LATE TRIASSIC BRACHIOPODS FROM THE LUNING FORMATION, NEVADA, AND THEIR PALAEOBIOGEOGRAPHICAL SIGNIFICANCE

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ABSTRACT. Brachiopods from the Late Triassic Luning Formation are described from localities in the Pilot and Shoshone Mountains, Nevada. The spiriferids *Balatonospira?* cf. *B. lipoldi*, *Zugmayerella uncinata*, *?Z.* sp., *Spondylospira lewesensis*, and the terebratulids *Plectoconcha aequiplicata*, *P. newbyi* sp. nov., *Rhaetina gregaria*, *R.* cf. *R. gregaria* and *Zeilleria* cf. *Z. elliptica* are described. This Luning fauna contains species known from western Europe (*Z. uncinata* and *R. gregaria*) and forms closely comparable to species known from western Europe are also present (*B.?* cf. *B. lipoldi* and *Z.* cf. *Z. elliptica*). Other species are only known from the Americas, *S. lewesensis* from displaced terranes in the cordilleran region of North America and from Peru, *P. aequiplicata* and *P. newbyi* sp. nov. from the displaced Paradise terrane of Nevada. Some of the brachiopods and associated corals, bivalves and foraminifers are conspecific with latest Triassic forms from central Europe. Ammonoids indicate the age of the fauna to be early Norian. The palaeobiogeographical distribution indicates existence of the Hispanic Corridor possibly as early as the Late Triassic which cannot be discounted as a possible migratory passage between Nevada and Tethys.

BRACHIOPODS were important benthic elements in shallow-water marine faunas during Late Triassic time. They are well known in Late Triassic sections of the former Tethys region in southern Germany, Austria and other Alpine regions farther east (e.g. Suess 1854; Zugmayer 1880; Bittner 1890; Dagys 1974). Along with sponges, foraminifers, corals, molluscs, and echinoderms, brachiopods are a common constituent of Late Triassic rocks in western North America. Many brachiopods occur in carbonate rocks, representing deposition in warm, relatively shallow-water environments of tropical to subtropical latitudes (Stanley 1979). Despite their local abundance, few monographic studies have been devoted to Late Triassic brachiopods of North America, although the works of Logan (1964, 1967) and Hoover (1991) are exceptions. Mostly they have been described in some of the pioneering studies on the western part of the continent (Gabb 1864; Hall and Whitfield 1877; Whiteaves 1889; Clapp and Shimer 1911; Smith 1914, 1927; Lees 1934). Brachiopods mentioned by the above authors included spiriferids, rhynchonellids and terebratulids, some of which were endemic to North America, while others have European and Japanese affinities (Ager and Westermann 1963). Late Triassic and Early Jurassic rhynchonellids from British Columbia were described by Ager and Westermann (1963), including a revision of some species originally described by Smith (1927).

Brachiopods in western North America frequently occur in reef-like buildups (Stanley 1979), few of which are comparable in terms of size and facies development to those of the Tethys region of western Europe (Stanley 1980, 1982). In North America, Late Triassic examples occur in rocks belonging to various displaced terranes, many of which have geological histories independent of the craton of North America (Coney *et al.* 1980; Nur and Ben-Avraham 1982). The significance of Triassic to Jurassic faunas in assessing the former positions of displaced terranes has been highlighted during the past decade (e.g. Tozer 1982; Hallam 1986; Smith and Tipper 1986; Stanley 1987; Newton 1988); ammonoids, bivalves and corals have been emphasized, excluding other commonly occurring faunal elements. Triassic brachiopods appear to be a group offering excellent possibilities for such studies but have so far been neglected; the group is among those that are being

used to investigate Permian palaeogeography of terranes from the American Cordillera (e.g. Stevens *et al.* 1990).

The Triassic brachiopod fauna described here (Text-figs 1–3) is the most taxonomically diverse known for the Mesozoic of North America probably because so little detailed collecting and systematic study has been done. The brachiopod fauna contains only spiriferids and terebratulids. The following have been identified from the Lower Member of the Luning Formation, in Dunlap and Cinnabar Canyons. Pilot Mountains (Text-figs 1, 3), *Balatonospira*? cf. *B. lipoldi*, *Zugmayerella uncinata*, ?*Z.* sp., *Spondylospira lewesensis*, rare *Plectoconcha aequiplicata*, *P. newbyi* sp. nov., *Rhaetina gregaria*, *R.* cf. *R. gregaria*, and *Zeilleria* cf. *Z. elliptica*. From West Union Canyon, Union District, Shoshone Mountains, *Spondylospira lewesensis*, *Plectoconcha aequiplicata*, small specimens of *Rhaetina gregaria*, and *Zeilleria* cf. *Z. elliptica* have been identified. Specimens collected from the Pilot Mountains by S. W. Muller in 1934 and by D. E. Cornwall in 1979 were also studied. Of the brachiopods described herein, *B*? cf. *B. lipoldi*, *Z. uncinata*, *R. gregaria*, and *Z.* cf. *Z. elliptica* have Tethyan affinities.

Muller and Ferguson (1936, 1939) recorded *Spiriferina gregaria* Suess, *Spiriferina peneckei* Bittner, *Terebratula debilis* Bittner, *Terebratula julica* Bittner and *Terebratula suborbicularis* Munster var. *typica* Bittner from the Luning of Dunlap Canyon, Pilot Mountains. The brachiopods listed by Muller and Ferguson are most likely referable to the following taxa described herein (followed by original designation): *Spondylospira lewesensis* (Lees), (*Spiriferina gregaria* Suess); *Zugmayerella uncinata* (Schafhaeutl), (*Spiriferina peneckei* Bittner); *Zeilleria* cf. *Z. elliptica* (Zugmayer), (*Terebratula debilis* Bittner); *Rhaetina gregaria* (Suess), (*Terebratula julica* Bittner, although Cooper (1983, pp. 51–52) has referred fifteen Late Triassic specimens from Table Mountain, Hawthorne quadrangle, Nevada, lacking dental lamellae, to 'Triassic genus and species undetermined'. The specimens of Muller and Ferguson (1939, p. 1599) were from Dunlap Canyon. *Rhaetina gregaria* lacks dental lamellae); *Plectoconcha newbyi* sp. nov., (*Terebratula suborbicularis* Munster var. *typica* Bittner).

In a broad overview of Tethyan faunas in North America Kristan-Tollmann and Tollmann (1983) recorded '*Spiriferina*' aff. *munsteri* Davidson, *Zugmayerella* aff. *uncinata* (Schafhaeutl), '*Rhynchonella*' cf. *austriaca* Suess, '*Rhynchonella*' sp. and '*Terebratula*' sp. from the Luning Formation of Dunlap Canyon, Pilot Mountains. The papers by Muller and Ferguson (1936, 1939) and Kristan-Tollmann and Tollmann (1983) lacked serial sections of the brachiopods.

TECHNIQUES AND CONVENTIONS

For this study transverse serial sections were taken to investigate the internal structures of a number of specimens. A full description of the technique and equipment used in the preparation of serial sections in the Palaeontology Laboratory, Department of Geology, University of Dayton was given by Sandy (1989), wherein additional references can be found. Images from acetate peels were drawn using a Nikon SMZ-10 binocular microscope and drawing tube. All serial sections are drawn with the brachial valve lowermost.

Annotations for synonymy lists and open nomenclature follow those proposed by Richter (see Matthews 1973).

The following dimensions are used: L = length; Lbv = length of the brachial valve; W = width; T = thickness; + = damage in that orientation. All dimensions are given in mm.

## STRATIGRAPHY

Lithostratigraphy

The Luning Formation is widely exposed within numerous thrust sheets in the Pilot Mountains, east of the town of Mina, as well as in the Garfield and Royston Hills, Shoshone and Cedar Mountains and Paradise Mountain Range to the north, west and east of the Pilot Mountains. In its type locality
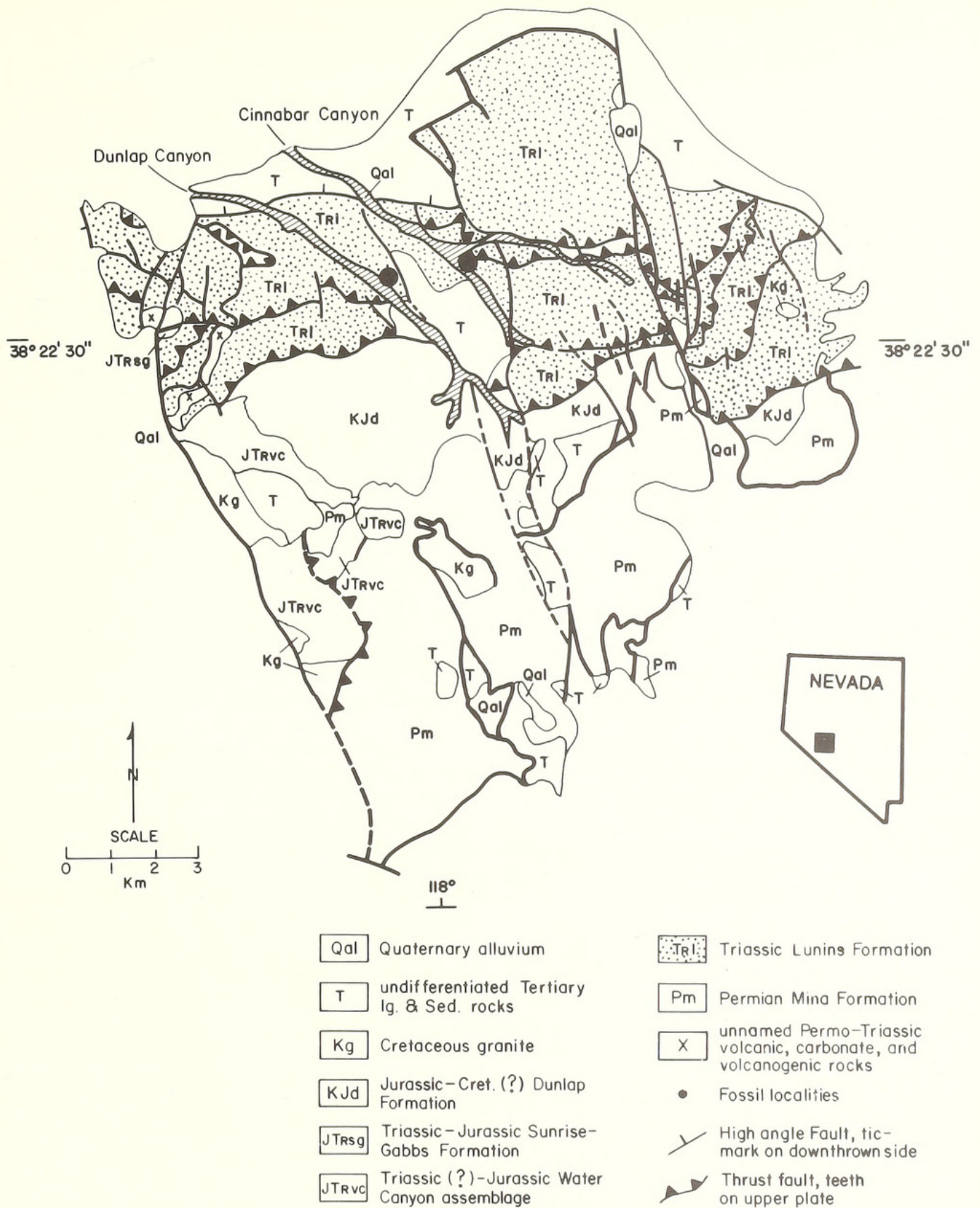
TEXT-FIG. 1. Geological map of a portion of the Pilot Mountains showing structural relations and approximate location of fossil localities in Dunlap and Cinnabar Canyons (black dots). Map from Oldow (1981). Outline of State of Nevada shown to bottom right of map, black square indicates location of Pilot Mountains.
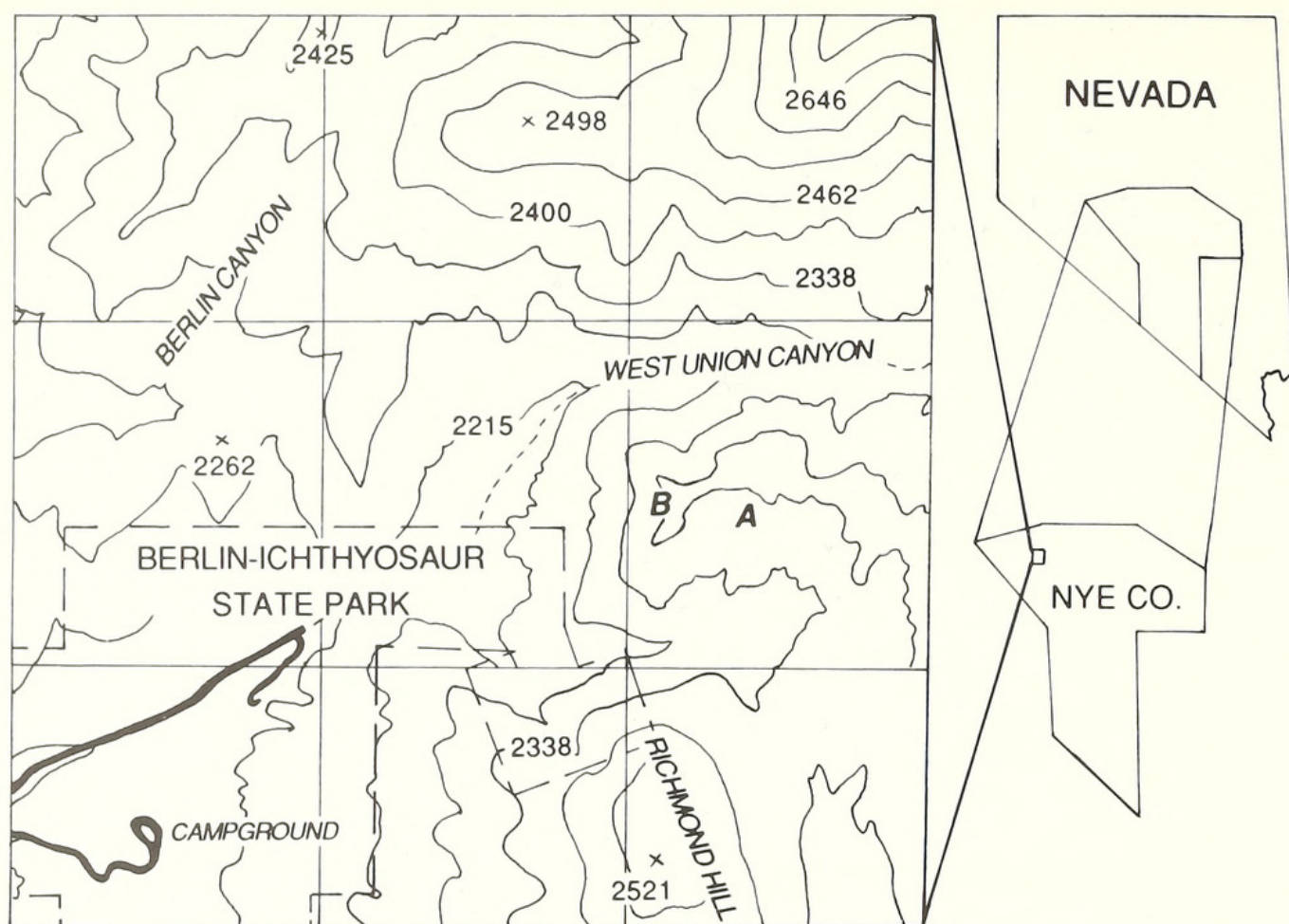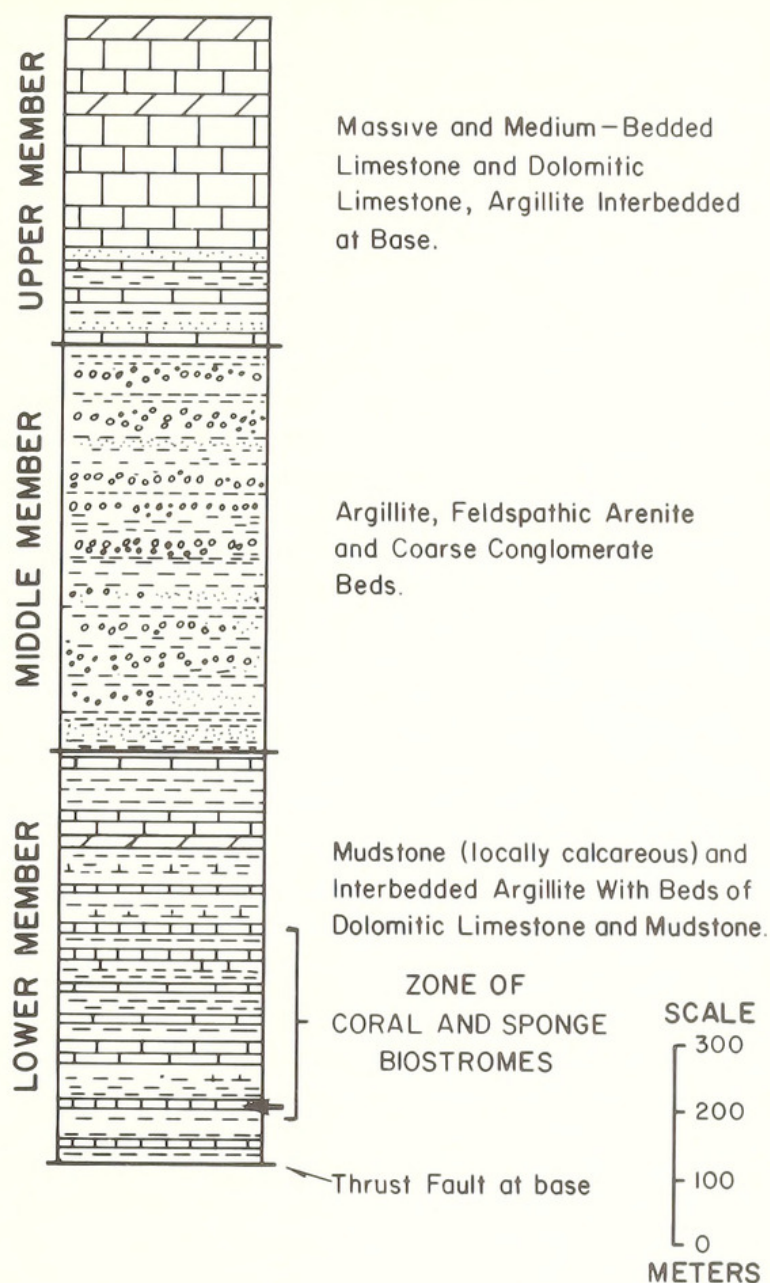
TEXT-FIG. 2. Location of collecting sites in West Union Canyon, Berlin-Ichthyosaur State Park, Nye County, Nevada. A = locality with large *Plectoconcha aequiplicata* (Gabb); B = 'Brachiopod Ledge' with small *Plectoconcha aequiplicata* (Gabb). Both localities in the limestone and secondary dolomite member of Silberling and John (1989), Luning Formation. Roads represented by solid black line, tracks by short dashed line, State Park boundary by long dashed line. Map based on Ione 15′ quadrangle map, Township 12 North, Range 39 East. Contour interval 60·96 m (200 feet). All elevations converted to metres.

the Luning Formation is more than 2·5 km thick, with lithologies ranging from limestone and dolomite to argillite, sandstone, and conglomerate. The type Luning is part of the Luning Allochthon (Oldow 1981) which includes a series of nappe thrusts moved considerable distances to the southeast as part of the Paradise terrane (Silberling 1990).

The brachiopods from the Pilot Mountains come from the so-called 'coral reef' facies in the Lower Member of the Luning (Text-fig. 3). According to Muller and Ferguson (1939), this facies occurs in a consistent stratigraphical position within the 775 m thick member and is therefore of value in correlating between different thrust blocks. Muller (1936) discussed the occurrence of 'coral reefs' in the Luning Formation from this area based on well-exposed outcrops in Dunlap Canyon. Here the facies is about 60 m thick, traceable as far as 130 km to the north. The rock and fossil associations within this interval in the Pilot Mountains were studied by Stanley (1979) who considered them not to be reefs but, small, bedded biostromal buildups of impure limestone which alternate with thin argillite and mudstone beds. Some of these limestones are dominated by abundant corals and sponges, while others are characterized almost entirely by a very large mytilid bivalve *Trichites* sp. and '*Ostrea*' *montiscaprilis*. Individual limestone beds of corals and sponges can be traced along strike for up to 1·5 km. They range from 1·5 m to 10·0 m thick, and pinch and thicken laterally along their outcrop (Stanley 1979, p. 10). At the top of one measured section

Massive and Medium–Bedded Limestone and Dolomitic Limestone, Argillite Interbedded at Base.

Argillite, Feldspathic Arenite and Coarse Conglomerate Beds.

Mudstone (locally calcareous) and Interbedded Argillite With Beds of Dolomitic Limestone and Mudstone.

ZONE OF CORAL AND SPONGE BIOSTROMES

SCALE
300
200
100
0
METERS

Thrust Fault at base

UPPER MEMBER

MIDDLE MEMBER

LOWER MEMBER

TEXT-FIG. 3. Generalized stratigraphy of the Luning Formation, Pilot Mountains, showing the subdivision into three informal members. The brachiopods described herein occur near the base of the Lower Member, within an interval of coral and sponge biostromes (horizons indicated by solid arrow). Stratigraphy generalized from unpublished field notes of J. S. Oldow.

(loc. MC, Stanley 1979, Appendix A) a massive limestone and dolomite interval 23 m thick contains bioclastic debris and cross-bedded oolitic zones. The Pilot Mountain fauna of Stanley (1979) consists of rare foraminifers, five species of chambered sponges, five species of spongiomorphs, twenty-three species of corals, and numerous and diverse bivalves; indeterminate gastropods, a nautiloid, ostracodes, echinoids, crinoids and brachiopods also occur. Notably absent from thin sections or sieved material in the argillites is any kind of involutinid foraminifer or calcareous algae which might be diagnostic of age or environment. From interbedded argillites, skeletal remains of large ichthyosaurs are common (Camp 1980). The sponges previously investigated by Seilacher (1962) have been revised (Senowbari-Daryan and Stanley 1992). Benthic foraminifers, sponges, corals, an ammonite, brachiopods and crinoid columnals were illustrated by Kristan-Tollmann and Tollmann (1983).

In Berlin-Ichthyosaur State Park the Luning Formation consists of four members – clastic, shaly limestone, calcareous shale and carbonate (Silberling 1959). Silberling and John (1989) redescribed four members of the Luning Formation in the Berlin Allochthon of the Paradise Range as 'clastic

rock member', 'shaly limestone and calcareous shale member', 'phyllite, grit and conglomerate member' and 'limestone and secondary dolomite member'. Hogler (1990) identified three biofacies in the formation, the 'benthic bivalve', 'ammonite/ichthyosaur/thin-shelled bivalve', and 'brachiopod/gastropod' biofacies. A velellid medusoid hydrozoan was reported from the Luning Formation of the Shoshone Mountains by Hogler and Hanger (1989). The brachiopods described here were collected from the 'limestone and secondary dolomite member' of Silberling and John (1989) ('carbonate member' of Silberling 1959, 'brachiopod/gastropod biofacies' of Hogler 1990) in West Union Canyon (Text-fig. 2). Large specimens of *Plectoconcha aequiplicata* were obtained loose from talus, while small specimens of the same species were obtained *in situ* from an exposure informally named 'Brachiopod Ledge' (Hogler, personal communication; Text-fig. 2). The diverse ammonoid fauna from Union Canyon (Muller and Ferguson 1939; Silberling 1959; Kristan-Tollmann and Tollmann 1983) occurs at stratigraphical levels below that of the 'limestone and secondary dolomite member'. Kristan-Tollmann and Tollmann (1983) also recorded four bivalves, a crinoid, and seven taxa of foraminifers.

Biostratigraphy

Corals from limestones of the Luning Formation in Dunlap Canyon were originally identified as of Jurassic age, but subsequently as Late Triassic (Norian) (Smith 1927, p. 9). Muller and Ferguson (1939) assigned the entire Luning Formation to the Carnian. Silberling and Roberts (1962) and Silberling and Tozer (1968) established the formation as a transgressive unit ranging from the latest Carnian into the mid and possibly late Norian. Silberling (personal communication) places the coral biostromes of the Lower Member of the Luning in the Pilot Mountains in the Kerri ammonite Zone (early Norian) based on the occurrence of *Mojsisovicsites kerri*; the brachiopod-bearing beds in the Shoshone Mountains range from the Kerri to Magnus ammonite Zones (early Norian). According to previous work, none of the Luning in the Pilot Mountains is any younger than the mid Norian. Ammonites are not common in the sections studied, but the association of spiriferid and terebratulid brachiopod species identified herein could be useful in identifying early Norian strata elsewhere.

Kristan-Tollmann and Tollmann (1983) illustrated ammonites from the Luning Formation at Union Canyon and the Pilot Mountains. At the latter locality, their discovery of *Pararcestes*, a genus also known from Austria in the Early Norian Kerri Zone, and in Union Canyon the occurrence of many species of ammonoid and halobiid bivalves, confirm previous assertions of a range from late Carnian into the early and mid Norian Stages. The presence, for example, of *Klamathites macrolobatus*, *Klamathites schucherti*, *Stikinoceras kerri* and *Guembelites jandianus* in the Union Canyon section (Silberling 1959) records the passage from the late Carnian to the early Norian in strata just below those of the brachiopod localities (Text-fig. 2).

Ager (1987, 1990) defended the Rhaetian as the last stage in the Triassic, contrary to Tozer (1980, 1988, 1990) and Silberling and Nichols (1988). There are similarities between the brachiopods described herein with those of the European Rhaetian, but the brachiopod-bearing part of the Luning can be assigned an early Norian age based on the ammonites. Some of the brachiopod taxa are long-ranging forms which were geographically widely dispersed. Mesozoic brachiopods are of use in biostratigraphy when conventional stratigraphically useful fossil groups such as ammonites and microfossils are absent. Ager (1979) suggested that rhynchonellids are the most useful brachiopods in Mesozoic stratigraphy.

Ager (1987, p. 10) considered that the brachiopods from the Pilot Mountains support a Rhaetian age for the Luning Formation. Ager reiterated this (1990, p. 9), with *Rhaetina* cf. *gregaria*, *Zugmayerella uncinata* and *Austrirhynchia*? sp. being named as characteristic Rhaetian forms. Of these, only the last named is restricted to the Rhaetian, *R. gregaria* and *Z. uncinata* are longer-ranging species of genera that also range beyond the Rhaetian. *Rhaetina gregaria* 'is without doubt the commonest and most widely distributed of the Rhaetian brachiopods' (Pearson 1977, p. 38) and it has been identified as a guide fossil for the Alpine Rhaetian, although it is probably not restricted to the Rhaetian. Therefore, its presence in the Luning Formation of Nevada does not support a Rhaetian age (*sensu* Ager 1990) for the Lower Member of the Luning Formation in the Pilot

Mountains. The identification of *Austrirhynchia*? sp. in the Late Triassic of Nevada was based on a few brachiopods collected by Stanley in 1975. Subsequent collections from the Luning in 1990 have allowed detailed taxonomic study of the brachiopods, including serial sections, and Ager's (1990) *Austrirhynchia*? sp. is now referred to *Balatonospira*? cf. *B. lipoldi* (Bittner) herein. *Balatonospira lipoldi* has been recorded from the Ladinian?–Carnian (Dagys 1974; Siblik 1988). *Balatonospira*? cf. *B. lipoldi* appears to be a closely related form from the early Norian. *Zeilleria* cf. *Z. elliptica* does not provide specific stratigraphical information, other than it has a resemblance to some Norian species.

Ager (1990) stated that the absence of *Halorella* in the Nevada brachiopod fauna was evidence for a Rhaetian age because this genus is typical of the Norian elsewhere. It is thought unlikely that this absence indicates a Rhaetian age. Of the other brachiopods, *Plectoconcha aequiplicata* was originally described by Gabb (1864) from the East Range, Nevada. It was recorded from the Dun Glen Formation, Magnus Zone, which is late early Norian (Silberling, personal communication). *P. aequiplicata* has also been collected from the Luning of Union Canyon and a few specimens from the Pilot Mountains, where *P. newbyi* sp. nov. also occurs. The genus may be indicative of the early Norian. Hoover (1990) suggested that *Spondylospira* was not restricted to the Norian and ranged into the earliest Jurassic of Central Peru.

PALAEOECOLOGY

According to Muller and Ferguson (1939), rocks of the Luning Formation in the Pilot Mountains can be divided into three distinct biofacies, each characterized by a distinctive faunal association. The first is a nearshore facies represented by bivalves, especially the large oyster '*Ostrea*', which locally forms thin 'banks'. The second facies was termed a 'coral reef' by these authors because of the predominance of abundant scleractinian corals and sponges. Brachiopods flourished during clearwater phases; they are closely associated with invertebrates that inhabited small-scale biostromes which existed in lagoonal environments offshore from areas of active deltaic and carbonate shelf sedimentation. The small-scale biostromes attained at best only a few metres of relief above the surrounding sea floor. Lack of algae and a predominance of low-energy (micritic mud) matrices indicate that the biostromes may have inhabited settings within deeper or turbid waters. Depths of up to 60–70 m were estimated. Ammonoids are rare from the biostromes and their associated sediments. The third facies type is argillaceous, bearing an ammonoid fauna and representing offshore, deeper water environments.

Palaeoecological zonation is apparent among the corals, sponges and other invertebrates in the biostromes, as indicated by vertical succession and quantitative point-count studies on bedding surfaces (Stanley 1979). Other palaeoecological relationships, including overgrowth encrustations by corals and sponges, substrate stabilization by thalamid sponges, boring by lithophagous bivalves, and cryptic niche habitats have been recognized. Episodic influxes of fine-grained (clay and silt-size) siliciclastic sediment were deleterious to the corals and other invertebrate organisms, periodically engulfing them. As outlined by Stanley (1979), frequent extermination is clearly evident in measured sections with at least five or six thin coral biostromes occurring within a 115 m interval. The top of each biostrome is draped by unfossiliferous mudstone and argillites, preserving *in situ* the invertebrate fauna.

The presence of pockets or cavities formed by overgrowth of encrusting and laminar corals was reported within some of the biostromes by Stanley (1979). Many of these cavities contained abundant spiriferid brachiopods, *Zugmayerella uncinata*, in gregarious 'nestled' associations. Presumably, therefore, these brachiopods had functional pedicles into adulthood (cf. Hoover 1983). Such 'nestled' associations within reef cavities seem good evidence for cryptic habitats and gregarious lifestyles for this brachiopod. One specimen of this species has an example of the trace fossil *Oichnus* Bromley (1981) towards the posterior end of the pedicle valve sulcus. It probably originated from predation on the living brachiopod and indicates that the pedicle valve was accessible for attack; the interarea of the pedicle valve may have been protected by being close to

a substrate. A few specimens of this brachiopod were collected from thin shale interbeds (c. 0·1 m thick) within unit 35 of Stanley (1979, p. 53). Three specimens were observed with their pedicle valve lowermost. If they were preserved in life positions, this may represent an alternative strategy for exploitation of a fine-grained clastic substrate. The terebratulids and other spiriferid brachiopods do not appear to show much in the way of life associations within the lower member of the Luning. Brachiopod-rich 'pockets' are apparent in the field, although life position is not suggested by the orientation of the specimens. They may represent little-transported, post-mortem accumulations within depressions on the substrate. However, one specimen of *Plectoconcha newbyi* sp. nov. was observed in Dunlap Canyon with its pedicle umbo and brachial valve resting directly on a flat, horizontal sponge, this may represent burial of a brachiopod while still attached to its substrate.

Rhynchonellids appear absent in the collections studied herein. *Plectoconcha aequiplicata* initially may be mistaken for a rhynchonellid, as did Gabb (1864) in his original description. Kristan-Tollmann and Tollmann (1983) recorded '*Rhynchonella*' cf. *austriaca* Suess (possibly *Balatonospira*? cf. *B. lipoldi* herein) and '*Rhynchonella*' sp. from the Pilot Mountains localities. The scarcity of rhynchonellids may be related to environment. The small, costate spiriferid *Balatonospira*? cf. *B. lipoldi* may be occupying the role of a rhynchonellid generalist in the fauna.

The three successive biofacies identified by Hogler (1990) in the Luning formation of the Shoshone Mountains were interpreted as indicating 1) a relatively shallow, normal marine, current-washed setting, 2) deeper, less well ventilated bottom waters, and 3) a return to shallower, more turbulent, and better oxygenated conditions.

PALAEOBIOGEOGRAPHICAL DISCUSSION

Dagys (1974) provided the most comprehensive evaluation of Triassic brachiopod biogeography. He identified three regions, the Boreal, Tethyan and Maori, for latest Triassic brachiopods (Dagys 1974), and pointed out that these had been established earlier in the Triassic. The Tethyan region is characterized by the greatest faunal diversity; about 80 per cent of the species belong to families not known outside this region, and two distinct faunas are identifiable. One is in the Alps, Carpathians, Crimea, Caucasus, Pamirs and Indochina; the other in Oman, the Himalayas and Indonesia, the latter characterized by less diversity. Endemism was high enough for Dagys to consider these regions as the Alpine and Indian subregions which equate with the northern and southern shores of the Mesozoic Tethys (Ager and Sun 1989). The Boreal region includes the northeastern area of Asia and Primor'ye and only the northeastern former USSR in the latest Triassic; rhynchonellids and spiriferinids predominate in this fauna. The brachiopod fauna of the Maori region (New Zealand and New Caledonia) differs from that of the Tethyan region by its sharply reduced diversity (Dagys 1974). Campbell (1985) reviewed the status of the Maori province.

The occurrence of some Triassic brachiopod species both in North America and European Tethys has been remarked upon. Smith (1927) commented on the very close resemblance of some species he described from the Triassic of the Western Cordillera of North America to species described from Europe. A number of the new brachiopod species he described probably represent taxonomic over-splitting and might obscure palaeobiogeographic relationships, and he incorrectly referred some rhynchonellids to the terebratulid *Dielasma* (Ager and Westermann 1963). Logan (1964) in describing *Spiriferina abichi* (Oppel 1865) from Ladinian to Carnian cratonal rocks of northeastern British Columbia provided an interesting species-level link between the North American craton and the Oman and the Himalayas. *Zugmayerella uncinata* has been recorded from the Late Triassic of Nevada and Europe (Stanley 1979; Text-fig. 4), and the rhynchonellid *Halorella amphitoma* Bronn var. *rarecostata* Bittner, 1890 from Oregon is con-subspecific with material from the Alps (Schenk 1934; Ager 1968; Ager and Sun 1989). In western North America *Halorella* has been recorded from east-central Oregon and north-west Nevada. The Oregon material is from the Fields Creek Formation and Rail Cabin Argillite in the Izee terrane (Schenk 1934; Dickinson and Vigrass 1965; Silberling, personal communication). However, Brown and Thayer (1977) interpreted this *Halorella* to come from limestone slide blocks probably derived from mélange areas to the northeast and

B   Balatonospira lipoldi
O   Oxycolpella oxycolpos
P   Plectoconcha spp.
R   Rhaetina gregaria
S   Spondylospira lewesensis
Z   Zeilleria spp.
Zu   Zugmayerella uncinata
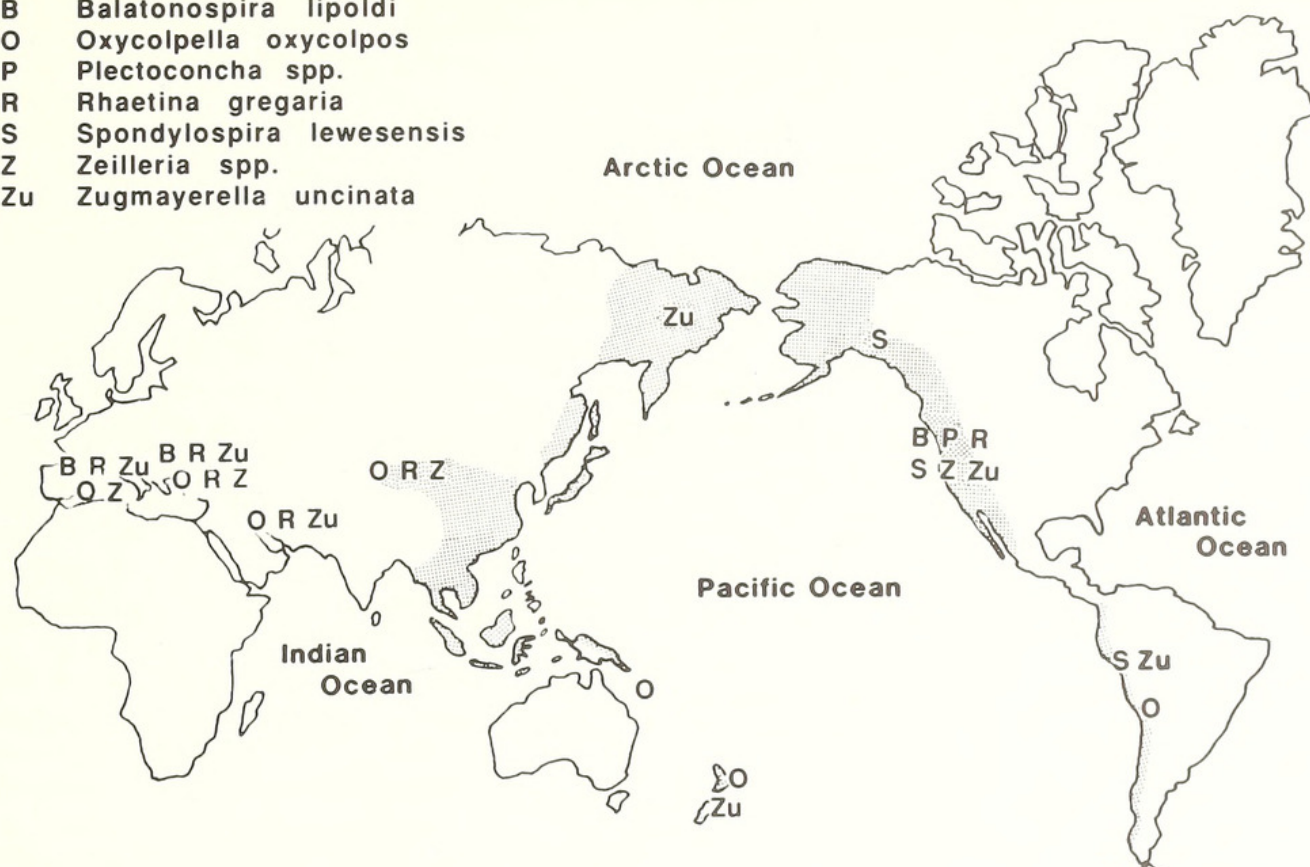
Mesozoic displaced terranes

TEXT-FIG. 4. Map showing present-day geography and the distributions of brachiopod genera and species recorded from the Luning Formation, Nevada, and *Oxycolpella* (from Kristan-Tollmann 1987). Key to letters given in top left corner of figure. B = *Balatonospira?* cf. *B. lipoldi* in Nevada. Sources of summaries of occurrence: *Balatonospira lipoldi*, Siblik 1988; *Rhaetina gregaria*, Pearson 1977; *Spondylospira lewesensis*, Hoover 1983, the genus has also been identified in the Koryak Range, north east former USSR; *Zeilleria* spp., Delance 1974; Ching *et al.* 1979; *Zugmayerella uncinata*, Pearson 1977; and *Oxycolpella oxycolpos*, as interpreted by Kristan-Tollmann 1987. Map adapted from Stanley 1988.

hence from the Baker terrane. *Halorella* also has been collected from the Jungo terrane in the vicinity of Muttlebury Pass, West Humboldt Range, north-west Nevada (Silberling, personal communication). In a recent study of cyrtinoid spiriferinacean brachiopods from western North America, Hoover (1991) considered that there were no species in common with Tethys. Our study, considering spiriferinaceans and other articulate brachiopods, reaches different conclusions.

Plectoconcha and *Spondylospira* have been interpreted as endemic respectively to western North America and North and South America (Text-fig. 4), although the latter genus has been identified in the Koryak Range (northeastern former USSR) by Bychkov and Dagys (see Hoover 1991, pp. 68, 81). The only genus that Cooper (1983) considered similar enough in its internal structures to belong in the same subfamily as *Plectoconcha* is the plicate *Merophricus*, from the Early Jurassic of the Middle and High Atlas, Morocco.

The circumtropic distribution of the Upper Triassic athyrid brachiopod *Oxycolpella oxycolpos* (Suess) has been emphasized by Kristan-Tollmann (1987). She recorded the species from the northern Calcareous Alps of Austria and Bavaria, the eastern Mediterranean (Turkey to Iran), the Himalayas, China, New Caledonia and New Zealand. It is interpreted as a species with a very

variable external morphology over its broad geographical range. A detailed taxonomic investigation including information on the internal structures of this species as interpreted by Kristan-Tollmann (1987) would be very useful to reduce the possibility of external homoeomorphy. If the distribution of *O. oxycolpos* considered by Kristan-Tollmann (1987, fig. 2) is plotted on a Late Triassic palaeogeographic base-map (e.g. Norian map in Scotese *et al.* 1987, cf. Text-fig. 4) representing present-day geography), then the distribution of this species falls mainly between the palaeolatitudes of 30° N and 30° S. Its occurrence in New Zealand gives a questionable southern high latitude record that could imply a circum-Gondwanaland distribution. However, displaced terranes of possible Tethyan origin are present in New Zealand (e.g. Bishop *et al.* 1985). *Halorella* is another Tethyan brachiopod recorded from New Zealand. It is known from the Torlesse terrane (Milne and Campbell 1969; Campbell 1985; Ager 1986). *Canadospira* appears to be a temperate or cool water form, known from the Canadian Arctic and the northeastern part of the former USSR (Dagys 1974).

The presence of a number of Triassic invertebrate species from a variety of fossil groups in both the Tethys of Europe and a number of displaced terranes from North America presents something of a palaeobiogeographical and palaeogeographical enigma. For example, many of the coral species from the Luning Formation are characteristic of the latest Triassic Rhaetian Reef Limestone, Koessen Beds and Dachstein Limestone of Austria and southern Germany (Stanley 1979). The same could also be said for some of the bivalve, brachiopod and spongiomorph species. These occurrences are not only possibly facies related, but also record earlier occurrences of some species in North America. A number of theories have been put forward to explain these occurrences (summarized from Stanley 1991): (1) beached funeral Viking ships, referring to tectonically transported fossil faunas across the Mesozoic Pacific (Panthalassa); (2) steady-state dispersal, where invertebrate larvae are transported across the Panthalassa by favourable currents and terranes do not need to be far travelled (Kristan-Tollmann and Tollmann 1981 suggested a North American–Tethyan dispersal; Newton 1988 favoured a Tethys–American dispersal); (3) stepping stones, a dispersalist approach, whereby a series of small volcanic terranes may have enabled steady state dispersal; (4) Staging Posts and Noah's Arks, a vicariance approach, with terrane dispersal by plate-tectonic processes with concomitant evolution of faunas and ultimately extension of biogeographical ranges (Flügel *et al.* 1989; Smith *et al.* 1990; Stanley 1988); and (5) Hispanic Corridor, an embryonic seaway thought to have been in existence between western Tethys and eastern Panthalassa, allowing exchange of faunas since the Early Jurassic (Smith 1983; Smith *et al.* 1990), but possibly operating since the Triassic. Palaeobiogeographical information for Late Triassic brachiopods of North America is as yet limited, but is discussed below in the light of the present study. A major consideration has to be the location of the Nevadan Paradise terrane during the Late Triassic and whether the biogeography of the fauna can assist in interpreting geography. The Paradise terrane is the most inboard terrane and during the Triassic probably was closer to North America than others.

Brachiopods are limited in their dispersal potential by their sessile, benthic mode of life and it has been suggested that like extant taxa, post-Palaeozoic articulate brachiopods possessed non-planktotrophic larvae (Valentine and Jablonski 1983). Similar limitations on dispersal were presented for Late Triassic dasycladacean algae from Oregon which show close taxonomic affinities with examples in Italy (Flügel *et al.* 1989). This would contrast with dispersal among other Triassic invertebrates such as ammonoids and bivalves which possessed planktotrophic larvae. Such differences in larval development would therefore make brachiopods suitable for palaeo-biogeographical investigation, as they would be likely to develop endemism should gene-flow become severed. Of the 'European' Tethyan spiriferid and terebratulid species occurring in Nevada, none is closely related to living brachiopods and it would be speculative to say they had non-planktotrophic larvae.

Until more is known about the taxonomic composition of North American brachiopod faunas through at least the Triassic it is not possible to comment in any detail on the role of the beached funeral Viking ships model as a post-mortem dispersal mechanism. It is thought unlikely that if

articulate brachiopods possessed non-planktotrophic larvae, they dispersed solely by ocean currents across the Triassic Pacific. However, it is clear that some Mesozoic articulate brachiopod genera were geographically widespread at times, through the low-latitudes of Tethys (e.g. Ager 1986; Sandy 1990), or from low to high latitudes (Sandy 1990, 1991*a*, 1991*b*). Ager and Sun (1989) suggested that some Mesozoic Tethyan taxa from southern Europe and North America were widespread at low latitudes, possibly crossing the Pacific by sea-mount hopping (also Ager 1986). By the Cretaceous, trans-Atlantic and trans-Arctic dispersal routes were established by more broadly latitudinally distributed genera (Sandy 1990, 1991*b*). A vicariance mode of dispersal utilizing island-hopping (which could include exotic terranes – newly formed seamounts and volcanic islands) aided by favourable currents could account for the occurrence of the Triassic 'European' species and endemic taxa in Nevada. Alternatively if accretion occurred during post-Triassic time in Nevada as suggested by Coney (1989), then the Paradise terrane could have acted as a beached funeral Viking ship.

The incipient central Atlantic Ocean began in the late Permian and during the Triassic tectonic activity resulted in crustal extension, volcanism and fault-controlled sedimentation, followed by the formation of a marine seaway (Hispanic Corridor) in the Triassic(?)–Jurassic which connected the western Tethys to the eastern Pacific. Sea-floor spreading started in the Middle Jurassic. The Hispanic Corridor (Smith 1983) was used to account for the distributions and dispersal directions of the earliest Jurassic molluscan taxa in the western Americas and Europe (Damborenea 1987; Damborenea and Manceñido 1979; Westermann 1981; Smith and Tipper 1986; Smith *et al.* 1990). The existence of marine basins west of southern Spain, open to the west and closed off from the Tethys to the east indicates an embryonic central Atlantic seaway during the Late Triassic. This is supported in part by stratigraphical and faunal occurrences (Martin and Braga 1987). The existence of an Atlantic seaway during Triassic time could explain some of the biogeographical relationships amongst the Nevadan faunas. While the presence of a Triassic marine connection between western Tethys and the eastern Pacific via the Gulf of Mexico region does not appear to be supported by stratigraphical data in central Mexico (Salvador 1987), the Late Triassic Barranca Group farther north in Sonora, has been interpreted as having been deposited in a rift-basin developed on the craton (Stewart *et al.* 1990). Undescribed marine invertebrates occurring at certain horizons show the existence of an east–west trending basin. Whether this basin connected eastward to other series of rift basins and eventually the Tethys is still open to discussion.

The relative timings of brachiopod occurrences is relevant to discussion of the Hispanic Corridor versus Panthalassa-bound dispersal. Both *Zugmayerella uncinata* and *Rhaetina gregaria* are known from the Norian of Europe (mainly western Tethys) and Nevada although they are typically Rhaetian in Europe. Delance (1974) recorded *Zeilleria elliptica* from the latest Triassic of Europe. *Zeilleria* cf. *Z. elliptica* is recorded here from Nevada. The Norian terebratulid *Plectoconcha* predates the probably-related *Merophricus* (Cooper 1983) from the Jurassic of the Middle and High Atlas, Morocco. These records of *Z. uncinata*, *R. gregaria*, *Z.* cf. *Z. elliptica* and *Plectoconcha* may indicate American–Tethyan dispersal. *Balatonospira lipoldi* is first known from the Ladinian?–Carnian of Europe and *B*? cf. *B. lipoldi* from the Norian of Nevada. The nature and timing of occurrences of these faunas might suggest a western Tethys–American migration. These indications of two-way exchange between faunas are not inconsistent with the operation of the Hispanic Corridor in the Norian to Early Jurassic. Other faunal elements from the Luning of Nevada (Pilot Mountains and Union Canyon) clearly indicate that Tethyan species are present (Kristan-Tollmann and Tollmann 1983): two halobiid bivalves, both Tethyan; seven sponges, mostly endemic (one known from the Stikinia terrane, two from Sonora and one from Tethys; Senowbari-Daryan and Stanley 1992); seven foraminifers, all Tethyan; seven corals, all Tethyan. Tethyan cephalopods are also present.

MUSEUM ABBREVIATIONS

The following repository abbreviations are used: GBV, Geologische Bundesanstalt, Vienna, Austria; MSM, Mackay School of Mines Geological Museum, University of Nevada, Reno, USA; UMIP, University of Montana, Missoula, Invertebrate Palaeontology Collections, USA; USNM, former United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA Duméril, 1806
Class ARTICULATA Huxley, 1869
Order SPIRIFERIDA Waagen, 1883
Superfamily SPIRIFERINACEA Davidson, 1884
Family SPIRIFERINIDAE Davidson, 1884
Subfamily BALATONOSPIRINAE Dagys, 1974

Diagnosis. Small shells with ribbed sulcus and fold. Septum high, dental plates reduced. Jugum complete. Spinate microsculpture absent.

Discussion. (After Dagys 1974.) This monotypic subfamily differs from the Spiriferininae in the absence of both spinate microsculpture and dental plates. Discrimination from the Punctospirellinae which is similar in the nature of its microsculpture, is quite clearly made on the nature of the jugal structure and apical apparatus. Also lacking in spinate microsculpture is the Pennospiriferininae, from which the Balatonospirinae differ sharply in external appearance (shell form, character of area, ribbing, etc.), structure of the apical apparatus, as well as in the complete jugum.

Genus BALATONOSPIRA Dagys, 1974

Type species. Spiriferina lipoldi Bittner, 1890, p. 139, pl. 28, figs 20–21, from the *Cardita* horizon, Carnian, of Hoch-Obir, Austria.

Diagnosis. (After Dagys 1974.) Slightly inequivalved shells of small size with a short hinge line and rounded hinge angles. Beak curved, area low, apsacline. Deltidial and chilidial plates disconnected. Lateral portions of valves, as well as fold and sulcus, are ribbed.

EXPLANATION OF PLATE 1

Figs 1–5. *Spondylospira lewesensis.* UMIP 6716; Lower Member, Luning Formation; from the low hills between Cinnabar and Dunlap Canyons, Nevada, north of the prominent andesite rhyolite hill (type locality of *Platyplateon nevadensis*); collected by Muller in 1934; brachial, pedicle, lateral, anterior and posterior views respectively. All × 1·5.

Figs 6–10. *Spondylospira lewesensis.* UMIP 20314 (sectioned, Text-fig. 10B); Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral, anterior and posterior views respectively. All × 1·5.

Figs 11–15. *Zugmayerella* cf. *uncinata.* UMIP 20348; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral, posterior and anterior views respectively. All × 1·5.

Figs 16–20. *Zugmayerella uncinata.* UMIP 20365; Lower Member, Luning Formation; Cinnabar Canyon, Nevada; brachial, pedicle, lateral, anterior and posterior views respectively. All × 2.

Figs 21–24. *Balatonospira?* cf. *B. lipoldi.* UMIP 20416 (sectioned, Text-fig. 7), Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1·5.

Fig. 25. *Balatonospira?* cf. *B. lipoldi.* UMIP 20328; Lower Member, Luning Formation; Dunlap Canyon, Nevada; anterior view. × 1·5.

Figs 26–30. *Balatonospira?* cf. *B. lipoldi.* UMIP 20350; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral, anterior and posterior views respectively. All × 1·25.

PLATE 1
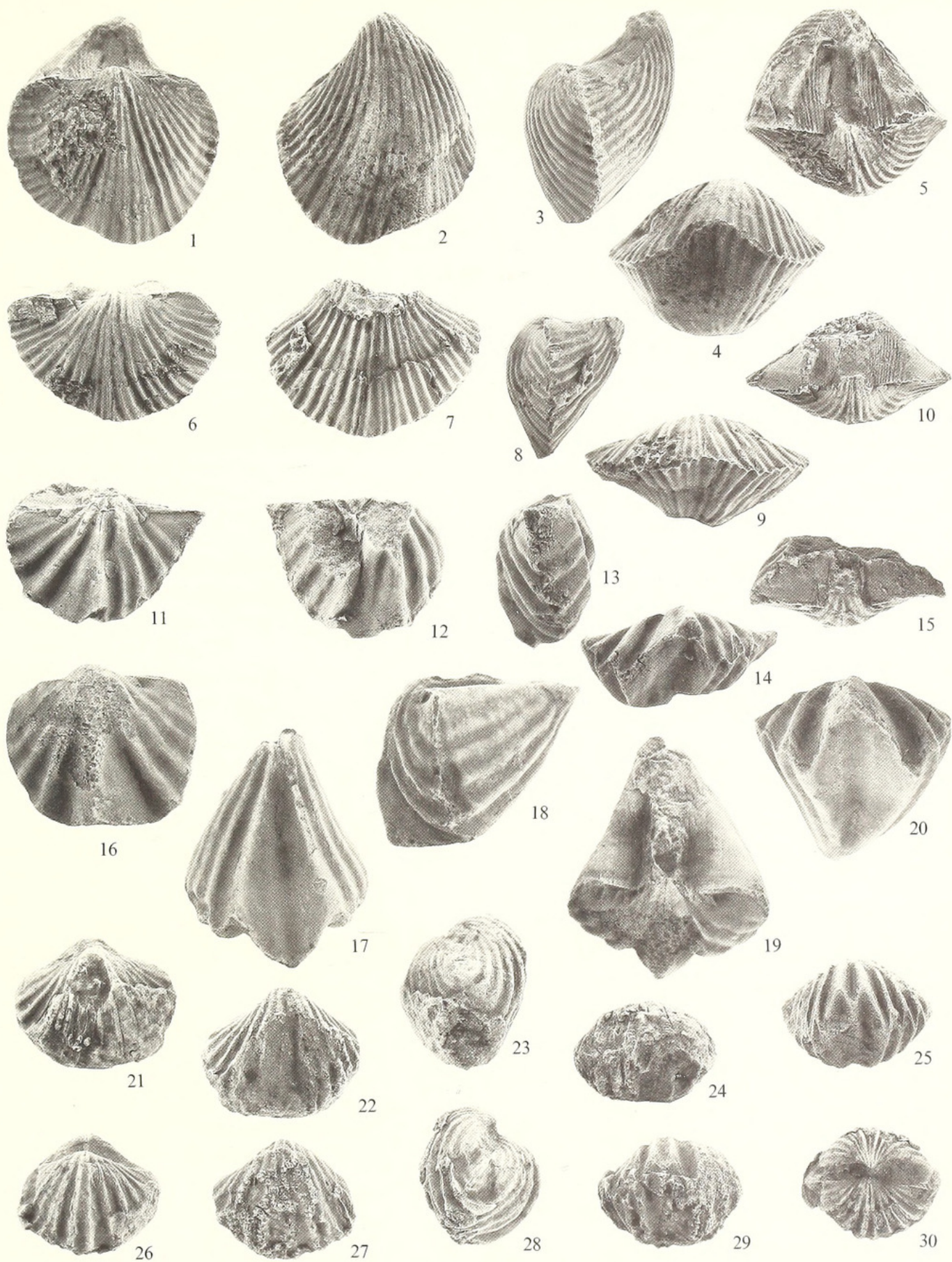
SANDY and STANLEY, *Spondylospira, Zugmayerella, Balatonospira*?

Discussion. It is possible that *Balatonospira* is a junior synonym of *Sinucosta* (see discussion for *B*? cf. *B. lipoldi*).

Occurrence. Ladinian?–Carnian stage of the Alps; Carpathians and Caucasus (Austria, Hungary, Bulgaria, Yugoslavia, Italy and Israel).

<div align="center">

Balatonospira? cf. *B. lipoldi* (Bittner, 1890)

Plate 1, figs 21–30; Text-figs 5–7
</div>

cf. 1890	*Spiriferina lipoldi* Bittner, p. 139, pl. 28, figs 20–21.
? 1972	*Balatonospira lipoldi* (Bittner); Detre, p. 89, pl. 1, fig. 2.
cf. 1974	*Balatonospira lipoldi* (Bittner); Dagys, p. 137, pl. 39, fig. 1.
? 1977	*Pseudospiriferina leopoldi* (Bittner) [*sic*]; Ching and Feng, p. 49, pl. 2, figs 16–21.
v cf. 1978	*Spiriferina* (= *Balatonospira*) *lipoldi* Bittner; Sieber, p. 170.
cf. 1988	*Balatonospira lipoldi* (Bittner); Siblik, p. 62.
v 1990	*Austrirhynchia*? sp.; Ager, p. 9.

Type material. The holotype is lost (Siblik 1988).

Material. Numerous specimens from the Luning Formation (beds 35 and 37 of Stanley, 1979, p. 53; Text-figs 1, 3), Dunlap Canyon; also common at Cinnabar Canyon. UMIP 6857, 20316, 20318, 20328–20331, 20335, 20341, 20345, 20350, 20361, 20371, 20379, 20384, 20386, 20396, 20400, 20404, 20415–20416 (sectioned), 20424, 20436.

Diagnosis. Medium sized spiriferinids, transversely oval, truncated outline, biconvex profile. Width greater than length; length greater than thickness. Incurved pedicle umbo, concave unornamented interarea. Triangular delthyrium with incipient deltidial plates. Ten to fifteen costae on each valve, two on brachial fold, one in pedicle sulcus. Punctate shell. Dental lamellae of brachial valve small, median septum persistent in pedicle valve. Dorsally directed crura.

Description. Small to medium sized spiriferids, up to 15 mm long, 18 mm wide and 12 mm thick (Text-fig. 5). Oval outline truncated by straight hinge line. Larger specimens have a strongly biconvex profile with an incurved pedicle umbo and an incurved, cataline pedicle valve interarea (see Logan 1967, text-fig. 6). Triangular delthyrium, incipient deltidial plates. Costae radiate from the umbos of each valve. Ten to fifteen costae on both valves (Text-fig. 6). Costate do not branch but are inserted laterally as the hingeline width
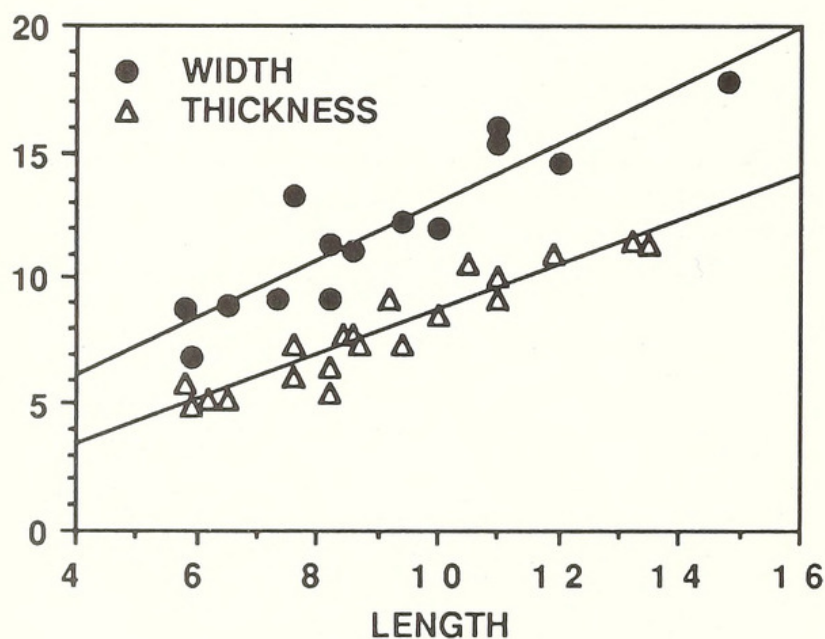
TEXT-FIG. 5. Plot of length versus width and thickness for *Balatonospira*? cf. *B. lipoldi* (Bittner); Pilot Mountains, Nevada. The correlation coefficient for length versus width is 0·830, and length versus thickness 0·883.
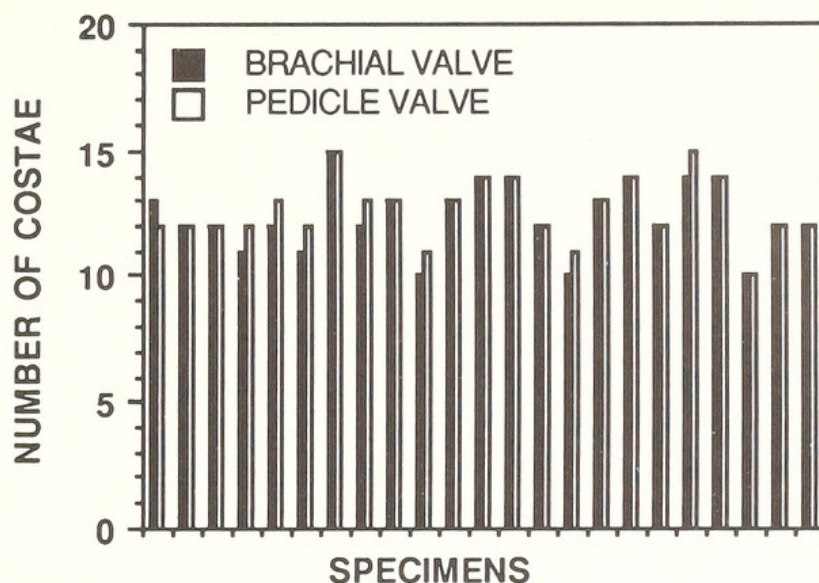
TEXT-FIG. 6. Bar graph of number of costae on brachial and pedicle valves of *Balatonospira*? cf. *B. lipoldi* (Bittner); Pilot Mountains, Nevada.

increases. Generally straight lateral commissure although may be some asymmetry. Anterior commissure gently uniplicate, costate. Punctae present.
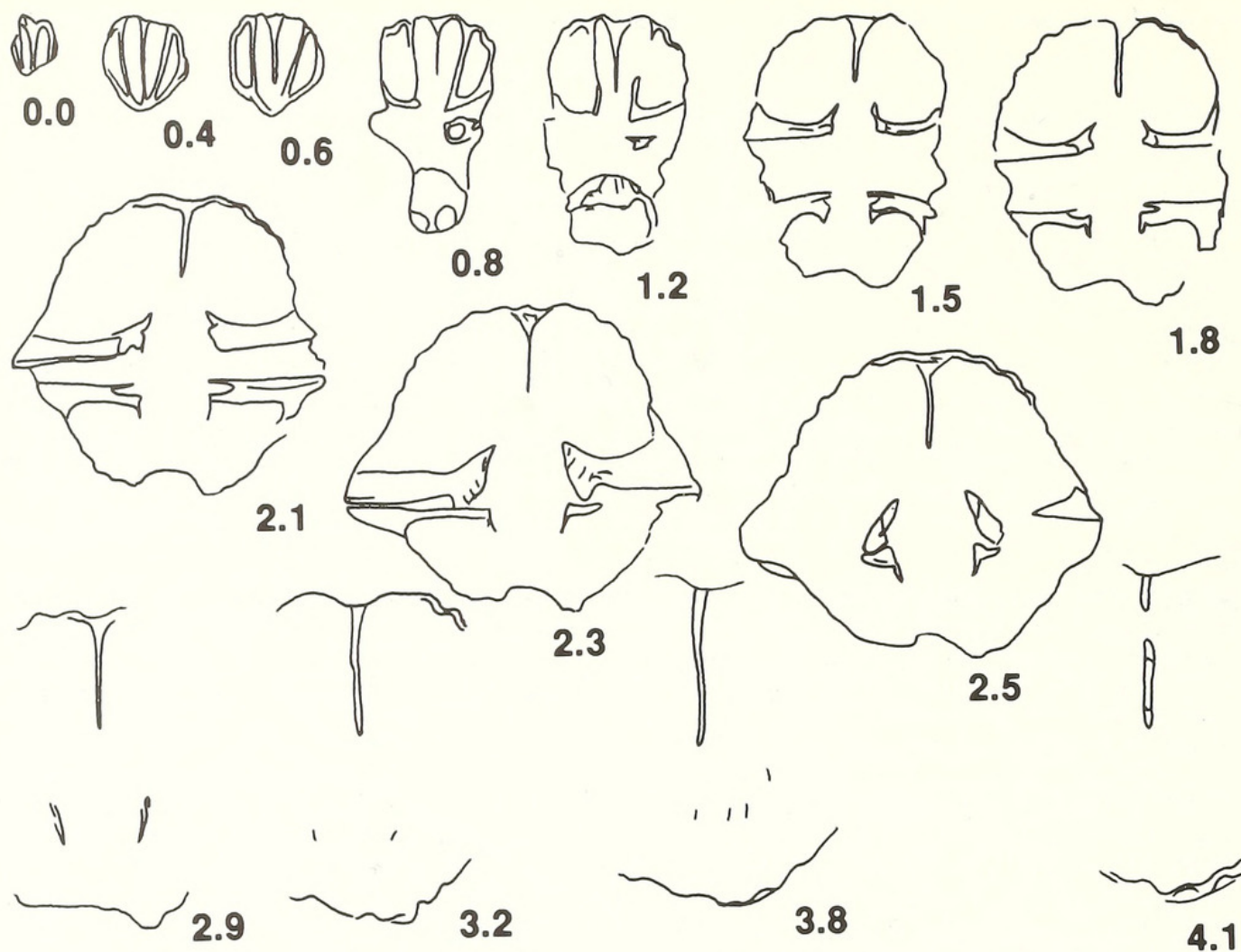
Transverse serial sections (Text-fig. 7) show the pedicle valve contains sub-parallel dental lamellae and a persistent median septum, traced to section 4.1 mm, after which it is a diminutive structure. Dorsally directed crura are attached to horizontal hinge plates (sections 1.8, 2.1). The spiralium is broken, traces of it may be present in section 3.8.

Discussion. The material of equivalent size from Nevada agrees very closely with the illustrations given by Bittner (1890), though our material reaches a larger size. Compared to *B. lipoldi* of Dagys (1974) our material tends to have a more incurved pedicle umbo and more marked pedicle sulcus; little significance is attached to these differences. The material from the former USSR is similar in size to Bittner's originals. Topotype material of *B. lipoldi* has been examined, in a block of pale yellowish brown (10 YR 6/2; Goddard *et al.* 1984) to pale yellowish orange (10 YR 8/6) weathering wackestone (GBV, number 1978/12/1); it also contained specimens of *Rhaetina* sp. Isolation of specimens for serial sectioning was not possible due to the friable nature of the fossils. However, it has been possible to grind the umbos of a few of them. In the brachial valve of one specimen a U-shaped hinge-trough or septalium was observed, but no additional details. The pedicle valve possesses a median septum, but no dental lamellae were seen. The shell is punctate. As dental lamellae have not been observed in topotype material of the species, the Nevadan specimens are referred to as *B*? cf. *B. lipoldi*. It may prove more appropriate to refer the Nevadan material to *Spiriferina*.

Pearson (1977) referred *Spiriferina lipoldi* Bittner, 1890 to *Sinucosta* Dagys, 1963. Dagys (1974) had previously referred the species to *Balatonospira*, in a monotypic subfamily. Pearson wrote his monograph prior to that of Dagys, although it was not published until after the latter appeared (see comment by Ager *in* Pearson 1977, p. 65). Dagys (1974, fig. 81) and Pearson (1977, fig. 1) both gave serial sections of specimens they referred to *Sinucosta emmrichi* (Suess). Both sets of sections show dental lamellae and a median septum in the pedicle valve. In his diagnosis of *Sinucosta*, Pearson (1977, p. 16) noted that the hinge line is shorter than maximum width. This is not the case with *lipoldi* where the maximum width is at or close to the hinge line.

The lack of a detailed description or serial sections of the material illustrated by Detre (1972) from the Carnian of the Bakony Mountains, Hungary, makes comparison with the Nevada specimens difficult. Similarly *Pseudospiriferina leopoldi* [*sic*] of Ching and Feng (1977) lacks serial sections. Two specimens of *B*? cf. *B. lipoldi* from Nevada were serially sectioned; the results from one specimen are given (Text-fig. 7). There are some differences between *B*? cf. *B. lipoldi* (Text-fig. 7) and *B. lipoldi* of Dagys (1974, fig. 92). Dental lamellae are not seen in the sections given by Dagys, the

TEXT-FIG. 7. Transverse serial sections through a specimen of *Balatonospira*? cf. *B. lipoldi* (Bittner); UMIP 20416; Lower Member, Luning Formation; Dunlap Canyon. Sections taken perpendicular to right lateral commissure and central costae on brachial valve. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Dental lamellae and median pedicle septum visible from 0.0, horizontal hinge plates (2.1–2.5) give rise to crura directed towards the floor of the brachial valve (2.1–2.9) and traces of the damaged spiralium (3.8). Last section taken through the median septum of the pedicle valve at 4·4 mm; last section taken at 4·7 mm. Magnification of sections, ×4. Dimensions of sectioned specimen: L = 12·4; W = 14·5; T = 10·9+ mm.

hinge plates are dorsally directed rather than horizontal and well-developed inner socket ridges are present. A ventrally arching cardinal process was observed in the other sectioned Nevadan specimen. The form of the median septum and crura are comparable in both series of sections from the Nevadan material. *Balatonospira* has punctae but no spinate microsculpture or dental plates, while *Sinucosta* has an impunctate shell with a micro-ornament of fine spines and divergent dental plates (Pearson 1977). In some of the Nevadan specimens where shell material has been partially lost, infilled punctae could be mistaken for a micro-ornament of fine spines. Type material of *S. emmrichi* (Suess, 1854) from Austria has not been investigated to examine the nature of shell ornament or structure in relation to that of *B. lipoldi* from Austria, or *B*? cf. *B. lipoldi* from Nevada. Yang and Yin (in Ching *et al.* 1979, p. 174, fig. 108) described *Balatonospira lipoldiformis* from China. The serial sections indicate the presence of well-developed dental lamellae and a ventrally arching cardinal process. There is therefore some doubt that the Chinese specimens belong to *Balatonospira*.

Occurrence. Lower Member, Luning Formation, Pilot Mountains, Nevada.

Family LABALLIDAE Dagys, 1962
Subfamily LABALLINAE Dagys, 1962
Genus ZUGMAYERELLA Dagys, 1963

Type species. Spiriferina koessenensis Zugmayer, 1880, p. 28, pl. 3, figs 2–3, 13, from the Rhaetian of Kitzberg, near Neusiedl, Piesting-Tal, Austria. Lectotype in the Palaeontological Institute of the University of Vienna (Pearson 1977).

Diagnosis. (From Pearson 1977, p. 23.) Medium sized pyramidal species. Beak tall; hinge line shorter than maximum width; lateral margins rounded. Sulcus and fold distinct, unribbed. Lateral slopes bear several ribs. Cardinal margin wholly or partially denticulate, area concomitantly ornamented with denticular ridges. Delthyrium open. Shell surface pustulose, possibly spinose. Dental lamellae fused with medium septum forming a spondylium-like structure. Cardinal process low, striate. Jugum as simple arch; descending lamellae of spiralia supported by plates. Punctate.

Discussion. Judging from the generic diagnoses for *Spondylospira* Cooper, 1944 and *Zugmayerella* given in Pitrat (1965) these genera are similar. *Zugmayerella* has a smooth fold and sulcus, i.e. only one costa forms the brachial fold, and no costa is present in the corresponding sulcus of the pedicle valve. Species of *Spondylospira* have more costae than those of *Zugmayerella*. The calcareous net supporting the descending lamellae of the spiralia in *Spondylospira* also appears to be present in *Zugmayerella*; 'the primary plates of the spiral are supported by net-like plates which, in turn, rest on low ridges in the valve bottom' (Dagys 1963, p. 99). A single pedicle valve from the Luning Formation, referred to ?*Zugmayerella* sp. (Plate 3, figs 5–6), appears intermediate between *Zugmayerella* and *Spondylospira*. It has strong costae and two costae in the sulcus. It casts some uncertainty on the validity of *Zugmayerella*.

Occurrence. Pearson (1977) recorded the genus from the Norian of Slovakia, east Bulgarian Balkan Mountains, Caucasus, Crimea and north east former USSR, and from the Rhaetian of the Northern Alps, Slovakia and north west Romania and probably the Carnian of Spitzbergen. Stanley (1979) recorded and figured *Z. uncinata* from Nevada. Newton (*in* Smith *et al.* 1990) recorded two species of *Zugmayerella* from the Late Triassic of Cordilleran America.

Zugmayerella uncinata (Schafhaeutl, 1851)

Plate 1, figs 11–20; Plate 3, figs 1–4; Text-figs 8–10A

  *1851   *Spirifer uncinatus* Schafhaeutl, p. 135, pl. 24, fig. 33.
  1880   *Spiriferina uncinata* Schafhaeutl; Zugmayer, p. 27, pl. 3, fig. 1.
  1963   *Zugmayerella uncinata* (Schafhaeutl); Dagys, p. 99.
  1977   *Zugmayerella uncinata* (Schafhaeutl); Pearson, p. 23, pl. 2, figs 6–10; text-figs 3–5.
  1979   *Zugmayerella uncinata* (Schafhaeutl); Stanley, p. 57, pl. 8, figs 10–12.
  1988   *Zugmayerella uncinata* (Schafhaeutl); Siblik, p. 75.
  1991   *Phenacozugmayerella mimuncinata* Hoover, p. 90, pl. 12, figs 6–24.

Type material. From 'Gervillien Schichten' of 'Hirschbühl hinter dem hohen Kramer bei Garmisch'; presumed lost (Pearson 1977, p. 23).

Material. Numerous specimens from Dunlap Canyon (Bed 35, Stanley 1979) and Cinnabar Canyon, Nevada (Text-figs 1, 3). Also from unnamed canyon 14·5 km east of Mina and from the Sonomia Quadrangle, south of Rose Creek, east of Auld Lang Syne Peak at approximately 2120 m, 23 m below top of the Dry Canyon Formation, East Range Mountains, Nevada. UMIP 6845, 6847, 6849, 6855–6856, 6858, 6861–6862, 6945, 20319–20321, 20334, 20338, 20343–20344, 20346, 20348, 20357, 20365–20366, 20368–20369, 20375, 20387, 20395, 20402, 20409, 20418, 20421, 20427.

Diagnosis. (From Pearson 1977, p. 23.) Ribs angular, three to five on lateral slopes of brachial valve. Cardinal margin partially denticulate; portion of area adjacent to delthyrium bears denticular ridges. Diagnosis otherwise as for genus.

Description. Pearson (1977, p. 23) gave a description of the species. Additional comments regarding the Nevada material are made here. Length is generally greater than width, which is greater than thickness. Brachial valve width is often greater than brachial valve length. The interarea width is generally greater than interarea height (Text-fig. 8). Interarea measurements are estimated in many cases and no account has been taken of the curvature of the interarea in the anterior–posterior plane. This results in a general underestimate of interarea heights, which may in fact be similar to interarea widths in more instances than indicated (Text-fig. 8). Five to nine costae were counted on brachial valves and five to ten on pedicle valves (Text-fig. 9). The brachial valve has one prominent costa marking the brachial fold, and no costae in the pedicle sulcus. A few specimens show fine capillae and many growth lines where the outer shell layer is preserved. Transverse serial sections have been
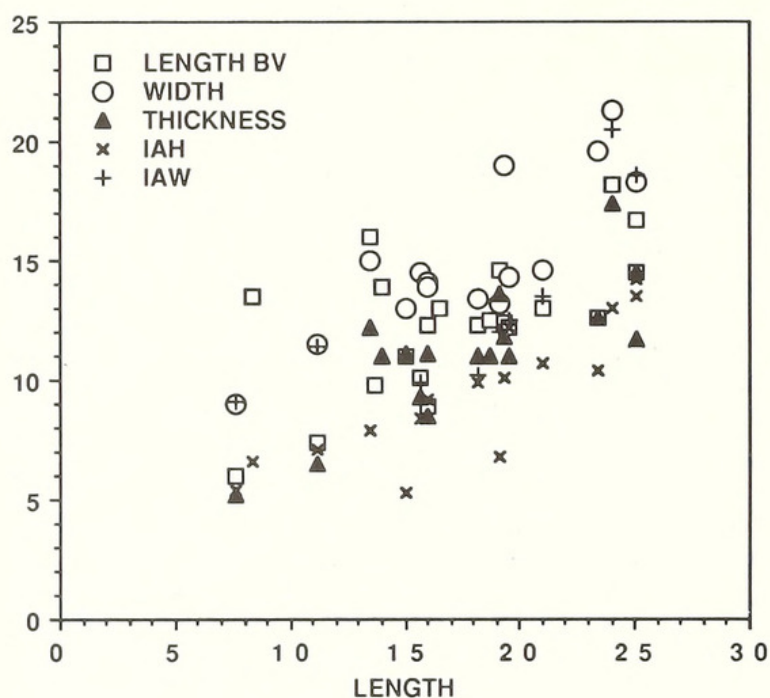
TEXT-FIG. 8. Plot of length versus width, thickness, length of brachial valve; interarea height; and interarea width for *Zugmayerella uncinata* (Schafhaeutl); Pilot Mountains, Nevada.
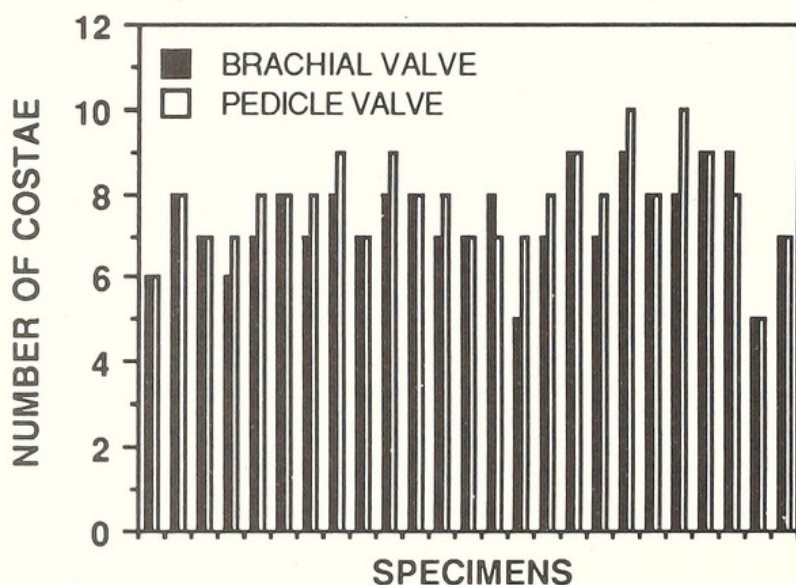
TEXT-FIG. 9. Bar graph of number of costae on brachial and pedicle valves of *Zugmayerella uncinata* (Schafhaeutl); Pilot Mountains, Nevada.

taken through one specimen (Text-fig. 10A). These show the dental lamellae fused to the median septum in the pedicle valve to form a spondylium-like structure (sections 1.5, 1.9, 3.0) with a median septum. Serial sections were taken for 3 mm from the initial section. The brachidium was not preserved in the sectioned specimen.

Discussion. In discussing the morphology of *Zugmayerella koessenensis* (Zugmayer), Pearson (1977, pp. 28–29) commented that this species is somewhat laterally compressed, both valves are characteristically elongate in outline, the prominent fold and sulcus are medianly flattened in all but the youngest specimens and rare adults and that the costae are narrow and rounded. At least four costae are present on the lateral slopes of the brachial valve of the smallest specimens with up to six in adult specimens (Pearson 1977). These characters have been used to distinguish *Z. koessenensis* from *Z. uncinata*. The number of costae counted on the Nevada specimens ranges up to nine on the brachial valve and ten on the pedicle valve (Text-fig. 9). However, using the number of costate present on a specimen to identify it has to be done with consideration of other characters because costation is a variable character. Only the dental lamellae, median septum and spondylium-like structure of the pedicle valve were seen in a series of transverse serial sections (Text-fig. 10A). Damage to the brachial valve umbo is the probable reason for the absence of the cardinal process (cf. Pearson 1977, fig. 4). Other details of the brachial valve's internal structures were not preserved.

Recently, Hoover (1991) described a new genus and species, *Phenacozugmayerella mimuncinata*. He commented that it is easily confused with *Zugmayerella uncinata*, differing from it by its capillate-cancellate surface micrornament, and in lacking the duplex interarea that is characteristic of the latter species. Many of the spiriferinacean brachiopods described by Hoover (1991) from western North America typically are silicified. Brachiopods collected from localities in the Pilot Mountains still retain calcitic shell material. It may be that the capillate-cancellate micrornament noted by Hoover as a distinguishing feature of *Phenacozugmayerella mimuncinata* is seen on these specimens because of their detailed preservation; perhaps cruder silicification does not preserve this fine surface ornament.

Occurrence. Lower Member, Luning Formation, Pilot Mountains, Nevada. Pearson (1977, p. 24) noted the characteristic occurrence of *Z. uncinata* with *Rhaetina gregaria* (recorded by earlier authors). Pearson (1977, p. 24) reported it from the Norian–Lower Lias of the French and Italian Alps, Slovakia, Polish sub-Tatra, northwest Iran, Romania and east Iran. He also noted its occurrence in the Lower Lias of northeast Turkey and the Pamirs and he thought that this species persisted into the Lower Lias of the German Alps.

<div align="center">

?Zugmayerella sp.

Plate 3, figs 5–6

</div>

Material. One pedicle valve, UMIP 6952.

Dimensions. L = 22·0+ ; W = 17·8+.

Description. The single pedicle valve has an incurved umbo and twelve costae. Many of the costae are strong. The sulcus contains two costae. The interarea appears smooth. In the pedicle valve dental lamellae unite with a median septum to form a spondylium.

Discussion. This single pedicle valve is distinguished from other brachiopods from Nevada by the strength of the costae and the smooth interarea. The strong costae and presence of a spondylium suggest affinities with *Zugmayerella*. The presence of costae in the pedicle sulcus distinguish it from *Z. uncinata* which possesses no costae in the sulcus. *Spondylospira lewesensis* has more numerous and finer costae than species referred to *Zugmayerella*. The interarea in *?Zugmayerella* sp. appears smooth, lacking the vertical striations typically found in *Zugmayerella* and *Spondylospira*. However, this may be due to poor preservation. A spondylium is present in the pedicle valve showing that the specimen is a homoeomorph of *Neoretzia superba* (Suess, 1856). The presence of strong costae on the pedicle valve and two in the sulcus of *?Zugmayerella* sp. suggests it may be intermediate between
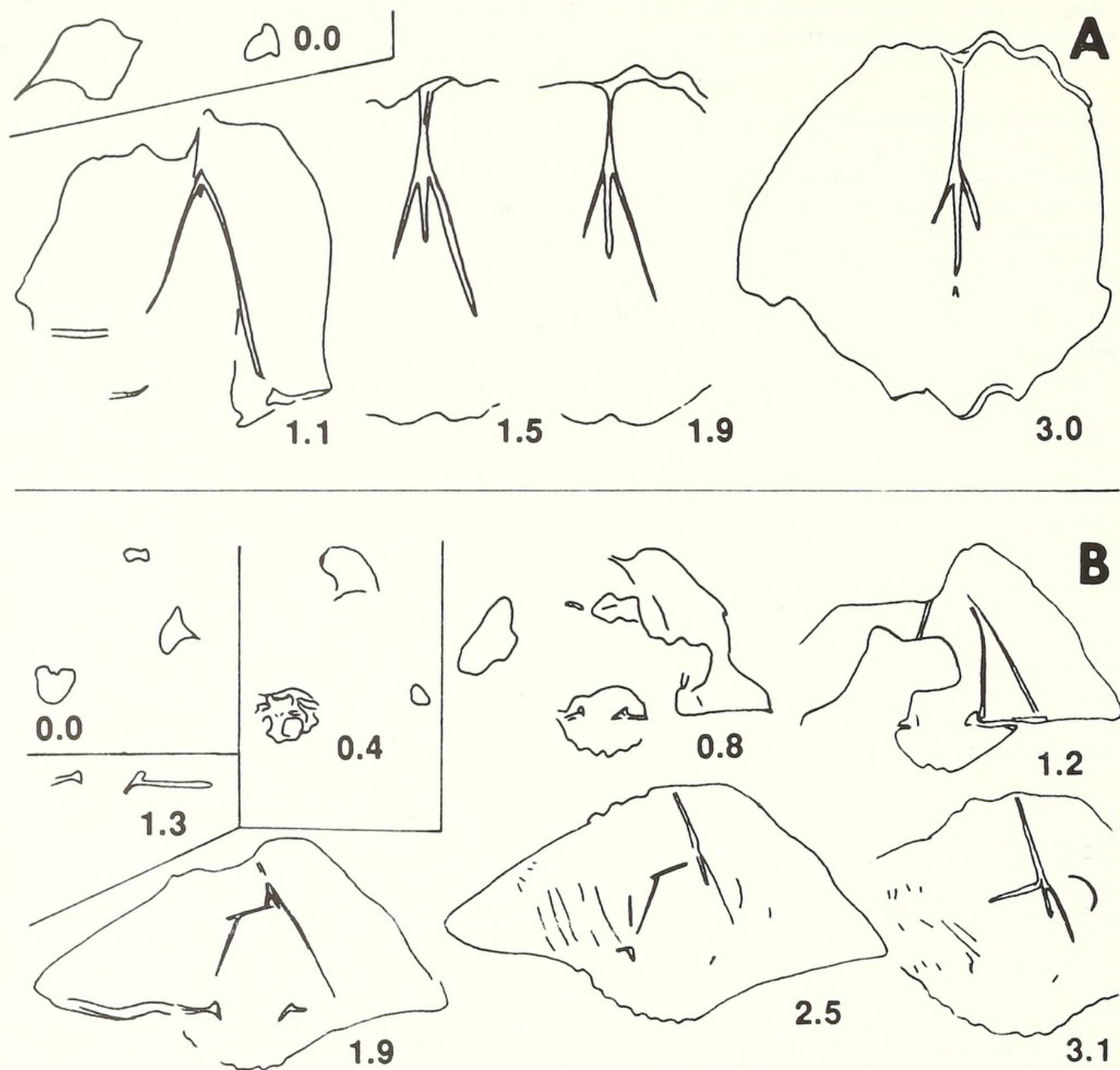
TEXT-FIG. 10. A. Transverse serial sections through a specimen of *Zugmayerella uncinata* (Schafhaeutl); UMIP 20320; Lower Member, Luning Formation; Dunlap Canyon. Sections taken perpendicular to posterior part of right-lateral commissure and central costae on brachial valve. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Spondylium-like structure (dental lamellae and extended median septum of pedicle valve) seen in sections 1.1–3.0. Last section taken through specimen at 3·0 mm. Magnification of sections, ×4. Dimensions of sectioned specimen: L = 17·9+; Lbv = 11·8; W = 13·6; T = 10·3 mm. B, Transverse serial sections through a specimen of *Spondylospira lewesensis* (Lees); UMIP 20314; Lower Member; Luning Formation; Dunlap Canyon, Nevada. Sections taken perpendicular to lateral commissure and brachial valve length. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Detail of hinge plates only shown at 1.3, damaged spondylium-like structure seen in sections 1.9–3.1, traces of damaged spiralium seen in sections 2.5–3.1. Last section taken through specimen at 3·6 mm. Magnification of sections, ×2.5. Dimensions of sectioned specimen: L = 18·3+; Lbv = 16·1; W = 25·1; T = 13·0+ mm.

Zugmayerella and *Spondylospira*. Alternatively, it may be derived independently from *Zugmayerella* (or *Spondylospira*). It casts some uncertainty on the validity of the genus *Zugmayerella*.

Occurrence. Luning Formation (probably Lower Member), unnamed canyon 14·5 km east of Mina, Nevada (locality MC of Stanley 1979).

Genus SPONDYLOSPIRA Cooper, 1942

Type species. *Spondylospira reesidei* Cooper, 1942, p. 232; 1944, p. 359, pl. 140, figs 43–47, from the Seven Devils Formation, Triassic, east side of Mission Creek, 1·5 miles (2·4 km) above Mission, 4·5 miles (7·3 km) above Jacques, about Section 15, Township 36 N, Range 3 W, Nez Perce County, Idaho.

Occurrence. Hoover (1983) recorded the genus from the Carnian to late Norian (Suessi Zone) of North and South America. In Central Peru it may also extend into the lowermost Jurassic (Hoover 1990).

Spondylospira lewesensis (Lees, 1934)

Plate 1, figs 1–10; Text-fig. 10B

*1934	*Cyrtina lewesensis* Lees, p. 35, pl. 1, figs 14–16.	
1937	*Spiriferina acrotamboensis* Körner, p. 168, pl. 11, figs 5–8.	
1942	*Spondylospira reesidei* Cooper, p. 232.	
1944	*Spondylospira reesidei* Cooper, p. 359, pl. 140, figs 44–47.	
1944	*Spondylospira alia* Cooper, p. 359, pl. 140, figs 48–51.	
1962	*Spondylospira lewesensis* (Lees); Tozer, p. 26, pl. 12, figs 11–13.	
1972	*Spondylospira lewesensis* (Lees); Tozer, p. 638, pl. 18, fig. 15a–c.	
1974	*Spondylospira reesidei* Cooper; Dagys, p. 145, pl. 41, figs 5–8.	
1974	*Spondylospira lewesensis* (Lees); Dagys, pl. 41, fig. 9a–b.	
1983	*Spondylospira lewesensis* (Lees); Hoover, p. 1026, figs 3G–s, fig. 5.	
1991	*Spondylospira lewesensis* (Lees); Hoover, p. 81, pl. 9, figs 10–38; pl. 10, figs 1–3.	

Holotype. USNM 10346a.

Diagnosis. (From Hoover 1983, p. 1027.) *Spondylospira* with strong costae on dorsal fold that increase initially by equal bifurcation, subsequently by equal or unequal bifurcation; fold and sulcus moderately to strongly developed; deltidial plates and bipartite cooperculum rarely preserved.

Material. Three complete specimens (UMIP 6716, 20314, 20428), one brachial (UMIP 6909) and two pedicle valves (UMIP 20389, 20420). UMIP 6716 and 6909 were collected from the low hills between Cinnabar and Dunlap Canyons, north of the prominent andesite rhyolite hill (type locality of *Platyplateon nevadensis*) by S. W. Muller in 1934. UMIP 20314, 20389, 20420 and 20428 were collected from Dunlap Canyon. One specimen from 'Brachiopod Ledge' (Text-fig. 2, locality B), Berlin-Ichthyosaur State Park (Hogler Collection). All specimens are from the Luning Formation.

Description. Dimensions of specimens: UMIP 6176: L = 27·9+; Lbv = 19·8; W = 23·9; T = 15·9; UMIP 20314: L = 18·6+, Lbv = 16·3, W = 25·1; T = 11·6; UMIP 20420: L = 25·0; W = 21·3. Counts were made of the number of costae on each valve. The counts are estimates, made at the commissure of each specimen. UMIP 6716: brachial valve costae (BVC) 29; brachial fold costae (BFC) 7; pedicle valve costae (PVC) 31; pedicle sulcus (PVS) 7. UMIP 20314: BVC 24; BFC 5; PVC 28; PVS 5. UMIP 20389: PVC 18. Neither the deltidial plates nor the cooperculum have been observed in any of the specimens from Nevada.

Discussion. *Spondylospira lewesensis* is highly variable in its external morphology (see Hoover 1983 for a recent discussion). It is externally homoeomorphic with *Sinucosta emmrichi* (Suess, 1854) figured by Pearson (1977, pl. 1, figs 9–14, and especially that of Zugmayer 1880, figured by Pearson 1977, pl. 1, fig. 9). *Spondylospira lewesensis* differs in its external morphology from *Sinucosta*

emmrichi by lacking the dense network of fine spines noted by Pearson for the latter species and in possessing a vertically striated interarea. The internal structures of one specimen have been investigated (Text-fig. 10B). They show the presence of dental lamellae (section 1.2) and a median septum (section 1.9) in the pedicle valve which are fused into a spondylium-like structure (sections 1.9, 2.5, 3.1). A small, flat cardinal process is present in the brachial valve (section 0.4). Crura are directed dorsally (sections 0.8, 1.2, 1.3, 1.9, 2.5) from horizontal hinge plates (section 1.3). The spondylium-like structure and the brachidium were damaged (sections 1.9, 2.5, 3.1).

Occurrence. Lower Member, Luning Formation, Pilot Mountains, Nevada. *Spondylospira lewesensis* was recorded from the late Carnian to late Norian (Suessi Zone) by Hoover (1983), from North America (Alaska, California, Idaho, Nevada, Oregon, Yukon Territory) and South America (Peru).

Order TEREBRATULIDA Waagen, 1883
Suborder TEREBRATULIDINA Waagen, 1883
Superfamily TEREBRATULACEA Gray, 1840
Family TEREBRATULIDAE Gray, 1840
Subfamily PLECTOCONCHINAE Dagys, 1974 (emended Cooper 1983)
Genus PLECTOCONCHA Cooper, 1942

Type species. Rhynchonella aequiplicata Gabb, 1864, p. 35, pl. 6, fig. 37, from the Cinnabar District, Humboldt Mountains, Nevada.

Diagnosis. (Modified from Cooper 1983, p. 38.) Medium to large, semicostate. Beak labiate. Anterior commissure rectimarginate to uniplicate. Outer hinge plates dorsally attached to crural bases. Loop short, wide.

Discussion. Despite records of *Plectoconcha* from China (Sun *et al. in* Ching *et al.* 1979) and the Soviet Union (Dagys 1974), our study confirms *Plectoconcha* as endemic to Nevada, USA. The only genus that Cooper (1983) considered similar enough to *Plectoconcha* to place it in the same subfamily is the plicate *Merophricus* from the Lower Jurassic of the Middle and High Atlas, Morocco. This is particularly interesting for palaeogeographical interpretation.

Occurrence. Luning Formation, Shoshone and Pilot Mountains and Dun Glen Formation, East Range, Nevada.

Plectoconcha aequiplicata (Gabb, 1864)

Plate 2, figs 1–8, 21–28; Text-figs 11–12

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*1864   Rhynchonella aequiplicata Gabb, p. 35, pl. 6, fig. 37.
 1914   Rhynchonella aequiplicata Gabb; Smith, p. 146, pl. 44, figs 9–11.
 1959   Plectoconcha cf. Plectoconcha aequiplicata (Gabb); Silberling, p. 22, pl. 11.
 1979   Plectoconcha aequiplicata (Gabb); Hoover, p. 10, pl. 2, figs 6–7.
 1983   Plectoconcha aequiplicata (Gabb); Cooper, p. 48, pl. 59, figs 11–14.
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Type material. Gabb's original figured specimen could not be located in the collections of the USNM (Thompson personal communication).

Diagnosis. (Modified from Cooper 1942, p. 233.) Terebratuloid, generally rotund and longer than wide; uniplicate with superimposed alternate multiplication. Foramen large, permesothyrid, labiate. Deltidial plates not exposed. Pedicle valve interior with large strong teeth not supported by dental plates. Pedicle collar strong. Cardinalia with strong inner socket plate and deep sockets. Broad cardinal process. Crural bases directed ventrally, crural processes close to end of hinge plates.

Crural processes high, subparallel. Loop short and wide, descending lamellae short and flaring laterally; transverse band high arched.

Material. Numerous specimens from red-weathering massive limestone beds, limestone and secondary dolomite member of the Luning Formation. Collected loose from the south facing slope, north of the Union Canyon Fault (Silberling 1959, p. 22, pl. 10) at the eastern end of West Union Canyon, at an altitude of approximately 2400 m above sea level, latitude 38° 52′ 30″ N, longitude 117° 34′ 00″ W, Nye County, Nevada (Text-fig. 2, locality A); UMIP 20447–20453. Numerous small specimens were collected from an exposure on the west facing slope to the north of the Union Canyon Fault (Silberling 1959, p. 22, pl. 10) at an altitude of approximately 2400 m above sea level. This exposure has been informally named Brachiopod Ledge by Hogler (Text-fig. 2, locality B); UMIP 20437–20442.

In addition there are approximately 140 specimens in the collection of the United States Geological Survey, Denver, Colorado from Berlin-Ichthyosaur State Park, locality LSJU 800-b (also labelled LSJU 2778, 2940, 2948). These were collected from the Luning Formation by S. W. Muller and N. J. Silberling on the east side of Union Canyon, about 1·6 km from the mouth of the canyon (Ione 15′ quadrangle map, Township 12 North, Range 39 East); this approximates to locality A (Text-fig. 2). In addition, a few specimens referable to *Plectoconcha aequiplicata* have been identified from the Luning Formation of the Pilot Mountains.

Description. Large terebratulids with round outline and evenly biconvex profile. Approximate maximum dimensions, length 35 mm, width 27 mm, thickness 28 mm. Length is greater than width and thickness. The pedicle umbo is suberect to erect, with a large rounded, labiate pedicle foramen. Both valves bear coarse costae (approximately 14) that run most of the length of the valves, although the number of costae is variable. The plicate anterior commissure may be broadly uniplicate. The specimens are generally poorly preserved, infilled with a dark grey (N 3, Goddard *et al.* 1984) micrite. Many valves are partly coated by a light brown to moderate reddish orange (5 YR 6/4 to 10 R 6/6, Goddard *et al.* 1984) layer of calcite, probably originating from recent surficial weathering. Internal structures show a cardinal process that has overgrown concave juvenile hinge plates (Text-fig. 11, section 3.2 mm). Anteriorly hinge plates are subhorizontal (sections 4.8, 5.2). Crural processes develop rapidly from free crural bases (sections 6.1–7.3). Transverse band high-arched (section 9.5).

Discussion. The species is represented by large and small forms collected from two different horizons. The large specimens from West Union Canyon agree well with material originally described and figured by Gabb (1864, pl. 6, fig. 37, reprinted in Smith 1914, pl. 44, figs 9–11) from the Cinnabar District, East Range, Nevada. Both show a rounded outline, biconvex profile, large, round pedicle foramen and a similar number of strong costae covering the valves. Cooper (1983, pl. 59, figs 11–12) figured a hypotype of *Plectoconcha aequiplicata* collected from the Luning Formation, 610 m ENE of Richmond Mine, 1·6 km from the mouth of Union Canyon, East side, Nye County. (A hypotype is a specimen described and/or illustrated after the establishment of the type lot; G. A. Cooper, personal communication). This specimen is certainly from the same locality and horizon from which the material described herein was collected. Cooper also figured an imperfect brachidium of a specimen of *P. aequiplicata* from Pershing County, Nevada (1983, pl. 59, figs 13–14, previously figured by Hoover 1979, pl. 2, figs 6–7), and a reconstruction (1983, pl. 66, figs 14–15). Comparing the serial sections of the Early to Middle Triassic species *P. variabilis* (Dagys, 1974) with the brachidium of the type species, Cooper (1983, p. 48) considered the Soviet species to belong to a different stock. '*P.*' *variabilis* possesses dorsally directed 'prefalcifer' crura and a centronellid stage in its loop development (translation from Dagys 1974, p. 197, *in* Cooper 1983, p. 38). These features, in addition to others considered by Cooper (1983), distinguish it at the genus and species level from the type species. The species from the former USSR is smaller and has a more elongate outline than *P. aequiplicata*.

Transverse serial sections have been taken through one large specimen of *P. aequiplicata* from Nevada (Text-fig. 11; described above). These confirm Cooper's observations on the differences between the American material and that from the former USSR. The sections also show that Chinese material referred to *Plectoconcha* by Sun *et al.* (*in* Ching *et al.* 1979, p. 196) does not belong in this genus. Sun *et al.* recorded a new species, '*P.*' *delicata* from the Triassic of China. It appears

to be smaller in size and with fewer costae than the type species, *P. aequiplicata*. The crura are falcifer-type (Sun *et al. in* Ching *et al.* 1979, fig. 132) and bear a similarity to the crura shown by Dagys (1974, fig. 143). Compared with the Soviet species the transverse band is low-arched in the Chinese species. Therefore, the genus *Plectoconcha* has only been substantiated in Nevada, USA.

Silberling (1959, p. 17) recorded abundant terebratuloid and rhynchonelloid brachiopods approximately 160 m above the base of the limestone and secondary dolomite member of the Luning Formation in the massive limestone bluffs near the crest of the ridge forming the southeast wall of West Union Canyon. On his plate 11 Silberling (1959) recorded abundant terebratuloid brachiopods from the carbonate member. The specimens of *Plectoconcha* were collected from these horizons, the smaller specimens from a ledge ('Brachiopod Ledge'; Text-fig. 2, locality B) in the massive limestone bluffs. The small forms are interpreted as juveniles of *P. aequiplicata*. It is interesting that the large and small specimens occur at different horizons (Silberling 1959; Hogler personal communication) and were therefore not synchronous. If the large and small forms are representatives of the same species, current-sorting or palaeoecological and palaeoenvironmental differences are indicated to account for the absence of small and large forms at the same horizon. The outline of the small forms ranges from subtriangular to rounded. Their profile is markedly biconvex. The costae are coarse and well developed. It has proved difficult to obtain many measurements for both large and small forms as they are often broken and the removal of adhering matrix from the small specimens is also a problem. The internal structures of one small specimen have been investigated (Text-fig. 12). These show a flat cardinal process (section 1.9 mm), hinge plates that are flat (section 2.0), to gently ventrally convex (section 2.6) and crural bases that project ventrally (section 3.2) and rapidly to the crural processes (section 4.6). The crural processes are incurved (section 5.0). This may reflect the form of the crural processes in juvenile *Plectoconcha*. It does not appear to be due to damage to the brachidium. A moderately arched transverse band was seen in another damaged specimen that was partially ground on a diamond wheel. These characters, both external and internal, support the assignation of these small forms to *Plectoconcha*, and indicate that they may be juveniles of *P. aequiplicata*.

Hoover (1979) created the new genus *Vex*, for '*Terebratula*' *semisimplex* White, 1880. The species is probably from the Portneuf Limestone Member of the Thaynes Formation, southeastern Idaho.

EXPLANATION OF PLATE 2

Figs 1–4. *Plectoconcha aequiplicata*. UMIP 20449; limestone and secondary dolomite member, Luning Formation; West Union Canyon, Berlin-Ichthyosaur State Park, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1.

Figs 5–8. *Plectoconcha aequiplicata*. UMIP 20448 (sectioned, Text-fig. 11); limestone and secondary dolomite member, Luning Formation; West Union Canyon, Berlin-Ichthyosaur State Park, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1.

Figs 9–12. *Plectoconcha newbyi* sp. nov. UMIP 20410, holotype; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1·3.

Figs 13–16. *Plectoconcha newbyi* sp. nov. UMIP 20322, paratype; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1·3.

Figs 17–20. *Plectoconcha newbyi* sp. nov. UMIP 20412 (sectioned, Text-fig. 14), paratype; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1·3.

Figs 21–24. *Plectoconcha aequiplicata*. UMIP 20441, juvenile; limestone and secondary dolomite member, Luning Formation; West Union Canyon, Berlin-Ichthyosaur State Park, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1·5.

Figs 25–28. *Plectoconcha aequiplicata*. UMIP 20439 (sectioned, Text-fig. 12), juvenile; limestone and secondary dolomite member, Luning Formation; West Union Canyon, Berlin-Ichthyosaur State Park, Nevada; brachial, pedicle, lateral and anterior views respectively. All × 1·5.

PLATE 2

SANDY and STANLEY, *Plectoconcha*
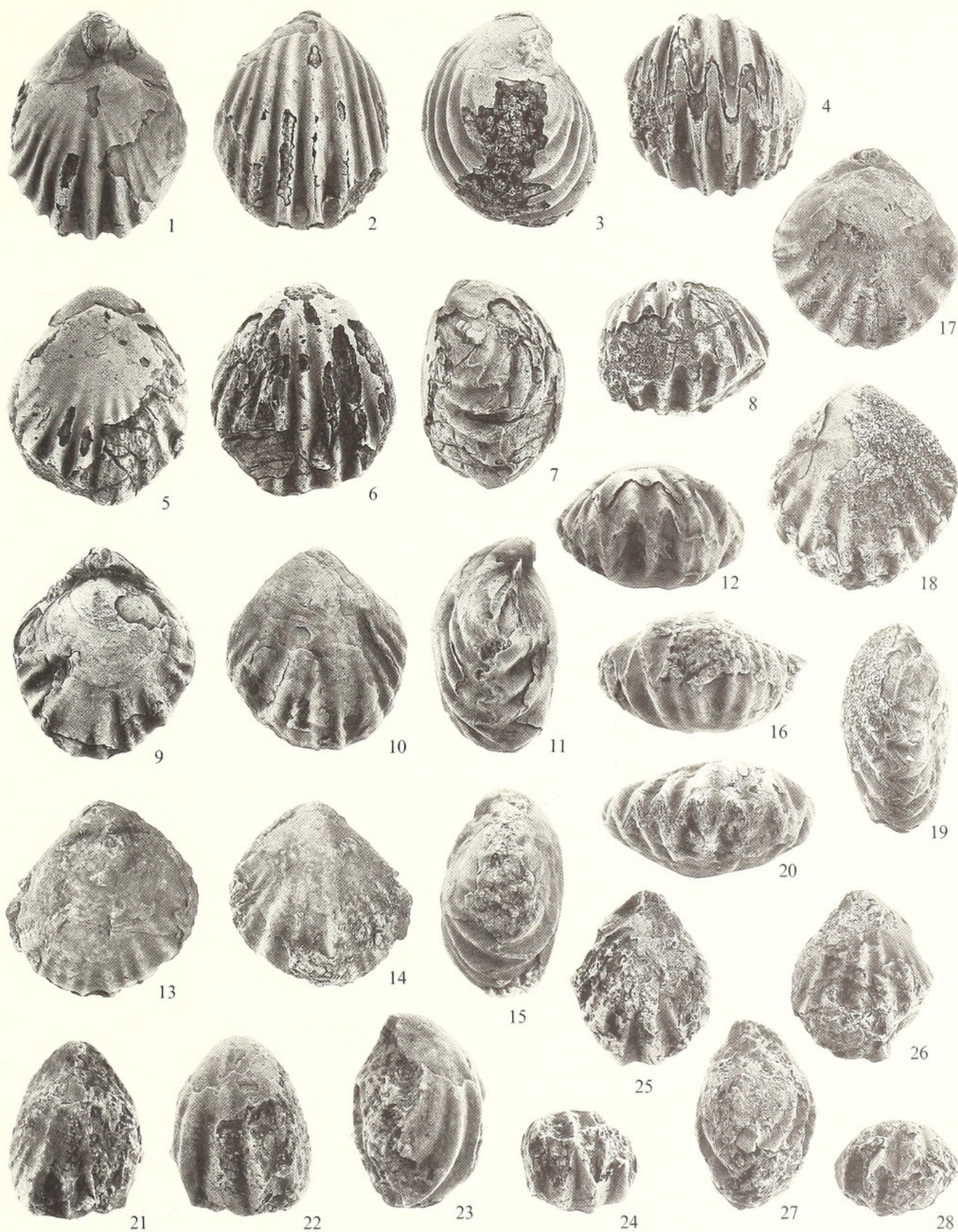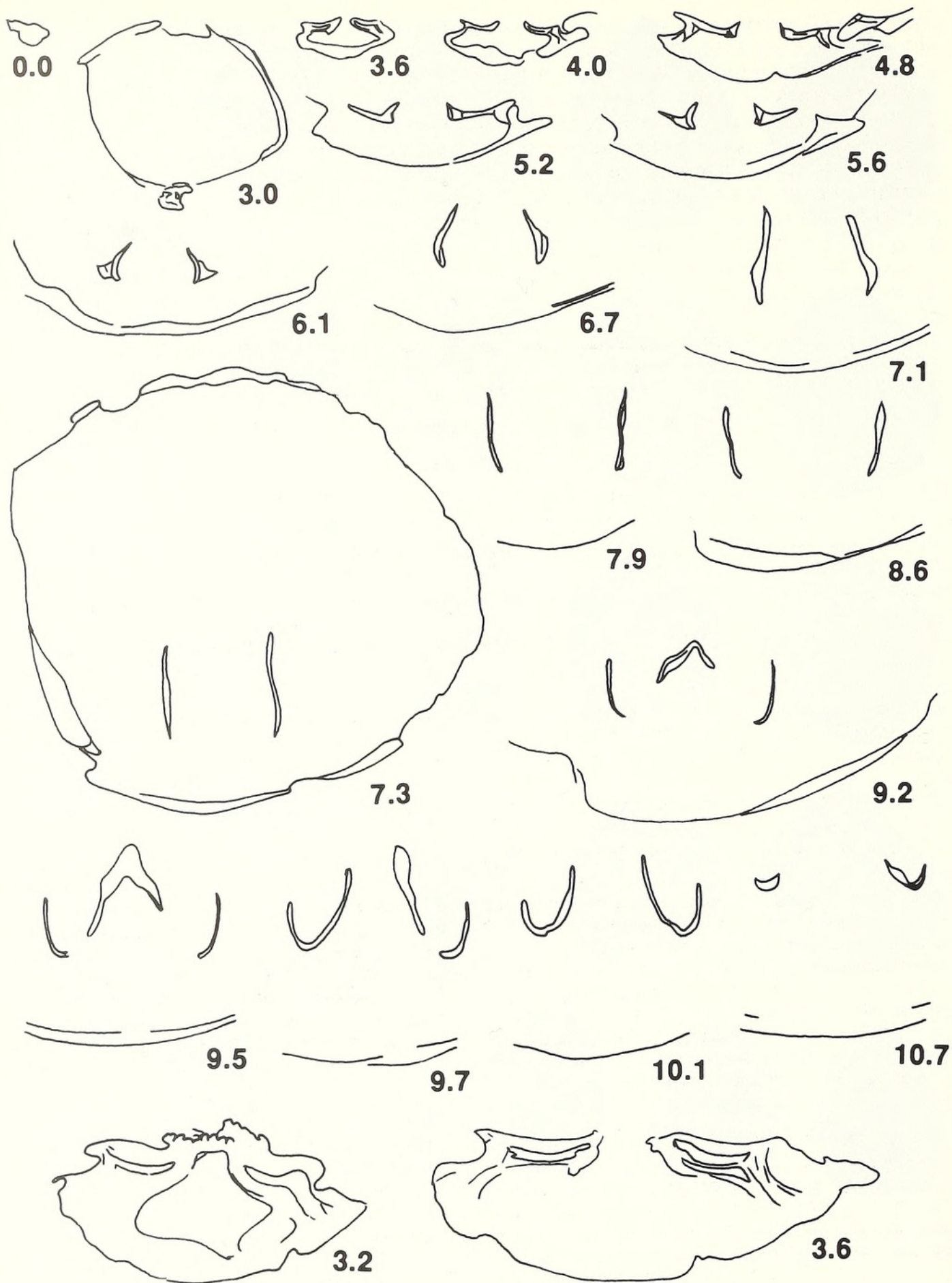
Hoover (1979, p. 10) commented on the similarities between *Vex* and *Plectoconcha*. He noted that the loops of both genera are not well known but that they are similar externally, with *Plectoconcha* commonly larger. Hoover (1979) referred *Vex* to the subfamily Plectoconchiinae (*sic*), but Cooper (1983) considered that it was not a terebratulid, and that there was no established family for the genus. Cooper commented (1983, p. 51) that the long loop of *Vex* was suggestive of *Zeilleria*, but that it lacked a median septum and dental lamellae found in the latter genus.

In the original description of *Plectoconcha aequiplicata*, Gabb (1864) figured a specimen from the Cinnabar district, East Range, Nevada. It was considered a Middle Triassic species (Smith 1914). Whilst the material described herein from the Shoshone Mountains is not topotypic (i.e. it is not from the East Range), it is probably from strata of a similar age. The material described by Gabb is from the Magnus Zone (late early Norian, Dun Glen Formation; Silberling, personal communication).

Occurrence. Limestone and secondary dolomite member, Luning Formation, West Union Canyon, Berlin-Ichthyosaur State Park, Union district, Nye County, Shoshone Mountains; Lower Member, Luning Formation, Pilot Mountains; Dun Glen Formation, Cinnabar district, East Range, Nevada.

Plectoconcha newbyi sp. nov.

Plate 2, figs 9–20; Text-figs 13–14

1979   Rhynchonellid, Stanley, pp. 14, 57, pl. 8, figs 5–6.
1979   Terebratulid, Stanley, pp. 14, 57, pl. 8, figs 8–9.

Derivation of name. For the late Paul Newby, of Esher, Surrey, England, family friend of M. R. S.

Holotype. UMIP 20410, Lower Member, Luning Formation, Dunlap Canyon, Pilot Mountains, Nevada.

Paratypes. UMIP 20322, 20354, 20358, 20412, 20425, Lower Member, Luning Formation, Pilot Mountains, Nevada.

Material. Numerous specimens from the Luning Formation of Dunlap and Cinnabar Canyons. UMIP 6852, 20323–20327, 20332, 20333?, 20342, 20351, 20353, 20360, 20362–20363, 20367, 20372–20373, 20378, 20383, 20398, 20403, 20408, 20414, 20426?, MSM 6172, 6182–6183, 6189.

Diagnosis. *Plectoconcha* of medium size, rounded outline, costate margins, smooth stage posteriorly, rectimarginate to uniplicate anterior commissure. Flat cardinal process, ventrally concave hinge plates, high crural processes, moderately arched transverse band.

Description. *Plectoconcha newbyi* has a rounded outline and biconvex profile. Maximum length is greater than width which is greater than thickness (Text-fig. 13). The anterior commissure is rectimarginate to uniplicate and may develop an incipient biplication. The lateral commissure is gently deflected towards the pedicle valve. The anterior half of both valves is costate, but smooth posteriorly. Approximately ten costae are present at the commissure of each valve. The pedicle foramen is round, permesothyrid and labiate and the beak erect. Internal characters show a flat cardinal process (Text-fig. 14, section 2.5 mm) that has overgrown horizontal to gently ventrally concave hinge plates (section 2.6). Crural bases are small, attached to hinge plates, crural processes are high and develop rapidly from the end of the hinge plates (sections 4.2, 4.9, 5.4). Transverse band is moderately arched and rounded (section 7.6).


TEXT-FIG. 11. Transverse serial sections through a specimen of *Plectoconcha aequiplicata* (Gabb); UMIP 20448; limestone and secondary dolomite member, Luning Formation; West Union Canyon, Berlin-Ichthyosaur State Park, Nevada. Sections taken approximately perpendicular to brachial valve length. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Cardinal process (3.0, 3.2), gently concave to subhorizontal hinge plates (3.2–5.6), high-arched crural processes (7.1) and transverse band (9.5) present. Last section taken at 11·7 mm. Magnification of sections 0.0–10.7, ×4; sections 3.2 and 3.6 also shown at ×16.
Dimensions of sectioned specimen: L = 29·6+; W = 25·2+; T = 20·4 mm.
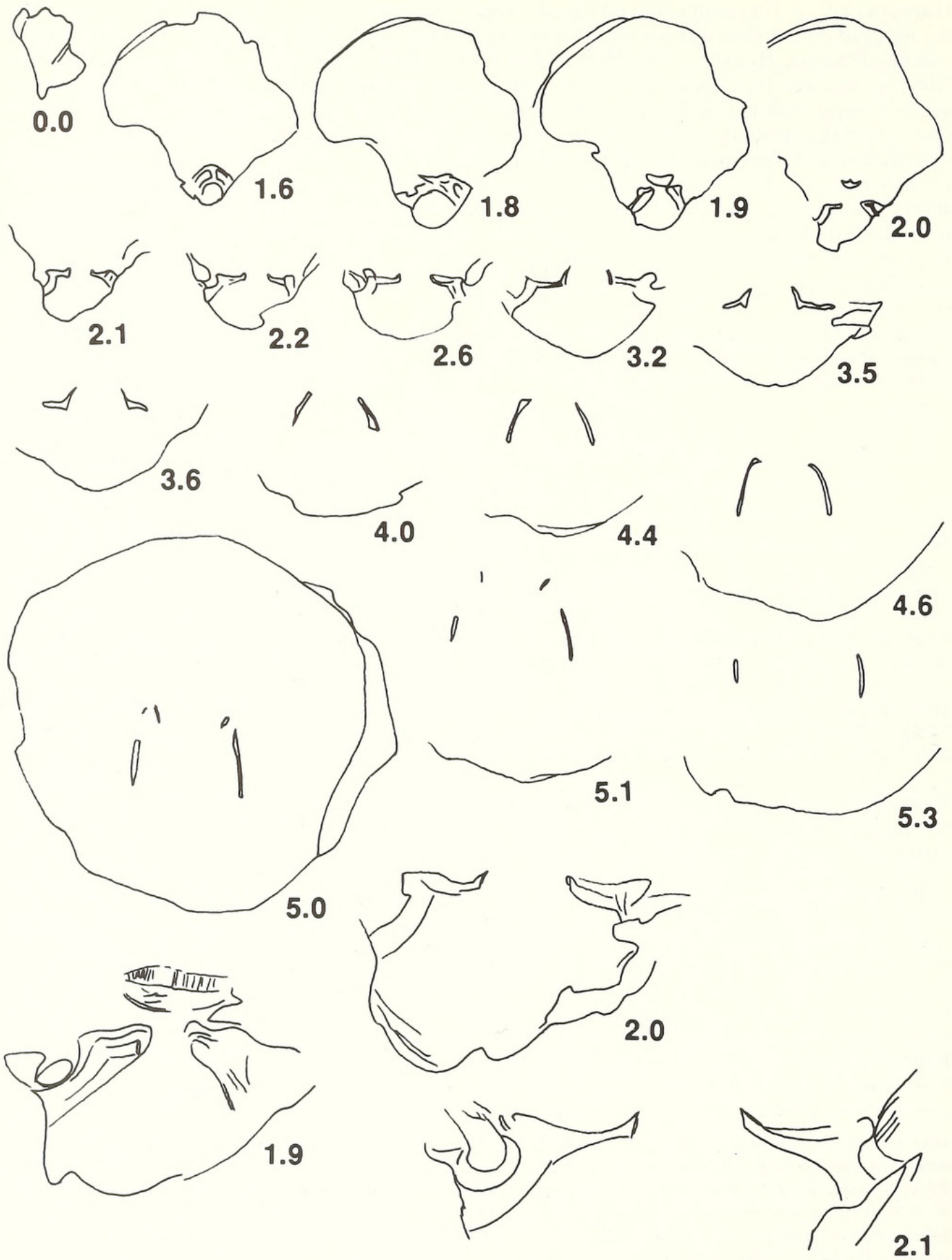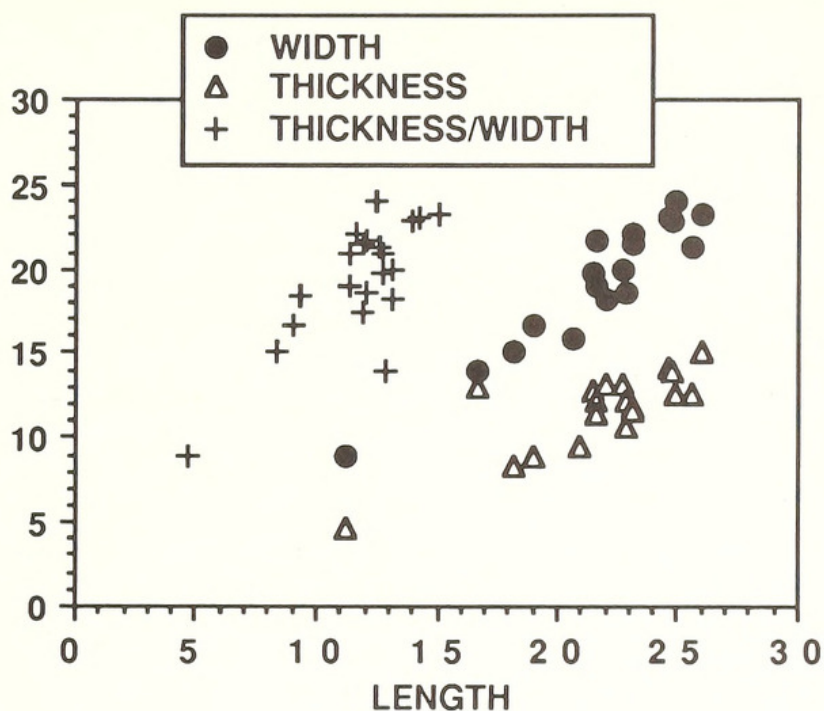
TEXT-FIG. 13. Plot of length versus width and thickness and of thickness versus width for *Plectoconcha newbyi* sp. nov.; Pilot Mountains, Nevada.

Discussion. Compared with *Plectoconcha aequiplicata*, *P. newbyi* sp. nov. is less strongly costate and has fewer costae, is smaller in overall length, width and thickness, and is not so markedly biconvex. The two species are probably very closely related.

The transverse serial sections of *P. newbyi* sp. nov. (Text-fig. 14) show some differences from those taken of *P. aequiplicata* (Text-figs 11–12). The presence of small crural bases posteriorly in *P. newbyi* sp. nov. could be significant. However, it might reflect that the specimen of *P. newbyi* that has been sectioned is a juvenile.

The similarities in external morphology between *P. aequiplicata* and *P. newbyi* (the form of pedicle foramen, costation) and their internal morphology (the form of the cardinal process, hinge plates, crural processes and transverse band) suggest that *newbyi* should be referred to *Plectoconcha*. It is possible that *P. aequiplicata* and *P. newbyi* sp. nov. represent ecophenotypic variation within one species. The latter species has not been identified at Berlin-Ichthyosaur State Park, Shoshone Mountains.

Occurrence. Lower Member, Luning Formation, Pilot Mountains, Nevada.

<div style="text-align:center">

Superfamily DIELASMATACEA Schuchert, 1913

Family DIELASMATIDAE Schuchert, 1913

Subfamily DIELASMATINAE Schuchert, 1913

Genus RHAETINA Waagen, 1882

</div>

TEXT-FIG. 12. Transverse serial sections through a juvenile specimen of *Plectoconcha aequiplicata* (Gabb); UMIP 20439; limestone and secondary dolomite member, Luning Formation; West Union Canyon, Berlin-Ichthyosaur State Park, Nevada. Sections taken perpendicular to maximum length. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Last section taken at 6.7. Cardinal process (1.9), gently concave to horizontal hinge plates (1.9–3.5) and high-arched crural processes (4.6) present. Magnification of sections 0.0–5.3, ×6·6; sections 1.9, 2.0 and 2.1 also shown at ×17. Dimensions of sectioned specimen: L = 18·0; W = 14·6; T = 11·4 mm.
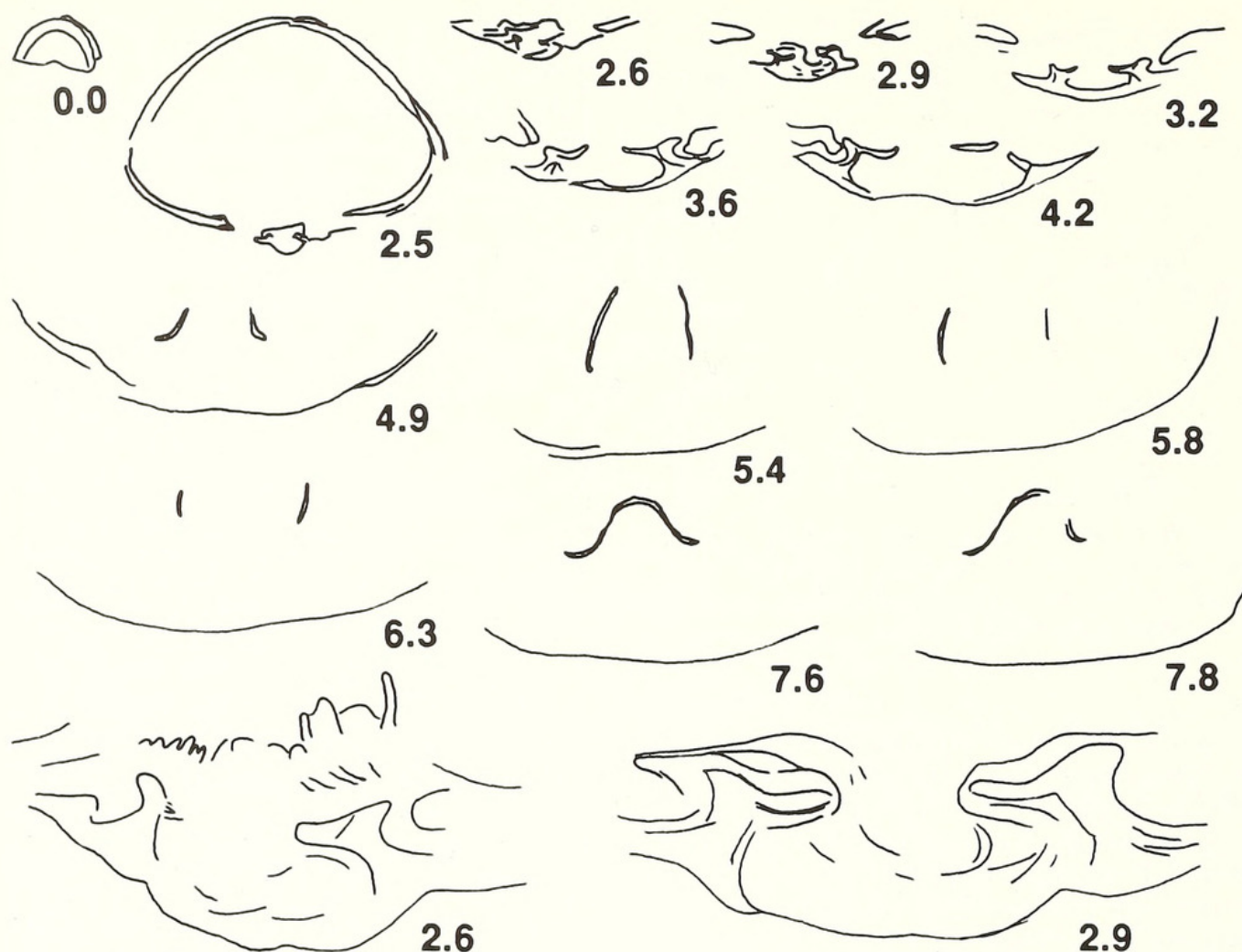
TEXT-FIG. 14. Transverse serial sections through a specimen of *Plectoconcha newbyi* sp. nov.; UMIP 20412, paratype; Lower Member, Luning Formation; Dunlap Canyon, Nevada. Sections taken perpendicular to maximum length. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Cardinal process (2.5, 2.6), horizontal to gently ventrally concave hinge plates (2.6–4.2), high-arched crural processes (5.4) and transverse band (7.6, 7.8) present. Last section taken at 8·6 mm. Magnification of sections 0.0–7.8, ×4; sections 2.6 and 2.9 also shown at ×17. Dimensions of sectioned specimen: L = 23·1; W = 21·4; T = 11·9 mm.

Type species. Terebratula gregaria Suess, 1854, p. 14, pl. 2, figs 14–15, from 'Mandling-Wand bei Wallegg'.

Discussion. Rhaetina is a very well known and abundant brachiopod genus of the southern Alpine Carpathian and Caucasian Late Triassic (Pearson 1977). Ching *et al.* (1979) recorded the genus from the Triassic of China. Pearson (1977) stated that the genus ranges from the Middle Triassic to the Early Jurassic. In addition, Hoover (1979) recorded the genus from the Early Triassic of Idaho, USA.

Rhaetina gregaria (Suess, 1854)

Plate 3, figs 7–22; Text-figs 15–16

<table>
<tr><td>*1854</td><td>*Terebratula gregaria* Suess, p. 14, pl. 2, figs 14–15.</td></tr>
<tr><td>v cf. 1864</td><td>*Terebratula humboldtensis* Gabb, p. 34, pl. 6, figs 35, 35*a–b*.</td></tr>
<tr><td>v cf. 1877</td><td>*Terebratula humboldtensis* Gabb; Hall and Whitfield, p. 282, pl. 6, figs 22–24.</td></tr>
</table>

v cf. 1914   *Terebratula humboldtensis* Gabb; Smith, p. 147, pl. 64, figs 3–5.
    1977   *Rhaetina gregaria* (Suess); Pearson, p. 35, pl. 4, figs 1–13 [with a detailed synonymy].
    1988   *Rhaetina gregaria* (Suess); Siblik, p. 97.

Type material. Suess's originals are lost. Pearson (1977) chose a lectotype from specimens figured by Suess (1854, pl. 2, fig. 14.)

Material. Lower Member of the Luning Formation, Cinnabar and Dunlap Canyons, Pilot Mountains, Nevada. UMIP 20311, 20315, 20352, 20359, 20377, 20401, 20411, 20413, 20422, MSM 6182. A few small, rare specimens from Berlin-Ichthyosaur State Park, Shoshone Mountains, Nevada (Hogler Collection).

Description. Specimens from Nevada have the characteristic slightly elongate outline of *Rhaetina gregaria*, broadest near the anterior end. The beak is prominent and erect, with a small pedicle foramen and rounded beak-ridges. The valves are smooth for two-thirds of their length, then two strong rounded costae develop on the brachial valve deflecting the anterior commissure.

The internal structures of two specimens of *Rhaetina gregaria* have been investigated, one a large, possibly mature adult specimen (Plate 3, figs 15–18; Text-fig. 15), the other a smaller, juvenile specimen (Plate 3, figs 19–22; Text-fig. 16). The larger specimen has a prominent cardinal process (Text-fig. 15, section 3.4). Anterior to the cardinal process is a large boss-like process (sections 3.5, 3.9), probably an extension of the cardinal process but lacking the typical comb-like muscle attachment structure. Hinge plates are attached to the floor of the brachial valve (sections 3.3–6.0), a characteristic feature of *Rhaetina*. One of the crural processes is damaged (sections 6.6, 6.9). The smaller specimen (Text-fig. 16) also has a well-developed cardinal process (section 1.9) but there is no sign of a boss-like process. The hinge plates also join the floor of the brachial valve (e.g. section 3.3). The crural processes are concave, and converge ventrally (section 4.7). The transverse band was not seen in either set of sections although it may be partially preserved in the smaller specimen (Text-fig. 16, section 6.9).

A few rare specimens share the external characters of *Rhaetina gregaria* but in addition have costae on their lateral flanks (Plate 3, figs 23–25). There are about four lateral costae on each side and are slightly sharper than those in the median fold. Such lateral costae have not been recorded in species of *Rhaetina*. The presence of these lateral costae may prove to be sufficient justification for erecting a new species. However, more material is needed for study of the internal characters. At the present time these specimens are recorded as *R.* sp. cf. *R. gregaria* (Suess). If *Plectoconcha newbyi* sp. nov. developed a strongly biplicate anterior commissure it might resemble this form. It is externally similar to *Misolia noetlingii* (Bittner, 1899) (e.g. in Hudson and Jefferies 1961, pl. 1, figs 5–8) although the extent of the costae across the posterior of the valves is difficult to determine for the poorly preserved figured specimen from Nevada (Pl. 3, figs 23–25).

Discussion. Pearson (1977, pp. 35–36) gave an extensive synonymy list for *Rhaetina gregaria*. Although all of his references have not been examined, the species is interpreted as variable, as did Pearson. '*Terebratula*' *humboldtensis* Gabb was originally described from the East Range, Nevada. It is probably from the Dun Glen Formation (Silberling, personal communication) which has also been dated as Kerri Zone (late early Norian), as has the lower member of the Luning Formation in the Pilot Mountains. Examination of Gabb's original figured specimens of '*T.*' *humboldtensis* (USNM 12533a–b) suggests that it is a junior subjective synonym of *R. gregaria* (Suess). The elongate outline of Gabb's original figure (1864, pl. 6, figs 35, 35a–b) resembles a zeillerid. The anterior commissure is commonly rectimarginate among zeillerids, not broadly uniplicate as seen in Gabb's illustrated specimen (1864, pl. 6, fig. 35a). Subsequently, Hall and Whitfield (1877, pl. 6, figs 22–24) and Smith (1914, pl. 64, figs 3–5, from Hall and Whitfield) described and figured '*T.*' *humboldtensis* Gabb. The figures by Hall and Whitfield (1877) and Smith (1914) confirm that USNM 12533a–b are those illustrated. The figures are somewhat idealized, but the specimens are 'distorted' (damaged) as Gabb recorded (1864, p. 34). Whiteaves (1889, p. 129) recorded '*T.*' *humboldtensis* Gabb from Nicola Lake, British Columbia. It is possible that '*T.*' *liardensis* described by Whiteaves (1889) from British Columbia may be referable to *Rhaetina*. Similarly, terebratulids recorded by Lees (1934) from the Yukon, and referred to *Dielasma suttonense* (Clapp and Shimer) and *T*? *piriformis* Suess, may prove to be *Rhaetina*. The median septal structures recorded by Whiteaves and Lees in the brachial valves of these species may reflect where the hinge plates attach with the floor of the brachial valve. Lees (1934, p. 33) recorded dental lamellae as

scarcely visible in his cf. *Dielasma julicum* (Bittner). Whiteaves and Lees' collections have not, however, been investigated during the present study.

Occurrence. Lower Member of the Luning Formation, Pilot Mountains, and the limestone and secondary dolomite member, Luning Formation, Berlin-Ichthyosaur State Park, Shoshone Mountains and also probably the Dun Glen Formation, East Range, Nevada. Pearson (1977) recorded this variable species from the Late Triassic–Early Jurassic of Central, Southern and Eastern Europe and the Middle East (see Siblik 1988, p. 88 for a detailed listing). Next to *Spondylospira lewesensis*, *Rhaetina gregaria* is the rarest element of the brachiopod fauna described herein from Nevada.

<div align="center">

Suborder TEREBRATELLIDINA Muir-Wood, 1955
Superfamily ZEILLERIACEA Allan, 1940
Family ZEILLERIIDAE Allan, 1940
Genus ZEILLERIA Bayle, 1878

</div>

Type species. *Zeilleria quadrifida* Lamarck, 1819, p. 253, fig. 35, from the Lias of France. Delance (1974, p. 178) considered the specimen in the Lamarck Collection, Museum of Natural History, Geneva, Switzerland, as the type.

Discussion. Delance (1974) made a thorough revision of *Zeilleria* and the species that occur in western Europe. He considered *Cincta* Quenstedt a subgenus of *Zeilleria*.

<div align="center">

Zeilleria cf. *Z. elliptica* (Zugmayer, 1880)

Plate 3, figs 26–33; Text-figs 17–18

</div>

cf. 1880   *Waldheimia elliptica* Zugmayer, p. 17, pl. 2, figs 6–8, 10.
cf. 1963   *Zeilleria elliptica* (Zugmayer); Dagys, p. 192, pl. 28, figs 10–13.

Type material. From the Rhaetian of Kitzberg, near Pernitz, Austria. A lectotype for the species has not been selected (Siblik 1988).

<div align="center">EXPLANATION OF PLATE 3</div>

Figs 1–4. *Zugmayerella uncinata.* UMIP 20320 (sectioned, Text-fig. 10A); Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All ×2.

Figs 5–6. ?*Zugmayerella* sp. UMIP 6952; Lower Member, Luning Formation, unnamed canyon, Nevada; pedicle and lateral views respectively. All ×1.

Figs 7–10. *Rhaetina gregaria.* UMIP 20315; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All ×1.

Figs 11–14. *Rhaetina gregaria.* UMIP 20311; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All ×1.

Figs 15–18. *Rhaetina gregaria.* UMIP 20359 (sectioned, Text-fig. 15); Lower Member, Luning Formation; Cinnabar Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All ×1.
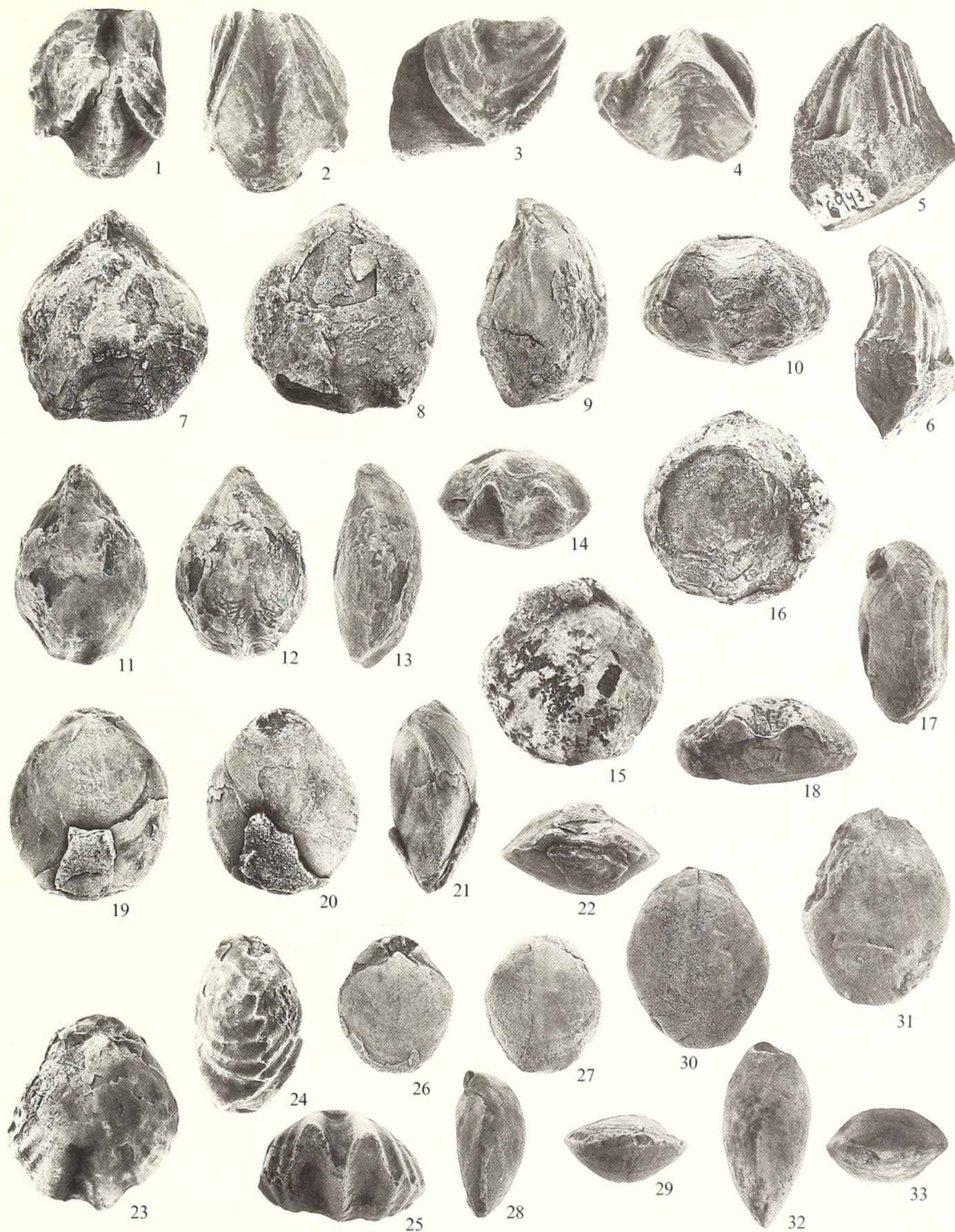
Figs 19–22. *Rhaetina gregaria.* UMIP 20413; (sectioned Text-fig. 16), juvenile; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All ×1.5.

Figs 23–25. *Rhaetina* sp. cf. *R. gregaria.* UMIP 20317; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, lateral and anterior views respectively. All ×1.

Figs 26–29. *Zeilleria* cf. *Z. elliptica.* UMIP 20336; Lower Member, Luning Formation; Dunlap Canyon, Nevada; brachial, pedicle, lateral and anterior views respectively. All ×1.25.
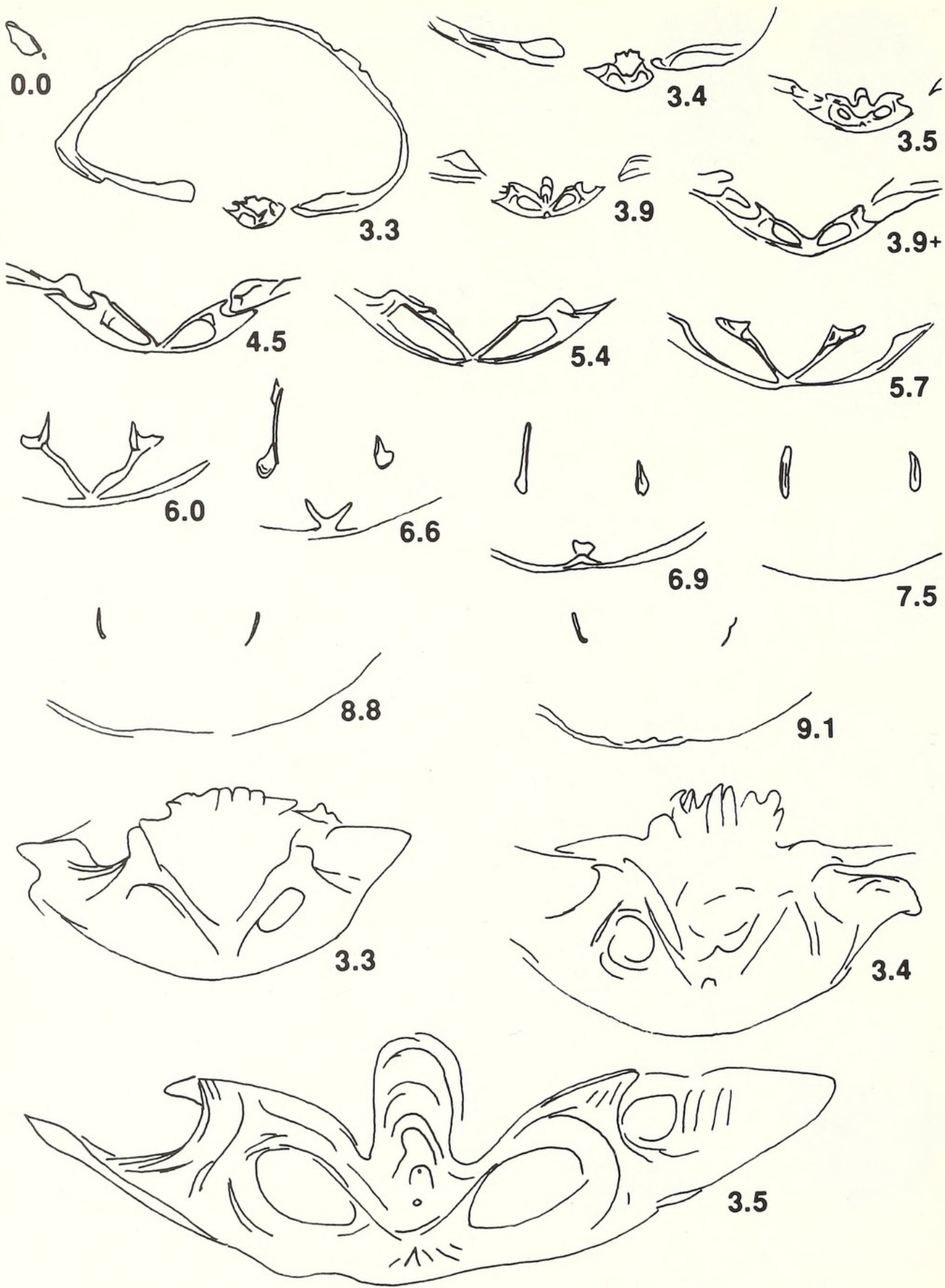
Figs 30–33. *Zeilleria* cf. *Z. elliptica.* MSM 6186 (sectioned, Text-fig. 18); labelled 'Luning Ls.' (= Lower Member, Luning Formation; probably from Dunlap or Cinnabar Canyon, Nevada); brachial, pedicle, lateral and anterior views respectively. All ×1.5.
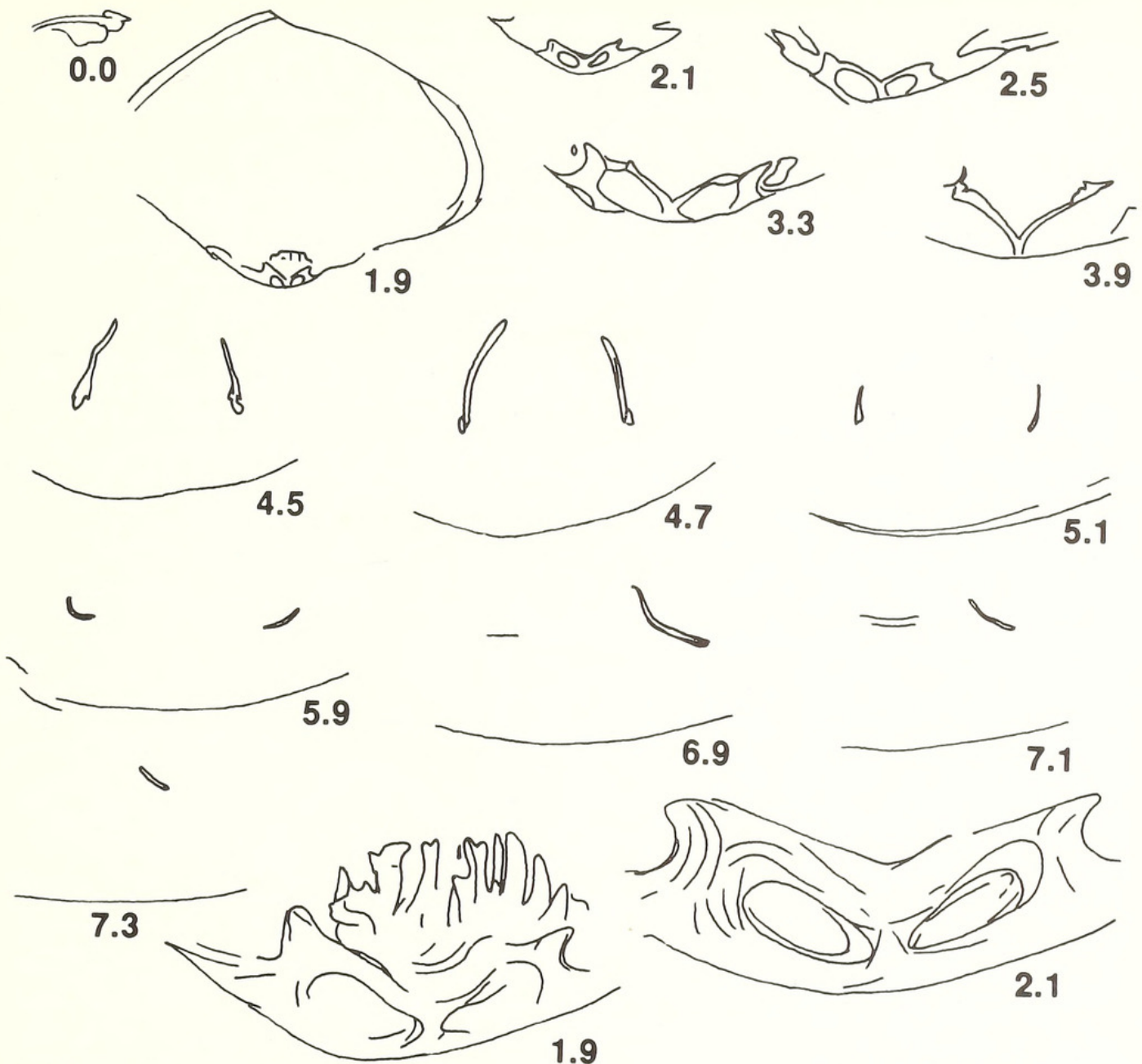
PLATE 3

SANDY and STANLEY, *Zugmayerella, ?Zugmayerella, Rhaetina, Zeilleria*

TEXT-FIG. 16. Transverse serial sections through a specimen of *Rhaetina gregaria* (Suess); UMIP 20413; Lower Member, Luning Formation; Dunlap Canyon, Nevada. Sections taken perpendicular to length of the brachial valve. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Cardinal process (1.9), dorsally inclined hinge plates (1.9–3.9), ventrally inclined crural processes (4.7) and transverse band? (6.9) present. Brachidium traced to 7·3 mm, last section taken at 7·7 mm. Magnification of sections 0.0–7.3; ×6·6, sections 1.9 and 2.1 also shown at ×40. Dimensions of sectioned specimen: L = 21·3; Lbv = 19·9; W = 17·5; T = 9·6 mm.

TEXT-FIG. 15. Transverse serial sections through a specimen of *Rhaetina gregaria* (Suess); UMIP 20359; Lower Member, Luning Formation; Cinnabar Canyon, Nevada. Sections taken approximately perpendicular to brachial valve length. Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. For some of the sections before section 3.9+ the base plate on which the specimen was sectioned was slightly out of alignment with the grinding surface. Up until 3.9+, sections probably represent about 0·2–0·3 mm less removed than the actual value shown. Cardinal process (3.3, 3.4), boss-like process (3.5–3.9), dorsally inclined hinge plates (3.3–6.0), dorso-ventrally directed crural bases (6.0) and crural processes (6.6) present. Brachidium traced to 10·3 mm, last section taken at 10·9 mm. Magnification of sections 0.0–9·1, ×4; sections 3.3, 3.4 and 3.5 also shown at ×25. Dimensions of sectioned specimen: L = 27·2+; W = 27·3; T = 13·6+ mm.

Material. Lower Member, Luning Formation, Cinnabar and Dunlap Canyons and limestone and secondary dolomite member, Luning Formation, West Union Canyon, Berlin-Ichthyosaur State Park, Shoshone Mountains, Nevada. UMIP 6854, 6863, 20336, 20345, 20349, 20356, 20370, 20382, 20397, 20405, 20407, 20417, 20423. Specimens in the collection of the University of Reno are probably from the Pilot Mountains, MSM 6172, 6186, 6189.

Diagnosis. Zeilleria of elongate-oval to elliptical outline, may have an anteriorly truncated outline. Both valves are smooth, with some growth lines discernible. The anterior commissure is rectimarginate to incipiently uniplicate. Pedicle foramen small, beak ridges sharp. The presence of dental lamellae and a median septum can be determined in a number of specimens from external examination. Hinge plates horizontal.

Description. Length is greater than width which is greater than thickness (Text-fig. 17). Transverse serial sections have been taken through one specimen (Text-fig. 18). Dental lamellae are present (sections 1.2, 1.4 mm). The median septum (section 1.4) is short, but a low median ridge continues anteriorly (section 3.8). The united hinge plates and inner socket ridges form a broad, ventrally concave septalium (sections 1.4, 2.2). Anteriorly the crura extend to crural processes (section 3.8). The descending branches of the loop are present until section 5.9. Beyond this it is difficult to trace the brachidium as the loop is believed to be broken.
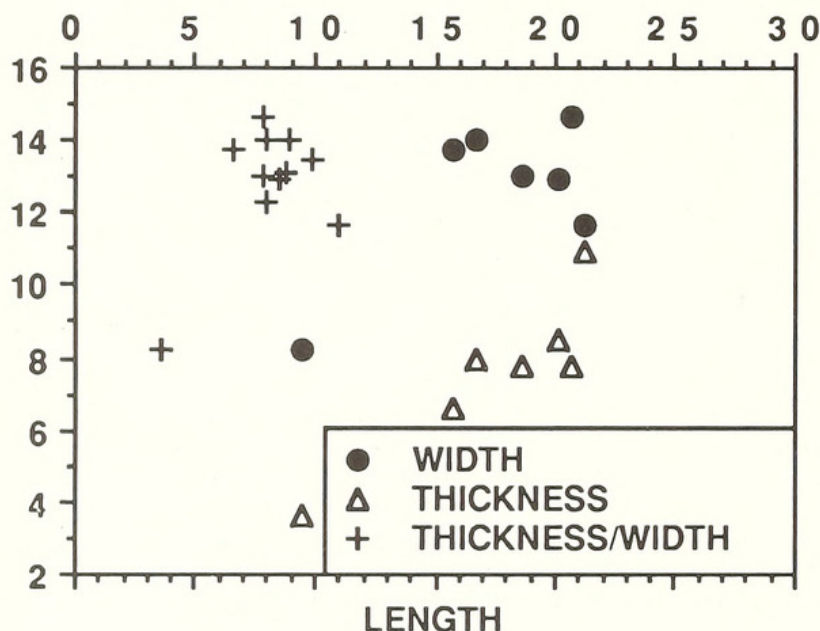
TEXT-FIG. 17. Plot of length versus width and thickness and of thickness versus width for *Zeilleria* cf. *Z. elliptica* (Zugmayer), Pilot and Shoshone Mountains, Nevada.

Discussion. Zeilleriid brachiopods are difficult to characterize at the specific level. Like many of the taxa already considered, they may show considerable variation, particularly in their most obvious and readily observable characters – shell outline and profile. The zeillerids available for study from Nevada show a wide range of variation in outline and profile and there may well be more than one species present. There are a number of zeillerid species that have been recorded from the Triassic and Jurassic that are similar to the American specimens.

One specimen of *Zeilleria elliptica* figured by Dagys (1963, pl. 28, fig. 12) is very similar in outline to the specimens of *Z.* cf. *Z. elliptica* figured herein (Plate 3, figs 26–33). A few specimens (MSM 6186) are very similar to *Z. bukowski* (Bittner, 1892) figured by Dagys (1963, pl. 28, figs 14–18). Generally though, *Z.* cf. *Z. elliptica* from Nevada is smaller, has a more angular outline and less inflated profile than typical specimens of *Z. bukowski*. The American specimens are comparable to *Z. perforata* (Piette, 1856) which has been recorded from the Early Jurassic, but Delance (1974) recorded very similar forms from the Triassic. *Z.* cf. *Z. elliptica* tends to be more elliptical and
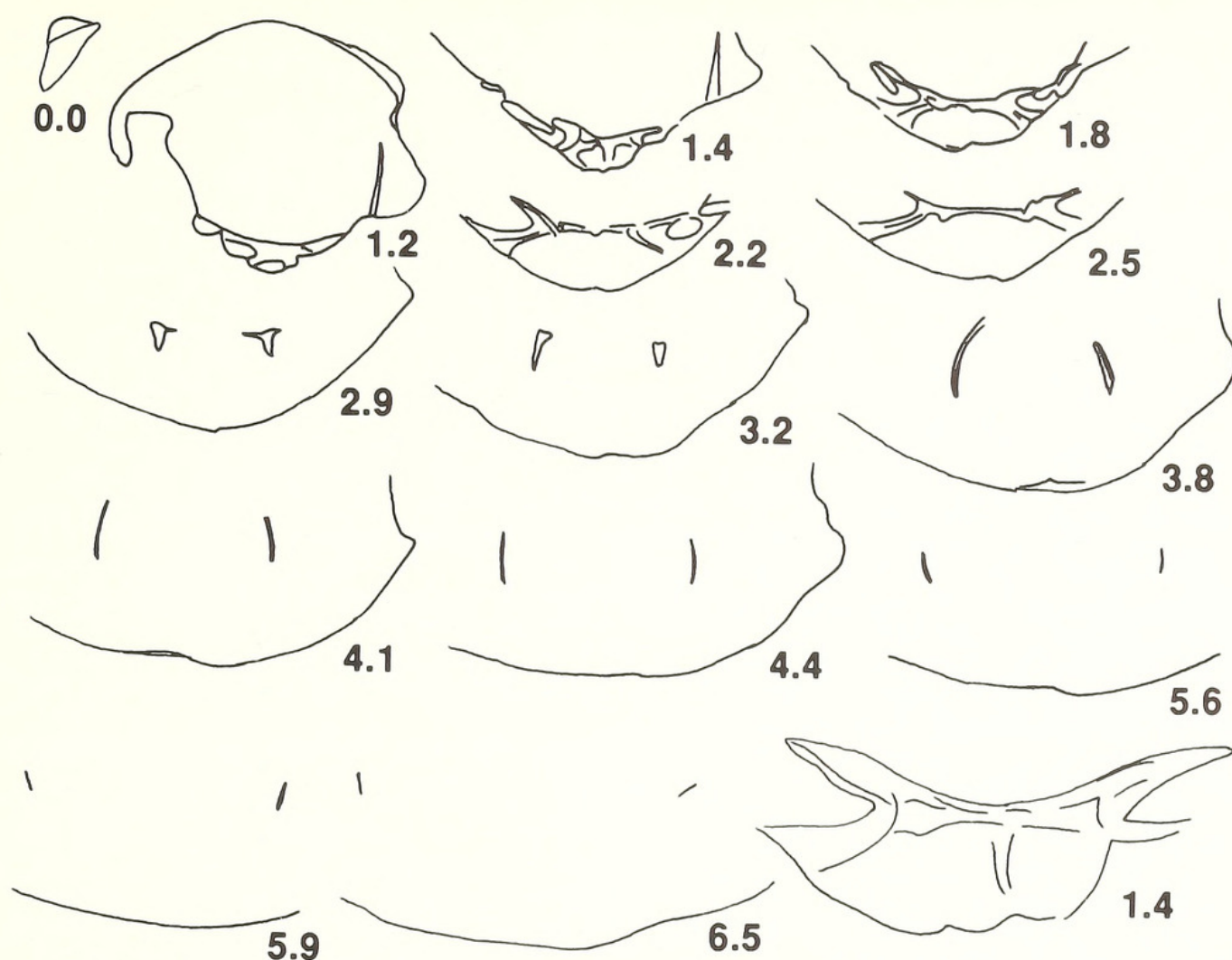
TEXT-FIG. 18. Transverse serial sections through a specimen of *Zeilleria* cf. *Z. elliptica* (Zugmayer); MSM 6186; labelled 'Luning Ls.' = Lower Member, Luning Formation; probably from Dunlap or Cinnabar Canyon, Nevada. Sections taken perpendicular to length and median septum of brachial valve (visible for 5·5 mm on exterior). Cumulative spacings given in mm from initial section 0.0 through pedicle umbo. Dental lamellae, median septum and broad septalium (1.2–1.4) and concave descending lamellae (3.2–5.9) present. Last section taken at 6·8 mm, brachidium damaged. Magnification of sections 0.0–6·5, ×4; section 1·4 also shown at ×25. Dimensions of sectioned specimen: L = 18·7+ ; Lbv = 17·7; W = 14·0; T = 8·9 mm.

laterally compressed than *Z. perforata*. Delance (1974, p. 391, fig. 21-1) recorded *Z. perforata* as ranging from the very bottom of the Jurassic in western Europe. In a phylogenetic diagram Delance regarded *Z. elliptica* as ancestral to *Z. perforata*. They are very similar in their morphology and presumably closely related. *Z. lingulata* Ching *et al.* (1979, p. 211, pl. 51, figs 4–9) is another zeillerid species that is similar in outline to *Z.* cf. *Z. elliptica*.

The septalium is not strongly developed or markedly concave in the sectioned specimen of *Z.* cf. *Z. elliptica* (Text-fig. 18). In many of the papers referenced above in which serial sections are given for the species discussed, the septalium is often markedly concave and the median septum well-developed. Sections of *Z. bukowski* in Dagys (1963, fig. 93) do show a broad, gently concave septalium. The concavity of the septalium is partly a function of the angle of sectioning and the incurvature of the umbo of the brachial valve, and the median septum is a variable character, liable to resorption during growth. A number of the Nevada specimens do show the presence of a median septum in the brachial valve, suggestive of *Zeilleria*, rather than the genus *Gusarella* Prosorovskaya, 1962, which lacks one.

Occurrence. Lower Member, Luning Formation, Cinnabar and Dunlap Canyons and limestone and secondary dolomite member, Luning Formation, West Union Canyon, Berlin-Ichthyosaur State Park, Shoshone Mountains, Nevada.

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