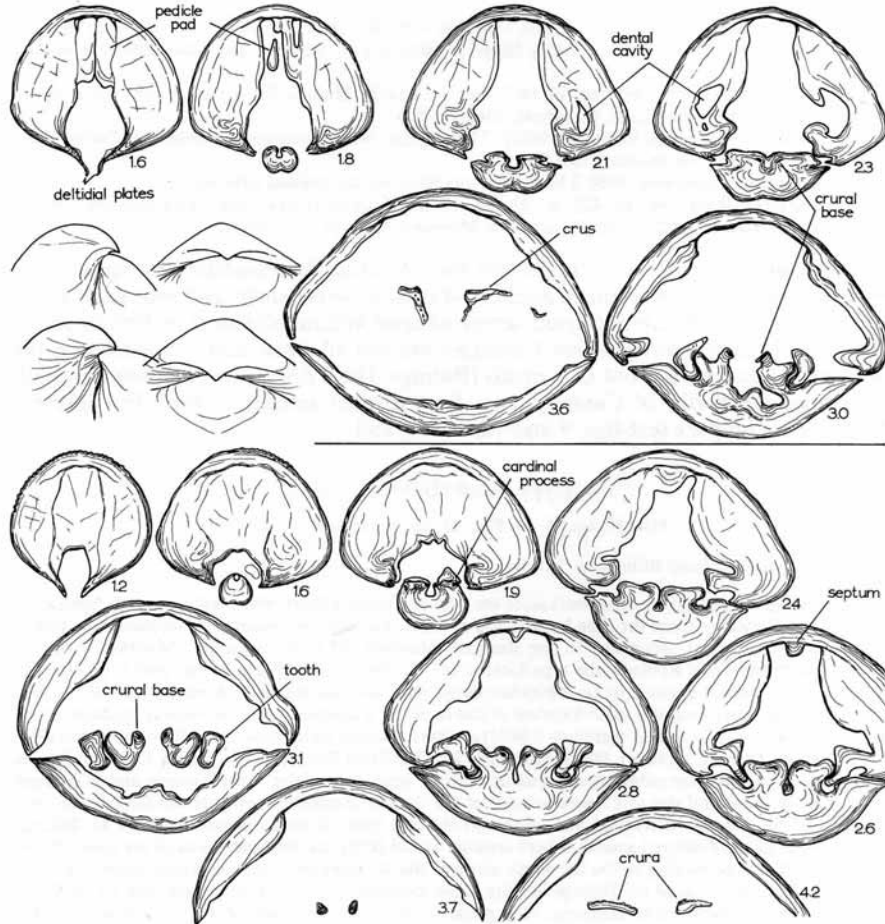
Plate 37, figs. 31–35; Plate 38, figs. 1–14; text-figs. 10–11

1862 *Athyris headi* Billings, p. 147, fig. 125.

Types. Holotype or syntypes lost, at least since the time of Foerste (1909), who mentioned that 'specimens collected by Whiteaves from the type locality are at hand, and may be regarded as replacing the types'. Whiteaves donated four specimens to the Redpath Museum (McGill University, Montreal RM801), which are labelled Trois Rivières, the type locality (Pl. 37, figs. 31–35). None of the four is identical to Billings's figure, which appears to be somewhat larger than life size (width = 19 mm). None of the four is ideal as a neotype, since the exact location of the material is unknown, but Whiteaves probably knew the type locality first hand and therefore RM801a is here selected as neotype. In collections of the Geological Survey, Ottawa, there are fifteen specimens labelled Trois Rivières, collected by J. Richardson in 1856. These specimens are substantially smaller than *C. headi headi* from Trois Rivières and Bécancour and similar in shape and size to *C. anticostiensis* of the Vaureal Formation on Anticosti Island. It is concluded that this suite is mislabelled and represents the lost types of *anticostiensis* described by Billings. The lectotype of the Anticosti species is here selected as GS 2038j, the best preserved of the suite (Pl. 38, figs. 15–19). The type locality is 'On the south shore of the St. Lawrence opposite Three Rivers' (Billings 1862). The exact location of the Billings locality is not possible to trace. Directly opposite Three Rivers at the present time there are no outcrops, only glacial erratics. At the Nicolet River section, some 14 km south of Trois Rivières, the 'gully section' of Foerste (1916, p. 18) probably contains the stratigraphically equivalent horizons (Pontgravé River Formation) with *C. headi headi*, but at present the gully section is not exposed. *C. headi headi* occurs abundantly at Bécancour, about 8 km north of Trois Rivières and a suitable restricted type locality may be NTS Bécancour 3118/W 01450:38880. The type horizon is 'Hudson River formation' (Billings 1862). The Nicolet River section equivalent is probably zones S and T of Foerste

(1916, pp. 18–19) which are in the Pontgravé River Formation ('Richmond'). The Bécancour material is in the same horizon.

Dr. Yvon Globensky, who kindly provided me with a large collection of specimens from Bécancour remarks that the *Catazyga* occur in limestone beds, interstratified with grey, sandy shales. At this locality *C. headi* occurs near the base of the Pontgravé above the Carmel River member. Associated with the atrypoids are solitary rugose corals, *Strophomena* and *Sowerbyella*. The *Catazyga* substrate during life was probably a soft calcareous mud, with specimens orientated beak-down, more due to thicker calcite



TEXT-FIGS. 10–11. Serial sections of two specimens of *Catazyga headi* (Billings, 1862) from Bécancour, Quebec, Canada (near Trois Rivières), NTS Bécancour 01450:38880. Top GS 45398; bottom GS 45397. Note the variation in pedicle deposits, typical of many later atrypoids. External views of the umbonal region are inset. Scale $\times 5$.

deposition in the umbonal region, than to anchoring. Sectioned specimens frequently show muddy infilling posteriorly and vugs or drusy calcite anteriorly.

Diagnosis. Medium sized to large, globose *Catazyga* with maximum width at mid-length, hypercline beaks, foramen and area obscured at maturity. Pedicle valve more convex than brachial valve, often with weak narrow anterior brachial valve sulcus and broad pedicle valve fold (over all weakly uniplicate). Internally distinctive muscle fields, thick pedicle callosities, small outwardly extended deltidial plates, dental cavities horizontally elongated, teeth massive, lacking accessory lobes, cardinal process irregular, bulky; crura thick. Spiralia-jugum unstudied. Spiridium reconstruction based on *C. anticostiensis* (text-fig. 9).

Description (based on Bécancour locality). Shells average width, peaks at 14 mm, maximum 19 mm, depth peaking at 9 mm, mostly longer than wide (text-fig. 6), apical angles 105–110° (average 108°). Pedicle area covered by beak in very early growth stages, before shell is 10 mm wide; sometimes pedicle opening expanded as slit in umbo. Ribs very fine posteriorly (at 5 mm, 25–30 ribs per 5-mm arc) but at 20 mm from umbo coarsening to 8–11 ribs per 5-mm arc; ribs round-broad crested and narrow-troughed. Brachial valve less convex but well-rounded; both valves usually sulcate with the pedicle valve having broad, flat sulcus. The adductor muscle fields are quite variable. The ventral adductor pad occupies about a quarter of the shell length, is wider than long, rectangular to rounded, and frequently skew or irregular; medially it is divided by a broad, low septum and laterally each side has three to four grooved lobes (usually three). The ventral diductors appear to be raised on two rounded irregular lobes, fusing posteriorly and sometimes raised off the shell floor. These structures may represent pedicle muscle callosity, and if that is the case the diductors possibly are located between the pedicle callosity and the adductor field. The dorsal muscle field is difficult to interpret. Adductors are in the form of two pairs, a posterior bean-shaped pair and an antero-medial pear-shaped pair divided by a rounded median septum. Closer to the hinge plate are one to three pairs of small depressions of unknown origin, possibly accessory diductors (text-fig. 9).

The serial sections illustrated (text-figs. 10–11) are largely self-explanatory. Most striking are the thick pedicle cavity linings (squared in outline) and massive hinge plates generally lacking in zygospirids. The axis of the dental cavity is dorso-anteriorly ventral posteriorly and horizontal anteriorly; teeth are simple stumps, free anteriorly. The pedicle opening is either hidden or sometimes expanded into the ventral umbo as a minute, narrow slit; deltidial plates are pointed dorsally rather than medially. A cardinal process is present in the form of thick irregular outgrowths capping the ends of the socket plate, expanding well into the pedicle cavity; the groove between the socket plates is narrow and slit-like. The crura arise from a point source hidden deep within the hinge plate, and are rounded in cross-section; anteriorly they stand free as thin, raised ridges and then direct themselves ventrally and sharply laterally. Further brachidial structures still unknown (see reconstruction of complete *C. anticostiensis* in text-fig. 9).

Remarks. *C. headi*, like all *Catazyga*, had a small functioning pedicle or loss of pedicle in maturity. Epifauna was very scarce on the shells examined, and where found, consisted of small serpulids (*Cornulites?*) and *Hederella* normally located

on the anterior central part of the pedicle valve. The probable mode of life of *Catazyga* was with the umbo down and shell vertical or angled with the pedicle valve uppermost, considering the evidence of epifauna, thick shell callosities posteriorly, and the usual posterior mud infilling of the shell after death. Slabs of *C. anticostiensis* which contain large numbers of presumably death-orientated shells show a prevailing umbo-down position; clusters of the same *Catazyga* show orientation towards a common point of fixation, and possibly indicate a thin, thread-like pedicle.

The species of *Catazyga* at present are no more useful as stratigraphic indicators than mentioned by Foerste in 1924 (pp. 129–130). According to Foerste (1916) *C. erratica* precedes *C. headi* in the Quebec–Ontario sequences. In Ontario, *C. filistriata* in turn appears to precede *C. erratica* and possibly the oldest *Catazyga* is *C. uphami* from Minnesota. If this sequence is correct, then no distinctive external trends are present in the *Catazyga* lineage, except possibly increasing size. Shape, convexity, and structure of the anterior commissure were random developments at different times and in different places. Lineages of *Catazyga*, which was a deeper quiet-water inhabitant, are rarely continuous in contiguous sections, and thus reflect water-depth variability and fluctuations in different regions. Such changes will be calculated when more data is available on over-all distribution. *C. headi* is not sufficiently distinct externally from *C. erratica* to warrant the separate genus *Orthonomaea* Hall, 1893 for the latter. The species of *Catazyga* also are not sufficiently well known to split off a new genus on the presence or absence of dental cavities (or ‘dental plates’), as with other Palaeozoic atrypoids.

EXPLANATION OF PLATE 39

All figures $\times 2$, except fig. 7, $\times 4$.

Figs. 1–2. *Catazyga filistriata* Sproule, 1936. ROM39a lectotype (one of six syntypes), ventral and dorsal views. ‘Upper 30 ft. of Cobourg strata’ (below Collingwood Black Shale). Locality unknown, possibly old quarry at Bowmanville (Sproule 1936, p. 99), Canada. Caradoc.

Figs. 3–7. *Pentlandella tenuistriata* Rubel, 1970. 3–6, GS 45395 hypotype, ventral, dorsal, lateral, and posterior views of adult specimen. 7, GS 45394, interior view of pedicle valve enlarged ($\times 4$) to show the arrow-shaped muscle field. Latikula, Estonia, U.S.S.R.; Adavere Formation. Upper Llandovery.

Figs. 8–12. *Pentlandella pentlandica* (Haswell, 1865). 8, BMNH 12630a hypotype, latex mould of external of pedicle valve. 9, BMNH 12730b, hypotype, latex mould, internal view of pedicle valve. 10, BMNH 12730c hypotype, latex mould, internal view of brachial valve. Pentland Hills, Scotland, Bed D, Esk section. Upper Llandovery. 11, BMNH 12632a, latex mould, internal view of pedicle valve. 12, BMNH 12632b, latex mould, internal view of brachial valve. Same horizon and locality.

Figs. 13–15. *Pentlandella haswelli* (Reed, 1908). 13, A32775b paralectotype, latex mould of internal of brachial valve. 14, A32271 lectotype, latex mould of internal of pedicle valve showing muscle field in hatchet-shape more comparable to *Catazyga*. 15, A32275a paralectotype, latex mould, external of pedicle valve. ‘The Frolic, Haverfordwest’, Dyfed, Wales. Lower Llandovery.

Figs. 16–19. *Tuvaella rackovskii* Chernyshev, 1937. GS 45393 hypotype, ventral, lateral, dorsal, and posterior views of adult specimen. Elegest River, Tuva, U.S.S.R. Wenlock. (See Vladimirskaia 1973.)

Figs. 20–23. Undescribed genus (Nikiforova, in press). GS 45396, hypotype, lateral, posterior, dorsal, and ventral views of adult specimen. Khrebt Shakhriomon, central Asiatic U.S.S.R., Ordovician O₃ (Ashgill). Affinities of this taxon are still unclear—may be ancestral to *Tuvaella*, or possibly a spirigerinid.



COPPER, Ordovician and Silurian Zygospiridae

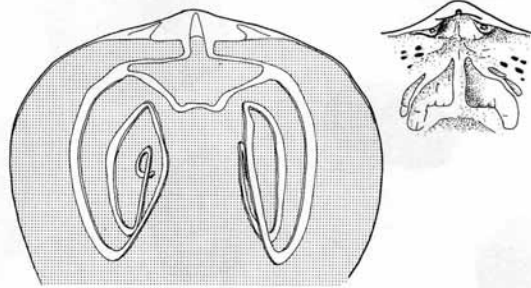
Genus PENTLANDELLA Boucot, 1964

Type species. *Rhynconella pentlandicus* Haswell, 1865 [sic], p. 31, pl. 3, figs. 9-10. (See Pl. 39, figs. 8-12.)

Range. Llandovery.

Distribution. Scotland, Wales, and Estonia.

Diagnosis. Small, globose, ventribiconvex, finely ribbed shells with hypercline beaks, minute foramina, and weak fold-sulcus. Ribs have micro-growth lines but no major interruptions; apically ribs are very faint to absent. Internally, the pedicle valve is thickened posteriorly; the brachial valve is also strong. Groove for ventral adductor and diverging diductors implanted into raised median septum. Dorsal muscle field flabellate, also divided by septum. No dental cavities or nuclei, teeth have wide bases, pointed extremities. Cardinal process apparently absent. Crura bases ball-like, thin crura rapidly spread laterally from crural bases. Jugum posteriorly located, joined almost at first spiral whorl, shaped like flattened W, or U with square corners. Spiralia with three to four whorls medially and medio-dorsally directed (text-fig. 12).



TEXT-FIG. 12. Reconstruction of spiralia and jugum in *Pentlandella tenuistriata* Rubel, 1970, based on text-fig. 13. Approx. $\times 7$.

Species assigned.

In addition to the type species, only two other species appear to be known:

Zygospira haswelli Reed, 1908 (pp. 434-435, pl. 14, figs. 4-9). Haverford Mudstone Formation (Lower Llandovery), 'Locality K, below the path SW. of Uzmaston Farm', Wales (label on lectotype A32771, Sedgwick Museum). Plate 39, figs. 13-15.

Pentlandella tenuistriata Rubel, 1970 (pp. 27-28, pl. 17, figs. 1-24). Adavere Horizon, Estonia, U.S.S.R. (Upper Llandovery), figured by Rosenstein 1941, p. 6, fig. 74a incorrectly as '*Catazyga furcata*' (Sowerby, 1839); the Sowerby species is not atrypoid.

Comparison. *Catazyga* is the most similar atrypoid genus, but differs in its muscle field and septal structures, simpler jugum and larger spiralia, and in its massive, bulbous tissue surrounding the crural bases. As the last-surviving catazyginid, ranging into late Llandovery time, and maybe the Wenlock, *Pentlandella* is not a widespread genus. It appears in Estonia to be a deeper-water inhabitant, like Ordovician *Catazyga*, which may explain its rarity in the Llandovery of Wales and

the Welsh Borderland. The genus is absent in richly fossiliferous Llandovery rocks of Anticosti Island, and those of the Siberian Platform, suggesting a provincial distribution. It is possible that the raised muscle areas of *Pentlandella* represent a trend towards a septally elevated muscle field such as in the mid-Devonian *Gruenewaldtia*. However, there are no connecting taxa, and raised muscle fields were independently developed in other different atrypoid lineages. The older *P. haswelli* has a hatchet-shaped ventral muscle field, becoming arrow-shaped in *P. pentlandica*.

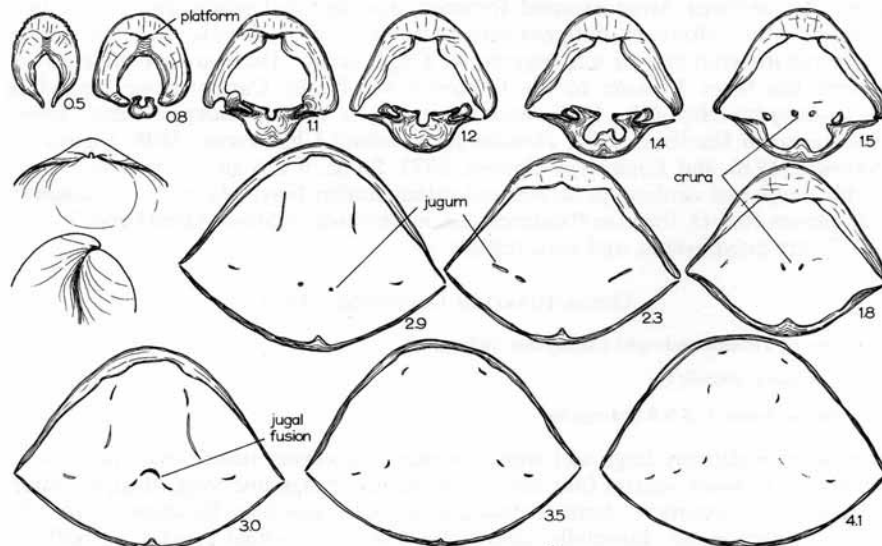
Pentlandella tenuistriata Rubel, 1970

Plate 39, figs. 3-7; text-figs. 12-13

Remarks. Rubel (1970) has well illustrated the external features of the Estonian species. Detailed internal serial sections, however, have not previously been available. Material for sectioning was made available to me by Dr. Rubel. The sections can now be compared adequately with those of *Catazyga* and other zygospirids (text-fig. 13). Note especially the thickened posterior shell wall portions, crura, and spiralia.

Subfamily TUVSELLINAE Alikhova, 1960 (emend.)

Vladimirskaia (1972) pointed out that *Tuvaella* had dorsally directed spiralia and would be more correctly placed in the Zygospiridae amongst the atrypoids, instead



TEXT-FIG. 13. Serial sections of *Pentlandella tenuistriata* Rubel, 1970 based on acetate peels. GS 45381, Adavere Horizon (Upper Llandovery); Latikula, Estonia, U.S.S.R. The type species of *Pentlandella* and related British species are preserved as moulds and unsuitable for sectioning. Scale $\times 5$.

of in the Orthacea. Alikhova (1960) had erected a special family, with a single genus, in the Orthacea to account for its peculiar morphology. Through the kindness of Dr. Vladimirskaia, who presented me with a suite of specimens, I was able to examine well-preserved specimens of *Tuvaella* from Tuva in the Asiatic U.S.S.R. This has led to a slightly revised diagnosis and some new discoveries.

The Tuvaellinae are unique in their stratigraphical distribution in rocks of latest Llandovery through Ludlow age. In addition to their size, and flattened dimensions, making them the largest known zygospirids, the Tuvaellinae are distinctive in several respects: they possess wide, flat interareas, a massive cardinal process and very thick hinge plates, and a dorsal jugum which comes to a blade-like, ventrally directed point between the spiral cones. They also differ from Zygospirinae by their lack of dental cavities or nuclei. They belong clearly to the Zygospiridae on two counts: firstly, their jugum is dorsal to the spiralia (as against ventral in all other atrypoid stocks), and secondly, the jugum is one piece (as opposed to two separated processes; see text-fig. 14). Otherwise, externally *Tuvaella* itself has a strong resemblance to the *Carinatina* group of the Devonian. It may have evolved independently in that direction, but other ancestors for the Carinatinae lie more in the range of *Neospirigerina* Rzhonsnitskaya, 1975.

A possible ancestor to the Tuvaellidae may be an undescribed genus (Nikiforova, in press; see Pl. 39, figs. 20–23) from late Ordovician rocks of central Asia (Shakhriom area). Poorly preserved material given to me by Dr. Nikiforova reveals a coarsely ribbed, large, weakly carinate, zygospirid shell, possessing a clear, relatively wide shelf-like interarea, large exposed foramen, and deltidial plates and orthocline-anacline beak. However, internal structures are still unknown, and the poorly preserved material may be a *Spirigerina* or *Eospirigerina*. There are probable phylogenetic ties from *Tuvaella* to the Devonian sub-family Carinatinae, including *Biconostrophia* Havlíček, 1956 (and its synonym *Davidsoniatrypa* Lenz, 1968), *Prodauidsonia* Havlíček, 1956, *Davidsonia* Bouchard-Chantereux, 1849, *Carinatina* Nalivkin, 1930, and *Eifelatrypa* Copper, 1973. Some, if not all, of these taxa have highly developed cardinal processes and rather similar hinge plates. If this assumption proves correct, then the Palaferellidae, in the sense of Struve (1961) and Copper (1973), are polyphyletic, and need restudy.

Genus TUAELLA Chernyshev, 1937

Type species. *Tuvaella rackovskii* Chernyshev, 1937, p. 12.

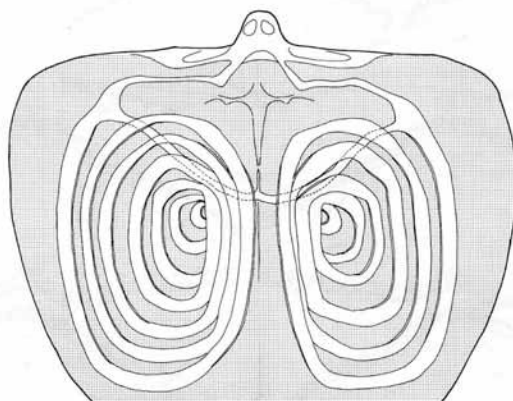
Range. Wenlock–Pridoli(?).

Distribution. Asiatic U.S.S.R., Mongolia.

Diagnosis. Relatively large and wide, coarsely and evenly ribbed zygospirids with somewhat carinate ventral fold and dorsal sulcus. Hinge line long, straight; interarea wide and extensive; beaks orthocline to partly anacline; foramen covered by thick deltidial plates. Internally solid teeth, a strong cardinal process, dorsally to medio-dorsally directed spiralia, and a jugum arising posteriorly with a central spine-like meeting point are characteristic of at least the type species (internals of other species not known).

Tuvaella rackovskii Chernyshev, 1937

Plate 39, figs. 16-19; text-figs. 14-15

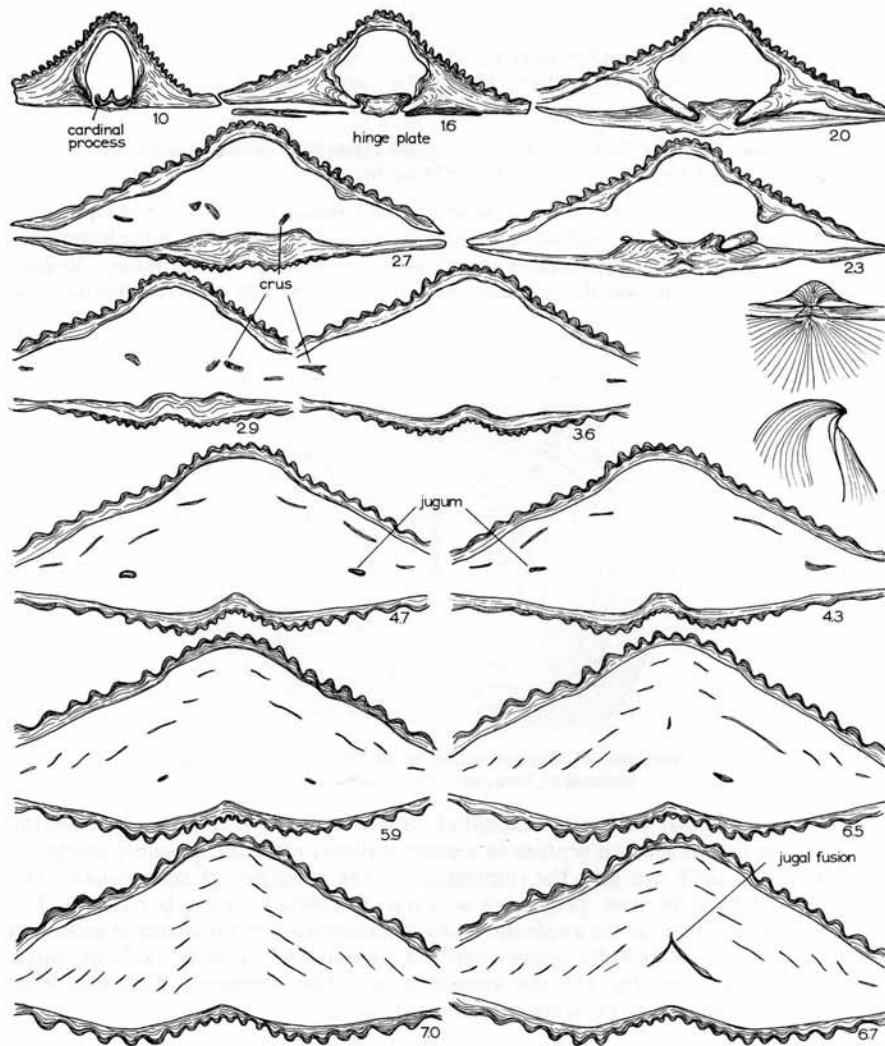
1937 *Tuvaella rackovskii* Chernyshev, pp. 12, 64, pl. 1, figs. 8-11.1972 *Tuvaella rackovskii* Chernyshev; Vladimirskaia, pp. 39-42, pl. 6, figs. 1-14.*Range.* Llandovery-?Wenlock or Ludlow.*Distribution.* Altai Mountains, Tuva, western Sayan, eastern Transbaikal, and north-east U.S.S.R. (Amur region), Mongolia. Not known outside U.S.S.R. and Mongolia.*Remarks.* Vladimirskaia (1972) provided the first detailed internal description of the type species of *Tuvaella*, including serial sections and photographs of the brachidia. Differential, partial recrystallization of the shells permitted Vladimirskaia to etch specimens to bring out specific features. At the same time this recrystallization alsoTEXT-FIG. 14. Reconstruction of the brachidia in *Tuvaella rackovskii* Chernyshev, 1937 based on text-fig. 15.

obscured the original shell and brachidial structure. I was unable to discover the canals in the dorsal median septum in unrecrystallized material: possibly recrystallization of the shell can give the impression of the existence of such canals. The enormous cardinal process, projecting well into the pedicle cavity is unusual. The crura do not geniculate at the angle shown by Vladimirskaia in the material sectioned by me. The jugum is broadly convex and not angular and projects medially into a remarkable blade (text-fig. 15), not known in any other atrypoids. This may have held mouth parts, or less possibly muscle structures.

Family ATRYPIDAE Gill, 1951

Subfamily CLINTONELLINAE Poulsen, 1943

Shells characteristic of this subfamily are biconvex, tubular-ribbed, usually non-carinate, non-lamellose, thin-walled, and with a narrow interarea, small beak, and



TEXT-FIG. 15. Serial sections of *Tuvaella rackovskii* Chernyshev, 1937 based on acetate peels. GS 45377, Wenlock; Elegest River, Tuva, U.S.S.R. Inset shows the pedicle structure. Scale $\times 5$.

small deltidial plates. Internally the group has relatively large dental cavities, thin hinge plates, delicate narrow crura, separated ventrally located jugal processes, and dorsally directed spiralia. This subfamily has characteristics similar to those of Devonian *Desquamatia*. Nikiforova and Modzalevskaya (1968) placed *Nalivkinia* (*Anabaria*), alongside *Alispira*, in the family Atrypidae, without special subfamily designation. Lopushinskaya (1965) assigned it to the Clintonellinae. Kulkov (1967) thought that *Nalivkinia* was related to the Karpinskiinae via *Eokarpinskia* Rzhonsnitskaya, 1964, and later referred it to the Atrypinae (Kulkov 1974). In 1973 I allocated *Nalivkinia* to the Atrypidae (erratum under Zygospiridae, p. 488) and *Alispira* and *Clintonella* to the Zygospiridae. Work on serial section internals convinces me that Lopushinskaya's interpretation is substantially correct, that is the Clintonellinae form a genus group including *Clintonella*, *Alispira*, and *Nalivkinia*. These are still believed to have evolved independently from the main *Atrypa* group as shown in Copper (1973). Because of the lack of brachidial data on the three clintonellinid genera, I am hesitant about suggesting other affinities. Possibly some of the Palaferellidae, like *Gracianella* and *Eokarpinskia*, are related to *Nalivkinia* (*Anabaria*). Alternatively affinities with Devonian *Desquamatia* or *Carinatinella* are suggested in morphology of the dental cavities and brachidia. The Clintonellinids lack the thicker, more massive shells of the palaferellids and their reinforced jugal processes, but may have moved in that direction by changing habitats from quieter marine to the higher-energy reef areas favoured by many palaferellids.

Genus NALIVKINIA Bublichenko, 1927

Type species. *Atrypa grünewaldtiaeformis* Peetz, 1901, pp. 147-148, 376, pl. 4, fig. 2a-c from the Sarachumysk River, Kuznetsk Basin, U.S.S.R.

Range. Upper Llandovery-Wenlock (possibly to the lower Devonian).

Distribution. Tuva, Altai Mountains, Salair, Kazakhstan, Central Asia.

Remarks. *Nalivkinia* ranging from Llandovery to the late Silurian and possibly into lower Devonian time, appears at present to have been found only in the U.S.S.R. Bublichenko (1927) recognized a new genus in the Peetz species and, in addition to the type, described a new species, *N. sibirica*, apparently from the same locality and horizon. Subsequently, Nikiforova and Andreeva (1961) described a species they called *Catazyga rara* from the Siberian platform, later identified by Lopushinskaya (1965) as belonging to a new subgenus *Anabaria* within *Nalivkinia*. Internally the only difference between them lies in the thicker muscle pads in *Nalivkinia* and externally in the greater globosity and beak incurvature. Identical features in the two taxa are the large dental cavities, 'hair-line' structures of the dental plate, and delicate crural bases and crural supports feathering distally. These similarities at present outweigh the differences on a generic level. The two subgenera are maintained because of lack of comparative brachidial evidence. The internal structure of these atrypids is more 'advanced' than the zygospirids and members of the *Atrypa reticularis* group in the presence of clearly definable socket plates, more delicate crura, and a striated cardinal process in the notothyrial pit.

Species assigned to Nalivkinia (Nalivkinia).

Inadequate data exists on the correct assignment of many Silurian atrypoid species referred in the past to *Nalivkinia*, *Gruenewaldtia*, or *Atrypa*. Any number of these could belong to *Nalivkinia (Nalivkinia)*: doubtful species are preceded by a question mark.

Nalivkinia sibirica Bublichenko, 1927 (p. 983, fig. 1; pp. 990–991, pl. 49, figs. 2, 7–8; pl. 50, figs. 4–10). This species occurs together with the Peetz type species in the same strata. It appears to be indistinguishable by its sulcus and more globose shell as described, and may be a population variant.

?*Nalivkinia linguata* Borisyak, 1955 (pp. 65–66, pl. 10, figs. 4–9; pl. 13, figs. 8–10). Llandovery–Wenlock of central Kazakhstan, U.S.S.R.

Nalivkinia minuta Menakova, 1964 (pp. 26–27, pl. 5, figs. 8–10). Daurich Mountains, U.S.S.R., Wenlock, Bed 'L'.

Nalivkinia (Nalivkinia) gruenewaldtiaformis Peetz, 1901

Plate 40, figs. 1–4; text-fig. 16

- 1901 *Atrypa gruenewaldtiaformis* Peetz, pp. 147–148, 376, pl. 4, fig. 2a–c. Holotype, Leningrad University Museum, specimen 81/90.
 1927 *Nalivkinia gruenewaldtiaformis* Peetz; Bublichenko, pp. 989–990, 1002–1003, pl. 50, figs. 1–3.
 1967 *Nalivkinia gruenewaldtiaformis* Peetz; Kulkov, pp. 106–108, pl. 18, figs. 1–2.
 1974 *Nalivkinia gruenewaldtiaformis* Peetz; Kulkov, pp. 61–62, pl. 21, figs. 3–6.

Remarks. Both Bublichenko (1927) and Kulkov (1974) illustrate a connected jugum for the type species of *Nalivkinia*. However, serial sections in Kulkov (1974, p. 62) indicate that the jugal processes are only very weakly joined together, and possibly recrystallization has obscured what may actually be disconnected structures. This is similar to many reconstructions for Devonian Atrypidae, which have been shown to be incorrect (Copper 1967). Jugal processes frequently come so close together that they are easily confused for being fused. More work is still needed on the interior of *Nalivkinia*. Significant apical internal structures of *N. gruenewaldtiaformis* are the large dental cavities, the presence of a thin true dental plate (appearing as a 'hair-line' structure in serial peels) along the inner margin of the pedicle cavity,

EXPLANATION OF PLATE 40

All figures $\times 2$, except figs. 19–20 approx. $\times 40$.

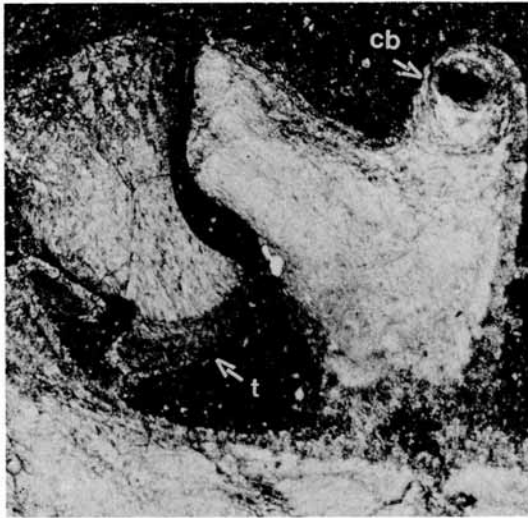
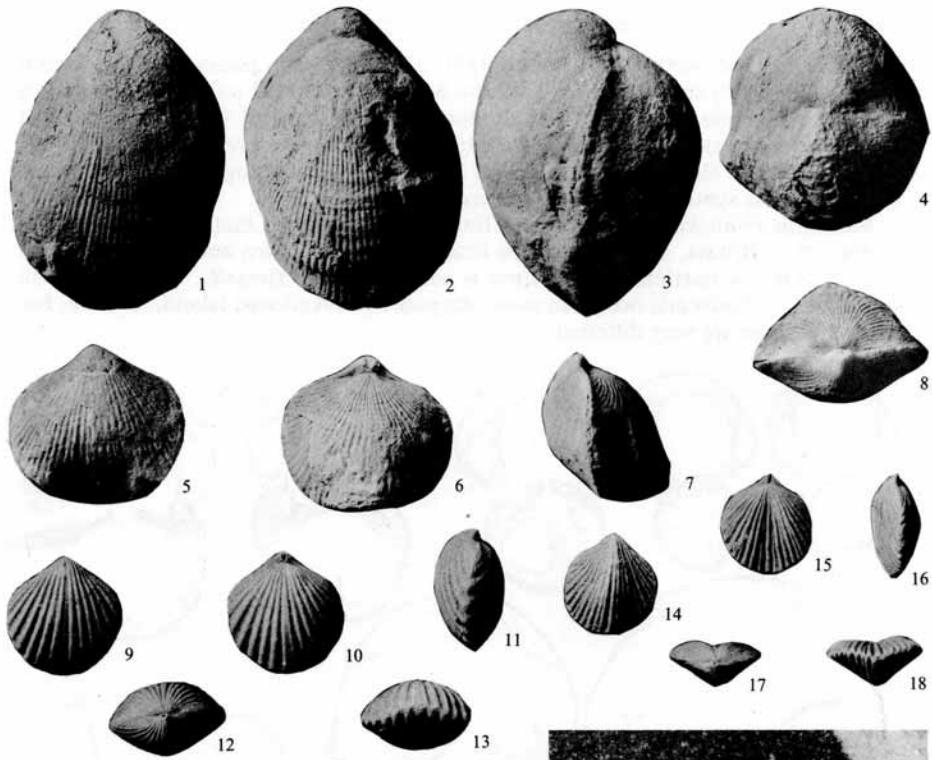
Figs. 1–4. *Nalivkinia (Nalivkinia) gruenewaldtiaformis* (Peetz, 1901). GS 45398 hypotype, ventral, dorsal, lateral, and posterior views of adult. Note that ribs have few anterior growth interruptions and lack frilly projections. Sara-chumysk, Salair, U.S.S.R. (locality K6710 Kulkov); marly limestones, Wenlock.

Figs. 5–8. *Nalivkina (Anabaria) rara* (Nikiforova, 1961). GS 45397 hypotype, ventral, dorsal, lateral, and posterior views of adult specimen. Ribs are tubular, lack frills. Omnutakh River, Siberian Platform, U.S.S.R. Wenlock.

Figs. 9–13, 20. '*Clintonella anticostiana* (Twenhofel, 1928). 9–13, GS 45399 hypotype, ventral, dorsal, lateral, posterior, and anterior views. Note lack of carination, accentuated mid-ribs. 20; GS 45392, photomicrograph of hinge plate and tooth structure (serial peel). NTS Jupiter River 75140:87850, Jupiter Formation (Zones 6–7), Anticosti Island, Canada. Upper Llandovery.

Figs. 14–18. *Alispira gracilis* Nikiforova, 1961. GS 45400 hypotype, ventral, dorsal, lateral, posterior, and anterior views of adult specimen. Note the carination, resulting in dorsal sulcus (contrast with figs. 9–13). Podkamennaya River, Tunguska, Siberian Platform, U.S.S.R. Llandovery.

Fig. 19. *Catazyga headi headi* (Billings, 1862). GS 45397 hypotype, photomicrograph of serial peel showing crural base (cb), hinge plate and tooth (t). NTS Bécancour 01450:38880, Pontgravé River Formation, Canada. Ashgill.



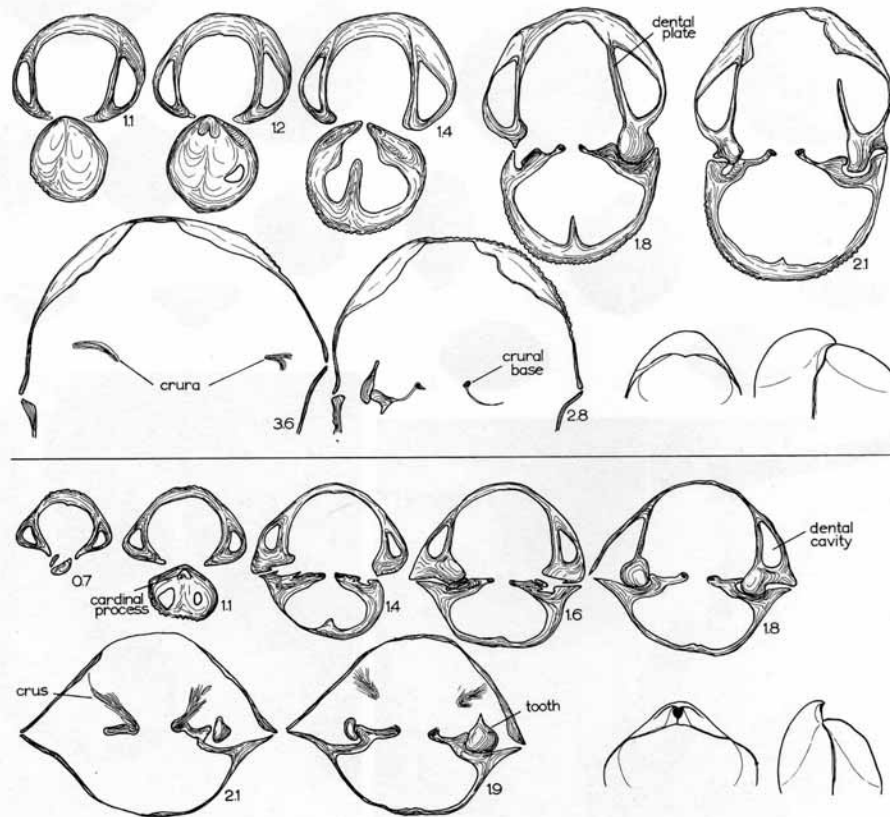
19

20

COPPER, Ordovician and Silurian Zygospiridae and *Alispira*

vertically aligned teeth, thin, horizontally aligned socket plates, delicate crural bases, and fibrous crural tips (text-fig. 16). Material sectioned was from the syntype collection of Peetz located in the Museum of the Historical Geology Section of Leningrad University, and made accessible by E. S. Poretskaya. The large syntype collection shows that a gradation exists in external morphology between the type species and the syntopic species *N. sibirica* Bublichenko, 1927.

Nalivkinia (*Nalivkinia*) has not been found on the Siberian Platform, in the Baltic region, or in Britain, and seems to be limited to the southern and Asiatic parts of the U.S.S.R. Its restricted distribution is comparable to *Tuvaella*. An external rib structure like *Nalivkinia* occurs in some atrypids from Anticosti Island, Canada, but internally these are very different.



TEXT-FIGS. 16-17. Serial sections of *Nalivkinia gruenewaldtiaeformis* (Peetz, 1901); (top), GS 45376, Wenlock, Sara-chumysk, Salair, U.S.S.R.; and *Anabaria rara* (Nikiforova, 1961) (bottom), GS 45375, Wenlock, Omnutakh River, Siberian Platform, U.S.S.R. Scale $\times 5$.

Genus NALIVKINIA Bublichenko, 1927
Subgenus ANABARIA Lopushinskaya, 1965

Plate 40, figs. 5-8; text-fig. 17

Type species. Catazyga(?) rara Nikiforova and Andreeva, 1961 (pp. 248-249, pl. 54, figs. 1-7). Wenlock, south-west Siberian Platform, Omnutakh River, U.S.S.R.

Remarks. Lopushinskaya (1965) correctly saw the affinity of *Catazyga(?) rara* to the genus *Nalivkinia*. The type species of *Nalivkinia*, *N. gruenewaldtiaformis* (Peetz, 1902) differs only slightly in its internal structure from the species *rara* (see this text). The only difference lies in external form, and in shell-wall thickness, which could be an infrageneric character. Externally, *Anabaria* has a less-incurved beak and a slightly flatter shell with broad sinus. The internal similarities are so striking that it is hard to tell them apart. Except for jugal processes and spiralia, which were not present in the material sectioned, the following items were identical in the two taxa: large dental cavities and straight hair-line structure (dental plate s.s.) on the inner side of the tooth, deltidial plates (small, hollow apically), cardinal process (thin lining in notothyrial pit), distinct thin socket plates, small crural bases expanding into thick, curved, feathery crura (text-fig. 17). The internal affinities of both *Nalivkinia* and *Anabaria* are with *Desquamatia* of the Devonian; internally *Nalivkinia* and *Anabaria* are so much alike it is probably better to classify them under the same genus and even subgenus. Beak incurvature is variable in the Sara-chumysk collections of Peetz. Beak incurvature and shell form are also infraspecifically different in Devonian taxa. However, until the jugal processes and spiralia are better known, it may be advisable to follow Lopushinskaya's separation. In looking at the serial sections particular attention should be paid to comparisons of *gruenewaldtiaformis* and *rara* (text-fig. 17).

Species assigned to Nalivkinia (Anabaria).

?*Nalivkinia kazachica* Borisyak, 1955 (pp. 61-63, pl. 10, fig. 3; pl. 11, figs. 17-19; pl. 13, figs. 1-3). Silurian, Central Kazakhstan, U.S.S.R. Lateral cavities and 'dental plates' seem to indicate *Anabaria* affinities.

?*Nalivkinia kassini* Borisyak, 1955 (pp. 63-64, pl. 10, figs. 1-2; pl. 13, figs. 6-7). Silurian, Central Kazakhstan, U.S.S.R. Serial sections not definitive.

?*Nalivkinia rhomboidalis* Borisyak, 1955 (pp. 64-65, pl. 10, figs. 10-13; pl. 13, figs. 4-5). Silurian, Central Kazakhstan, U.S.S.R. More coarsely ribbed, possibly an *Alispira*.

Genus ALISPIRA Nikiforova, 1961

Plate 40, figs. 14-18; text-fig. 18

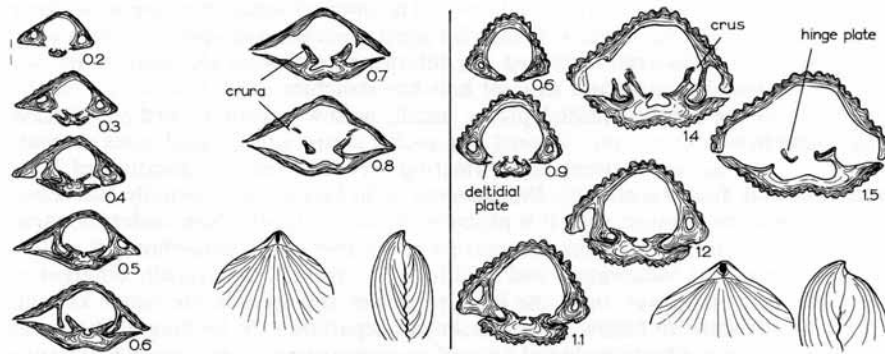
Type species. Zygospira (Alispira) gracilis Nikiforova, 1961, pp. 244-247, pl. 53, figs. 1-8; text-fig. 41.

Range. Llandovery-Wenlock.

Distribution. U.S.S.R. (Siberian Platform, Estonia). Not known from Britain, the Baltic, or other well-known Llandovery-Wenlock sections.

Remarks. The atrypoid relationships of this genus are without doubt, as confirmed by Nikiforova (1961) and Nikiforova and Modzalevskaya (1968). However, since the detailed internal structure of the poorly preserved, synchronous North American

genus *Clintonella* is yet unknown (see Boucot and Johnson 1970), doubt remains if *Alispira* is a junior synonym of *Clintonella*. If both taxa are characterized by carination, and if internal structures are similar, there may be no way of telling them apart. Clinton-age material in eastern North America is generally either silicified or preserved as moulds and casts, and sheds no light on the significant internal structures. The Jupiter River Formation of Canada yields *Homeospira anticostiana* which is probably atrypoid (see Pl. 40, fig. 20; text-fig. 19); but whether this is synonymous with *Clintonella* is not clear, since the Anticosti material lacks carination. Serial sections of topotypic *Alispira* (text-fig. 18) and the Anticosti material of '*Clintonella*' (text-fig. 19) is compared side by side. Note the disposition of the hinge plate and crura in both species.



TEXT-FIGS. 18-19. Serial sections of *Alispira gracilis* (Nikiforova, 1961); (left), GS 45382 from the Podkamennaya River, Tunguska, Siberian Platform; Llandovery; (right), *Clintonella? anticostiana* (Twenhofel, 1928), NTS Jupiter River 75140:87850; Zones 6-7, Jupiter Formation (Upper Llandovery). Compare the apical structures in the two species. Scale $\times 5$.

Genus CLINTONELLA Hall and Clark, 1893

Type species. *Clintonella vagabunda* Hall and Clarke, 1893, pp. 159-161, pl. 52, figs. 1-11. Original material derived from 'drifted and decomposed block of sandstone found without label among the collections presented to the New York State Museum'. Probably derived from the Clinton group in Orleans county (ibid., p. 161).

Range distribution. Llandovery and possibly Wenlock, North America.

Remarks. The affinity of this genus is still unsettled. Hall and Clarke (1893) intimated a close relationship with *Zygospira* on the basis of the hinge plate and muscle impressions. However, they stated that no spiralia had been found in any material examined. Boucot and Johnson (1970), despite new material, came no closer to an answer on affinities, since they, like Hall and Clarke before them, failed to find spiralia. Nevertheless, they were able to establish a more precise age for some *Clintonella* specimens, namely Llandovery C₃ to C₄, though leaving open the question of relations with the Zygospiridae or Atrypidae. *Clintonella* has affinities with the Siberian Llandovery *Alispira* Nikiforova, 1961 in sharing a carinate pedicle valve and sulcate

brachial valve (see Pl. 40, figs. 14–18 for topotypic material of *Alispira*). This carination is not always marked in illustrated material of *A. gracilis tennicostata*. *Alispira* possesses dental cavities, dorsal atrypoid spiralia, postero-ventral jugal processes (separated), and somewhat unusual hinge plates (see Modzalevskaya's serial sections in Nikiforova 1961, p. 246; compare with text-fig. 18). Nikiforova pointed out that some North American '*Homeospira*', e.g. '*H.*' *anticostiana* Twenhofel, 1928 and *H. subcircularis* Savage, 1913 were similar to *Alispira*. This is a problem still under investigation, particularly in regard to Anticosti material (Pl. 40, figs. 9–13, 20; text-fig. 19). A number of North American taxa assigned to '*Homeospira*' may be true atrypoids, and may belong to a new genus of clintonellinid lacking carination of any kind. Provisionally it is better to retain North American atrypoids of this type under *Clintonella*.

Clintonella? anticostiana (Twenhofel, 1928)

Plate 40, figs. 9–13, 20; text-fig. 19

1928 *Homeospira anticostiana* Twenhofel, p. 220, pl. 20, figs. 1–3.

Remarks. Text-fig. 19 serializes the apical structures of a typical specimen from Anticosti Island. Calcified material has not yet revealed spiralia. Dental cavities are distinct, small deltidial plates about the apex of the brachial valve, teeth are dorso-medially directed and simple in design. The hinge plate is somewhat similar to *Alispira*, but crura develop rather differently from crural bases (see Pl. 40, fig. 20; text-fig. 18). The inner part of the hinge plate is unique for atrypoids, in having medially pointed blades; the significance of this is not clear. Some *Alispira* (e.g. *A. rotundata* Nikiforova and Modzalevskaya, 1968, pp. 59–61, pl. 2, figs. 1–7) also have a similar hinge plate development.

CONCLUSIONS

Before atrypoid taxonomy can reach a satisfactory major scheme, a number of problems need to be solved. Most of these solutions rest on a better knowledge of internal structures, especially of the brachidia and pedicle structures. The theme of this paper is that the early atrypoids, the Zygospiridae (mostly of Ordovician age), were all 'designed' with a similar dorso-medially pointed spiralia and a dorsal, fused jugum. This implies a common method of solving the problems of food-gathering and waste disposal. In terms of external morphology, the zygospirids lacked many of the refinements of the Devonian atrypoids (the Silurian representing a transitional stage in morphology). Zygospirids did not develop specializations for settling or anchoring on soft muddy bottoms (e.g. frills, spines, planation or elongation of one or both valves, cementation, pedicle peculiarities). The zygospirinids were probably the ancestors of the Atrypidae, the tuvaellinids possibly of the Carinatininae, and the catazyginids were possibly the ancestors of the Palaferellinids (s.s.) and the Karpinskiinids. Knowledge is needed of the interior of different species assigned at various times to transitional generic forms, e.g. '*Eospirigerina*', '*Clintonella*' (or '*Homeospira*'), '*Alispira*', '*Zygospira*', etc. There is ample scope for further work.

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