

# LOOP DEVELOPMENT AND THE CLASSIFICATION OF TEREBRATELLACEAN BRACHIOPODS

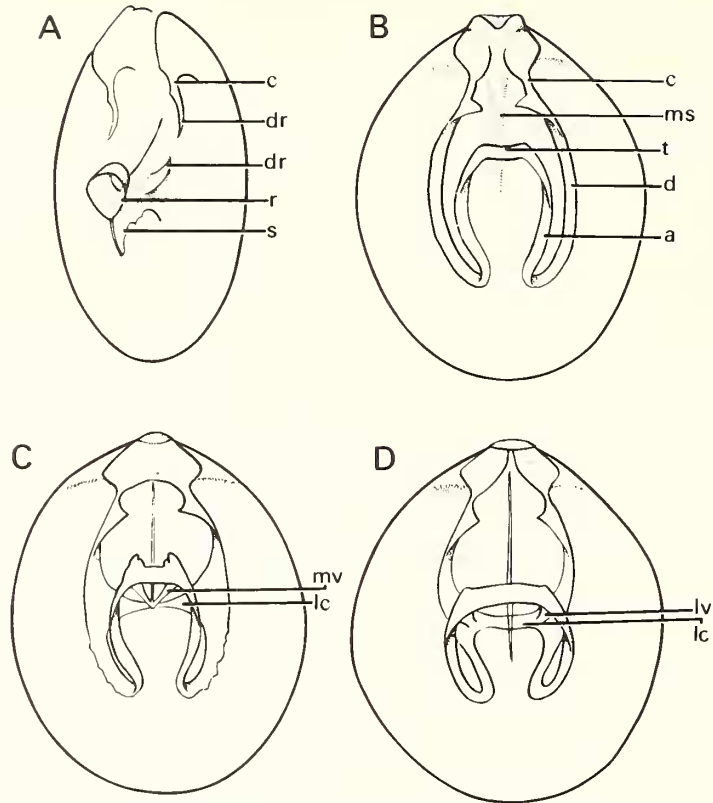
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**ABSTRACT.** The classical separation of Cainozoic long-looped brachiopods into two groups of genera, dallinid and terebratellid, according to certain early developmental features of the loop, does not withstand critical examination. These studies confirm the high taxonomic value of developing loop patterns but consider features of the developing loop, used previously to separate families, to be invalid. The dallinid sequence as defined previously is shown herein to include two groups of genera differing in the loop patterns exhibited during intermediate phases of development. These two groups of genera differ from each other and from terebratellid genera in the manner of resorption of parts of the ring and the stage at which it is freed from the septum. These factors govern the presence in one group (Dallinidae) of descending branches with double anterior limbs and in the other group (Laqueidae) of vertical connecting bands, neither of these structures occurring in the development of the Terebratellidae. The growth phases of the loop are identified by a simpler terminology using descriptive in place of generic adjectives. Two subfamilies, the Dalliniinae and Nipponithyrinae, are retained in the Dallinidae and four subfamilies, the Kingeniinae, Pictothyriinae, Macandreviinae, and Terebrataliinae (nov.), are included in the Laqueidae.

THE form of the loop is of prime importance in brachiopod classification. The dominant brachiopod faunas of the Cainozoic possess long loops and they are noted for the complex ontogenetic sequences from which adult loop patterns derive. The development of long-looped brachiopods from any geological age culminates in a loop possessing the same elements, descending branches and a transverse band uniting ascending branches; crura attach the loop to the cardinalia (the collection of structures in the dorsal valve concerned with articulation). This loop form is achieved by a series of metamorphoses of structures derived from the crura and a median septal pillar in most Mesozoic and Cainozoic genera and from the crura alone in Palaeozoic genera. In the Cainozoic genera reviewed here the crura give rise to the posterior segments of the descending branches and a ring gives rise to the ascending branches and the transverse band. The development of a long loop ultimately free of the septum may include the formation of three pairs of connecting bands linking the loop and the septum, one pair of horizontal bands (lateral connecting bands), and two pairs of vertical bands (medio-vertical and latero-vertical connecting bands).

Developmental features of the loop have long been used to differentiate two ontogenetic sequences, dallinid and terebratellid, within the superfamily Terebratellacea. Three families, namely the Dallinidae, Laqueidae, and Macandreviidae, are alleged to show dallinid development while the terebratellid sequence characterizes the Terebratellidae. The remaining terebratellacean families possess loops thought to be neotenous derivatives of the more complex structures seen in dallinid and terebratellid families.

Different authors have proposed a number of features to distinguish the loop development of dallinid and terebratellid genera. Fischer and Oehlert (1892) and Beecher (1895) claimed that during dallinid development lacunae appear in the



TEXT-FIG. 1. Semi-diagrammatic views of interiors of dorsal valves of four long-looped brachiopods to show: A, the loop rudiments; B, a loop free of the septum as in *Magellania insolita* (Tate); C, a loop with lateral and medio-vertical connecting bands as in *Paral dingia woodsii* (Tate); D, a loop with lateral and latero-vertical connecting bands as in *Frenulina pumila* (Tate).

Abbreviations: a = ascending branches; c = crura; d = descending branches; dr = descending branch rudiments; lc = lateral connecting bands; lv = latero-vertical connecting bands; ms = median septum; mv = medio-vertical connecting bands; r = ring; s = septal pillar; t = transverse band.

anterior regions of the ring which is freed from the septum at an earlier stage than in terebratellid genera. In 1927 Thomson extended these differences stating that early dallinid development is characterized by a hood enveloping the crest of the septum and descending branches arising from the crura only while in terebratellids the septum bears a lamellar ring and descending branches arise from both the crura and the septum. With further reference to early developmental phases, Konjoukova (1948, 1957) states that anterior division of the septum is characteristic of dallinid development. Elliott (1953, 1965) did not include this distinguishing feature in his review of methods of loop development in which he reaffirms the differences previously summarized by Thomson. In addition, Elliott states that since early loop

calcification is more extensive in dallinids, the greater resorption necessary to produce the final loop pattern results in different intermediate loop patterns (with lacunae perforating segments of the ring) from those seen in terebratellid genera.

None of these reviews incorporates or comments upon the observation of Friele (1877) that there is a pronounced difference in the loop development of, on the one hand, *Macandrevia* and *Frenulina* and on the other *Dallina* and *Glaciarcula*. Following Beecher's review (1895) these genera have been grouped together as displaying typically dallinid development and ironically there has been extensive use of Friele's illustrations to support such a claim. The position of lacunae in determining different intermediate loop patterns in these two groups of genera has not been included in any classification based on loop development. What has happened is that the presence of lacunae *ipso facto* has become one of the chief differentiating factors in methods of loop development. Any genera displaying lacunae during intermediate phases of loop development are regarded as dallinid while lacunae have not been described in any stage in the development of any terebratellid.

Studies on the development of a number of species (Richardson 1973a, in press) have led the author to the conclusion that lacunae may be present in the developing loop of all genera (which in their ontogenies reach intermediate loop patterns) including those attributed to the Terebratellidae. These studies have also led to the conclusion that the pattern described previously as dallinid is a confusing conglomerate of two different patterns of development. Hence an unnecessarily complex picture of the supposed dallinid sequence has evolved and with it a most formidable terminology. All accounts of loop development in different species indicate that three developmental patterns are evident in terebratellacean genera and that the key factors differentiating these are the stage at which the ring is freed from the septum and the manner in which the ring is resorbed. The origin of the descending branches and the presence of lacunae, a hood, a ring, or of a bifurcating septum are not factors which separate types of loop development.

#### THE DIFFERENTIATION OF DALLINID AND TEREBRATELLID LOOP PATTERNS

##### *Origin of the descending branches*

The first author to introduce the method of origin of the descending branches as a differentiating factor in terebratellid and dallinid growth patterns was Thomson in 1927. At that time growth stages prior to the completion of the descending branches had been figured for only two species. Fischer and Oehlert in 1892 described the development of *Terebratella dorsata*, Thomson in 1915 that of *Waltonia inconspicua*. In both species the descending branches arise from both the crura and the septum. Since the publication of Thomson's monograph, developmental stages incorporating the method of growth of the descending branches have been described for four dallinid species *Macandrevia cranium* by Atkins (1959a), *Frenulina sanguinolenta* by Richardson (1973a), *Gemmarcula humboldtii* (Hagenow), and *Trigonosemus pulchellus* (Nilsson) by Steinich (1965), and for five terebratellid species. *Magellania flavescens* (Lamarck), *Neothyris lenticularis* (Deshayes), *Pirothyris vercoi* (Blochmann), *Jaffaia jaffaensis* (Blochmann) by Richardson (in press), and *Magas chitoniformis*

(Schlotheim) by Steinich (1965). These species are characterized by the double origin of the descending branches with the single exception of *Macandrevia cranium* in which the descending branches arise from the crura only and therefore is the only species known in which this phenomenon occurs. *Macandrevia* is also characterized by pocket-shaped hinge plates and by the loss of the median septum in adult forms, features which distinguish it (together with *Notorgymia* recently described by Cooper 1972) from the large group of other genera referred to the Dallinidae. It does not seem advisable to use the mode of origin of the descending branches as a differentiator in the loop development of families when this is known from only one species which is somewhat aberrant in other morphological features.

### *Hood and ring*

The case of the hood versus the ring is difficult to clarify because these terms and their application do not seem to have been defined, with respect to loop development, by any author. In describing the earliest growth stage observed by him of *M. cranium*, Friele refers to the septum as bearing 'a tube, the posterior end of which is enclosed' and later that 'the first visible change occurs by an opening in the closed end of the tube' (1877, p. 381). In the same paper Friele describes the development of *Dallina septigera* stating that, apart from the shape of the septum, the early appearance of the loop accords with that of *M. cranium*. Fischer and Oehlert refer to the earliest structure on the crest of the septum of *Terebratella dorsata* as 'une petite boucle' (1892, p. 289) and in both *M. cranium* and *D. septigera* as 'une très petite boucle comprimée latéralement' (p. 306). Beecher in describing the development of *Dallinella obsoleta* refers to a 'small cylinder' (1895, p. 393) arching over the septum and, in a general account of loop development, states that in both terebratellid and dallinid genera the appearance of a small ring on the septum is the precursor to the ascending branches. Neither Douvillé (1879) for *Neothyris lenticularis* nor Deslongchamps (1884) for *Frenulina sanguinolenta* refer to the hood/ring before it fuses anteriorly with the descending branches.

In 1927 Thomson introduced the possibility of differences in the hood/ring in differing types of loop development. 'A hood, instead of a ring, is only rarely developed in the Magellaniinae and its lower sides do not project so far forward as in the Dalliniinae' (1927, p. 234). However, when discussing the development of *Waltonia inconspicua* (with *Terebratella dorsata* then the only terebratellid species whose loop development was known) he states that in the earliest stage observed a small hood lies on the back of the septum and 'this hood passes into a ring by absorption of its posterior dorsal portion, but it may persist as a hood in shells up to a length of 6 mm' (p. 262).

To quote such statements would seem to be labouring the point in minor matters of semantics had not Elliott stated that 'apart from the major difference of dalliniform hood and terebratellid ring, the development of the two families differs in the early growth of the descending branches' (1953, p. 269). These differences are reaffirmed in the Treatise by both Elliott and Hatai.

In the absence of specialized knowledge one would expect the hood to be a tube with one closed end and the ring one with both ends open. It seems clear that this is how Thomson interpreted the terms. If these definitions are acceptable then, in all

examples known of early development, the first structure to arise on the septum is a hood which by the resorption of its posterior end gives rise to a ring. That is, both a hood and a ring are characteristic of dallinid and terebratellid development and, since one structure is translated into the other, the hood always precedes the ring. There are differences in the shape and extent of these structures in different species as observed and noted above by Fischer and Oehlert and by Thomson. In general, the hood/ring occupies a greater part or length of the crest of the septum at a comparable growth stage in some of the genera attributed to the Dallinidae (*Dallina*, *Campages*) than in terebratellid genera, and this seems to be the feature which Elliott wishes to emphasize. However, the Dallinidae (as defined in the Treatise) also includes genera such as *Frenulina* in which the dimensions of the band making up the ring are similar to those seen in most terebratellid genera. In addition both *F. sanguinolenta* and those terebratellid species studied show variation in the width of the band in different specimens at comparable growth stages.

### *Lacunae*

Since Fischer and Oehlert published a comparative account of loop development in 1892 all authors have grouped together those genera in which lacunae perforate the ring during development. It is claimed that these genera show a dallinid pattern of loop development while genera not demonstrated to possess lacunae in the developing loop display a terebratellid pattern. Elliott (1953) accounts for the presence of lacunae by claiming that the developing loop of dallinid genera shows a greater degree of calcification thus requiring more extensive resorption to achieve the adult pattern.

These differences are not apparent in studies made by me (Richardson, in press) in which lacunae perforate parts of the loop in most species studied. Species in which lacunae are shown to occur are *Magellania flavescens*, *Neothyris lenticularis*, and *Waltonia inconspicua* all of which have been said to show a characteristic terebratellid pattern. Species which do not display lacunae during development, *Jaffaia jaffaensis* and *Pirothyris vercoi*, are characterized by adult loops which do not progress beyond the magelliform stage as defined on page H147 in the Treatise. Differences do exist in the number of lacunae present, in their position, the stage of development at which they occur, and in their duration, differences in this last factor probably accounting for the fact that they have not been described hitherto in any genus attributed to the Terebratellidae.

### *The median septum*

*Bifurcation.* Konjoukova (1948, 1957) has suggested that one of the principal factors distinguishing dallinid and terebratellid loop patterns is the anterior division or splitting of the median septum during early growth stages in dallinid genera. This method of differentiating the two groups has not been incorporated in any other review of loop development. However, Atkins (1959b) in an account of the development of *Terebratalia transversa* states:

It would seem therefore that *T. transversa* cannot remain in the Dallininae, although it agrees with those of the sub-family in which a number of growth stages are known, *Macandrevia cranium* (Müller) (Friele, 1877; Elliott, '48; Atkins, '59b), *Dallinella obsoleta* (Dall) (Beecher, 1895), *Frenulina sanguinolenta* (Gmelin)

(Eudes-Deslongchamps, 1884, as *Terebratella sanguinea* (Chemnitz)), *Dallina septigera* (Lovén), (Friele, 1877), *Fallax dalliniformis* Atkins '60, and also with *Laqueus californicus* (Koch) (Konjoukova, '57) a member of the Laqueidae, in the anterior splitting or bifurcation of the septum. In *Terebratalia transversa*, however, this occurs later than in the other species mentioned, and the forks are peculiarly heavy and clumsy. *T. transversa* also possesses the dallinid character of anterior spinous projections of the septum (pp. 422-423).

Atkins statement is quoted in full because it is important that it be examined carefully as it is felt that there is confusion in understanding the relationship between the septum and the fused attachments of the ring and the descending branches; if the septum splits there is an implication that the septum itself is a contributor to the bands making up the loop. In the first place the development of those species cited by Atkins must be reviewed.

Beecher describing an early growth stage of *Dallinella obsoleta* (1895, pl. 3, fig. 10) states that 'The ascending lamellae from the septum already have begun to divide or separate anteriorly' (p. 394) and makes no reference to the condition of the septum. Friele describing a 4.5 mm growth stage in *Macandrevia cranium* states that 'The united lamellae then begin to split apart at the anterior end' (1877, p. 381). In the same paper Friele describes the development of *Dallina septigera* which in the early growth stages is similar to *M. cranium* 'The only essential differences are in the form of the septum and the size' (p. 383). At this growth stage the ventral valve of *D. septigera* is 5.5 mm in length and the median septum has a much longer attachment to the valve floor than is the case in *M. cranium*. Both Beecher and Friele give lateral views of the developing loop in addition to ventral views, a factor of great assistance in assessing the relationship of different parts of the loop. This practice would have helped to clarify Konjoukova's figures (1957) of *Laqueus californianus* in which she states there is anterior bifurcation of the septum but her illustrations could just as easily represent the anterior fusion and separation of descending branch and ring attachments with the simultaneous resorption of anterior portions of the septum.

In her account of the development of *Fallax dalliniformis* Atkins states that at a growth stage of 5.4 mm 'The hood, or ascending branches of the loop, had widened greatly: slight anterior bifurcation was evident with short spines bordering it (Text-fig. 10)' (1960a, p. 84). Text-fig. 10 is a ventral view of the loop at this growth stage (no lateral view provided) and shows the septum extending well beyond the anterior limits of the loop, consequently the anterior bifurcation described by Atkins refers to the ascending branches. Of the dallinid species cited above by Atkins only the development of *Frenulina sanguinolenta* has been studied by me (Richardson 1973a). These growth stages have been compared with those observed by Deslongchamps who does not refer to the bifurcation of the septum nor was this observed by me in any growth stage of *F. sanguinolenta*.

In all cases of loop development observed by the present and previous authors the attachments to the septum of the ring and of the descending branches lie parallel to each other (text-fig. 3). The first step in the formation of the adult loop from these separate structures is their anterior fusion so that the descending branches and the anterior segments of the ring (future ascending branches) become continuous. This fusion follows the gradual approximation of their lines of attachment to the septum and proceeds in an anterior to posterior direction until the full lengths of the attach-

ments of the ring are fused with the descending branches. While these processes of fusion and consequent medial separation are going on the anterior border of the median septum undergoes gradual resorption. As noted in accounts of the development of *F. sanguinolenta* and of *Magellania flavescens*, *Waltonia inconspicua*, *Neothyris lenticularis* (Richardson 1973a, in press) it is difficult to assess from isolated growth stages whether the fusion and separation of the anterior segments of the loop involves the septum. In many specimens observed the anterior fusion of the attachments occurs simultaneously with the resorption of those parts of the septum adjacent to the fused lines of attachment of ring and descending branches. Therefore it may appear that a component derived from the septum contributes to the regions of fusion of the ring and the descending branches, a process of inclusion which would be aided by a previously split septum. However, in all species studied other growth stages were observed in which the fusion of the attachments occurred while the septum extends beyond the anterior and ventral limits of these attachments, i.e. while the septum partition-like separates the two sides of the loop. Therefore it appears that in some species at least, the septum does not contribute to the bands of the loop and that one of the variables to be considered in loop development is the stage of fusion of the attachments relative to the degree of resorption of the septum.

By means of whatever agency, splitting or fusion, the anterior division of the loop occurs, it should not be confused with the appearance of the septum in *Terebratalia transversa*. Atkins describes two specimens, 6.1 mm and 6.4 mm in length, in both the septum projects anteriorly beyond the separate attachments of the former and the fused attachments of the latter. As Atkins remarks 'There is evidently some variation in the way in which the anterior ends of the ascending branches free themselves from the septum' (1959b, p. 413) but does not expand this statement. Furthermore, she states that the bifurcation of the septum in *T. transversa* is 'peculiarly heavy and clumsy' (p. 422) and this appearance of the septum in *T. transversa* is comparable with the same structure in some growth stages of *Magellania flavescens* (Richardson, in press), i.e. thick ventrally with a jagged anterior edge.

The septum may split anteriorly in some species. It seems clear that this is the case in *Macandrevia cranium*. In *M. cranium* Atkins (1959a) describes the occurrence of an anterior split in the septum before the development of the hood. In this species the hood emerges at a late stage, relative to other structures, it rapidly becomes converted to a ring and its attachments fuse with the descending branches almost simultaneously. In *M. cranium* anterior septal splitting could be an aid to compensate for lost time in the development of the hood. The septum does not split in any of the species observed by me and whether it splits in *Dallinella obsoleta*, *Fallax dalliniformis*, *Dallina septigera*, and *Laqueus californianus* is doubtful, in these species the appearance of splitting could be confused with the anterior fusion of attachments of the ring and the descending branches.

The anterior split in the septum of *M. cranium* is preceded in ontogeny by a groove running the full length of the crest of the septum. This groove is also linked with the hood, Atkins commenting for *M. cranium* that 'grooving precedes formation of the hood' (1959a, p. 341). The precursor of the hood of *Frenulina sanguinolenta*, *Magellania flavescens*, *Waltonia inconspicua*, *Neothyris lenticularis*, *Pirothyris vercoi*, and *Jaffaia jaffaensis* is a groove which is restricted to the posterior section of the septal crest.

It seems reasonable to assume that these grooves are comparable and that they differ in the extent to which they occupy the crest of the septum. This assumption is supported by the fact that the groove defines the area to be occupied by its successor, the hood. That the groove is the precursor of the hood is also supported by the change in position of the early septal flanges (see p. 293) after the formation of the hood. These flanges, seen first as plates on the posterior border of the septum, become extensions of the posterior corners of the hood. In *M. cranium* the septum develops late in ontogeny and is short in length so that the hood even in occupying its full length is not appreciably wider than any of the species cited above in which the hood does not occupy more than the posterior half of the crest of the septum. A number of Mesozoic species indicate that full grooving of the septal crest with anterior bifurcation may be a more primitive condition than that seen in most Recent species in which the groove is restricted to the posterior segment of the septum. Elliott (1947, 1950) has described such a septum in the early loop phases of *Gemmarcula aurea* and of *Hamptonina buckmani* (Moore), Cooper (1955) in *Gemmarcula arizonensis* Cooper, Baker (1972) in *Zeilleria leckenbyi* (Davidson), and Steinich (1965) in *Gemmarcula humboldtii* (Hagenow) and *Trigonosemus pulchellus* (Nilsson).

*Shape and spinosity.* Other septal features upon which comment has been made in the above discussion are shape and spinosity. Friele (1877) noted that the median septum had a much longer attachment to the dorsal valve in *Dallina septigera* than in *M. cranium* while Beecher claimed that the septum is generally low in dallinid genera and projecting above the loop in terebratellid genera. Atkins (1959a) also drew attention to the dallinid character of anterior spinous projections.

The use of septal shape as a distinguishing feature would be very unsatisfactory. The shape changes so rapidly in early developmental phases in almost every species examined that the chances of matching the same growth phase in even two different species would be remote. However, there are differences in groups of genera in the extent of the septum. These differences are associated with growth or resorption during intermediate growth stages and are referred to below (p. 308). In all loop developmental series observed by me the anterior border of the septum is spinous during resorptive phases in this area.

*Origin.* In a recent study of the loop development of the Jurassic brachiopod *Zeilleria leckenbyi*, Baker (1972) describes the microstructure and derivation of the median septum. He states that the median septum of the adult plays no part in the development of the ascending elements of the loop. Baker refers to the earlier studies of Muir-Wood (1934) and shows that the median septum of adult shells is a bicomponent valve element resulting from the fusion of a septal pillar and septalial plates. The septal pillar comprises the anterior section and bears the future ascending elements of the loop, the septalial plates arise posteriorly as extensions of parts of the cardinalia. The septalial plates post-date and engulf the remnants of the septal pillar after the resorption of the last connections with the loop.

Studies on Recent terebratellid species (Richardson, in press) indicate that those axial structures culminating in the adult loop and septum arise in the same manner as described by Baker for the Jurassic zeilleriid brachiopods. The microstructure of the developing loop in these species has not been examined but even in the absence of



such a study it is clear that the adult median septum is a composite structure. The median septum of *Frenulina sanguinolenta* has also been shown (Richardson 1973a) to be derived from twin sources. Baker states that he has taken great care to avoid the use of the term median septum in the description of ontogenetic stages. He uses the term septal pillar to describe the earliest axial structure bearing the ascending elements of the loop and reserves the term median septum for the adult structure arising from the fusion of the septal pillar and septalial plates and which is also free of the loop. Although I am in complete accord with Baker's findings there are difficulties in applying these definitions at this stage. In the first place there are genera such as *Frenulina*, *Jaffaia*, *Pirothyris*, *Waltonia*, in which the adult loop is not free of the septum and in which it is not yet clear whether parts of the early septal pillar are engulfed by septalial plates. Secondly, the descending branches in all species studied also arise from both the cardinalia and the septal pillar; whether or not there are similar differences in microstructure as are evident in the septum is not known. Thirdly, there seems to be some confusion in the use of the terms, septalium, septalial plates, cruralium and their relationship to each other and to septal structures in brachiopods from different geological eras. Finally, the term median septum permeates the literature pertaining to Cainozoic brachiopods to such an extent that until a thorough morphological and ontogenetic study can be made of these structures it is preferable, for sheer convenience, to retain the term median septum to be used in the general sense in which it has been employed in the past. However, in the description of new material the terms septal pillar and median septum should be used where they can be clearly differentiated.

*Septal flanges.* Atkins (1959b) has provided a comprehensive and critical review of the occurrence of septal flanges in different species. These flanges arise on the posterior border of the median septum, they then become lateral expansions of the hood and finally are seen as postero-lateral horns on the transverse band. This sequence has been shown to occur in *Gemmarcula aurea* Elliott by Elliott (1947), *Gemmarcula humboldtii* (Steinich 1965), and in *Frenulina sanguinolenta* (Richardson 1973a). These flanges occur during development but are lost in the more advanced loop stages of the Recent species *Terebratalia transversa* (Sowerby) and of *Dallinella obsoleta* as described by Atkins (1959b) and Beecher (1895) respectively. They also occur in the Cretaceous species *Trigonosemus pulchellus* as described by Steinich (1965). Atkins noted that horns present on the transverse band of *Macandrevia cranium* are not preceded by flanges on the septum or the hood during the development of this species. Atkins states that their presence in *M. cranium* is due to the narrowing of a wide, transverse band by resorption of its mid-posterior margin. Horns are present also on the transverse bands of two genera, *Paralidingia* and *Jolonica*, whose loop development is unknown but is presumed to be similar to that of *Frenulina* (Richardson 1973a). In describing the hood of the Lower Cretaceous genus *Belothyris*, Smirnova (1960) compares the lateral flanges seen with those of *Gemmarcula aurea*. Owen (1970) also noted horns on the transverse bands of species of *Kingena* but does not consider them to be analogous with those seen in *G. aurea* because they show a different angle of deflection.

Thus the occurrence of flanges is described, in even doubtful cases, only in dallinid genera. Although the development of eight terebratellid species has been described

none has included a description of septal flanges or of the structures derived from them. These structures are termed 'pre-campagiform flanges' in the Treatise Glossary (Williams *et al.* 1965, p. H150).

Their presence has not been shown in any species of *Campages* nor in the development of *Fallax dalliniformis* Atkins which exhibits the same adult loop pattern as *Campages*. Consequently it is preferable to refer to these structures as septal flanges which in later developmental stages become lateral flanges on the hood then horns or ears on the transverse band whether or not they are ultimately resorbed. However, the presence of horns on the transverse band does not necessarily indicate that they have been preceded in development by septal flanges.

#### AN ACCOUNT OF FRIELE'S OBSERVATIONS AND THEIR SUBSEQUENT MISINTERPRETATION

Friele (1877) stated that the developing loop of *Macandrevia cranium* displayed a method of ring resorption different from that of *Dallina septigera*. Friele maintained that the early stages of loop development were similar in both species but that during the 'megerlia' stage of *M. cranium* 'the lateral walls of the ring were broken down by an aperture appearing in the middle of each and widening backwards'; in *D. septigera* 'the breach occurs to the contrary on the posterior end of the walls and extends in a forward direction' (Friele 1877, p. 383).

Friele also noted that young adult loops of *Frenulina sanguinolenta* were comparable with the megerliiform loop pattern of *M. cranium* and that developmental stages of *Glaciarcula spitzbergensis* (Davidson) were allied with those of *D. septigera*. Deslongchamps (1884) also noted these differences in methods of loop development after a study of *F. sanguinolenta* and noted certain similarities apparent in the adult loops of *Frenulina* and of *Laqueus*.

Contrary to the statements of Friele and Deslongchamps, Fischer and Oehlert (1892) claimed that *M. cranium* and *D. septigera* followed the same pattern of loop development and that each species passed through a series of stages termed centronelliform, ismeniiform (= megerliiform of Friele), terebratelliform, and magellaniiform. Fischer and Oehlert did not study the loop development of either *M. cranium* or *D. septigera* and they employed Friele's figures to demonstrate their theories. An examination of those figures from Friele, reproduced by Fischer and Oehlert, of *M. cranium* and *D. septigera* at the so-called ismeniiform stage reveals the apparent cause of error (text-fig. 2).

In the figures of these species lacunae are depicted in parts of the developing loop. However, the presence of these lacunae is not comparable in *M. cranium* and *D. septigera*. In *M. cranium* the lacunae appear in the dorsal bands of the ring while it is still attached (at least posteriorly) to the septum resulting in the delimitation of vertical connecting bands posteriorly; in *D. septigera* the lacunae appear after the dorsal segments of the ring are freed from the septum. A comparative study of Friele's figures of the developing loop of *M. cranium* and of *D. septigera* clearly demonstrates the differences both in the position of the lacunae and in the relative position and stage at which they appear in these two species.

Fischer and Oehlert's assertion that *M. cranium* and *D. septigera* display the same

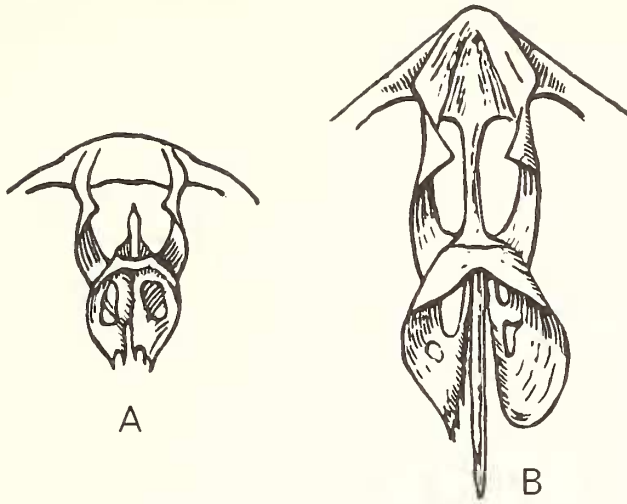


Fig. 20 a. *Macandrevia cranium*, Müller.—  
 b. *Magellania septigera*, Lovén. Appareils au  
 stade *Ismenia* montant la soudure annulaire  
 de l'appareil ascendant avec le septum.

TEXT-FIG. 2. Reproductions of the text and figures of Fischer  
 and Oehlert (1892), p. 308, fig. 20a, b.

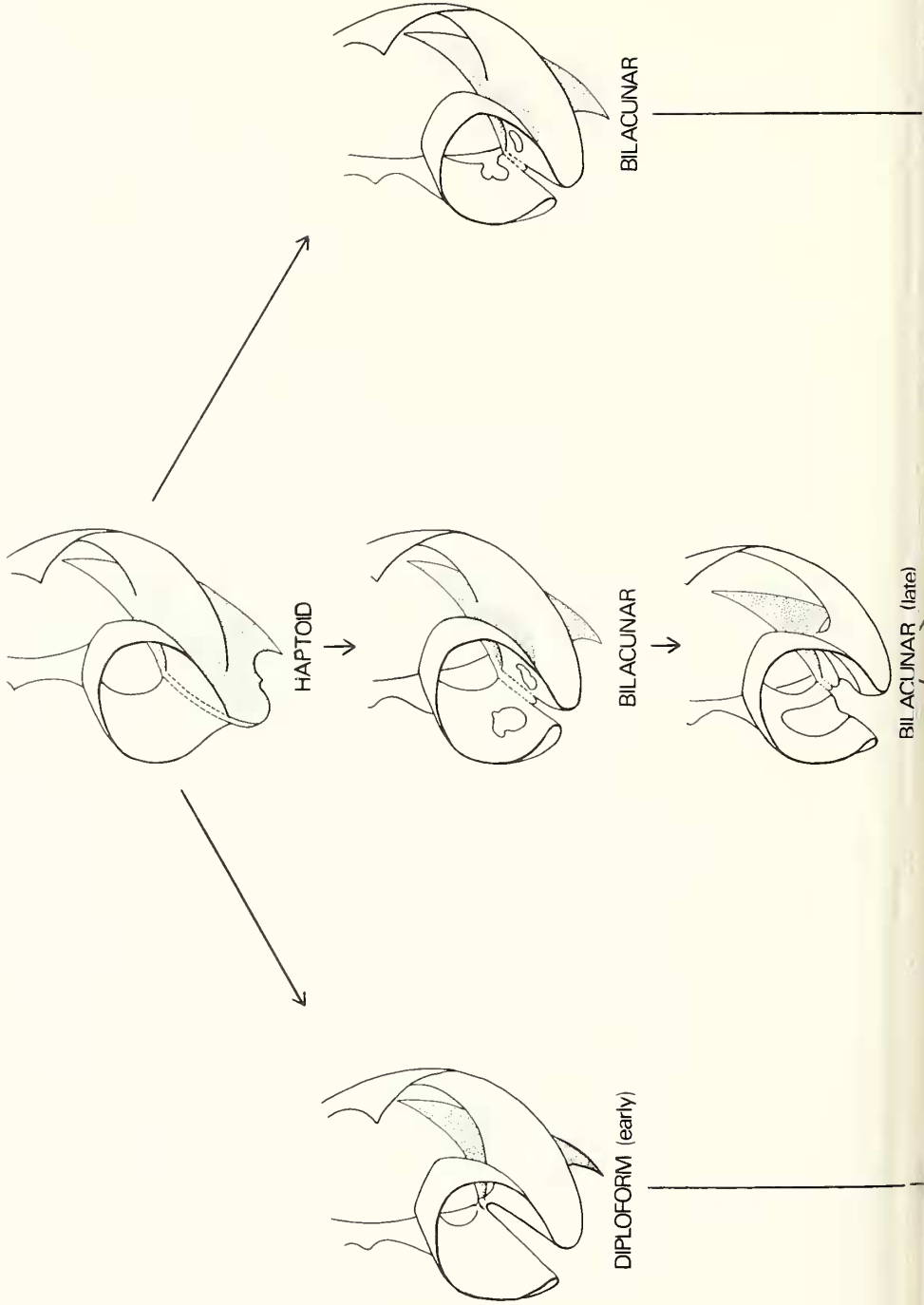
pattern of loop development has remained unquestioned by subsequent authors, Beecher (1895) using their supposedly uniform pattern of development as one of the principal factors differentiating these dallinid genera from terebratellid genera. Thus Fischer and Oehlert followed by Beecher formulated the basic classification of the terebratellacean brachiopods which has resulted in the present confused picture of loop development and generic relationships.

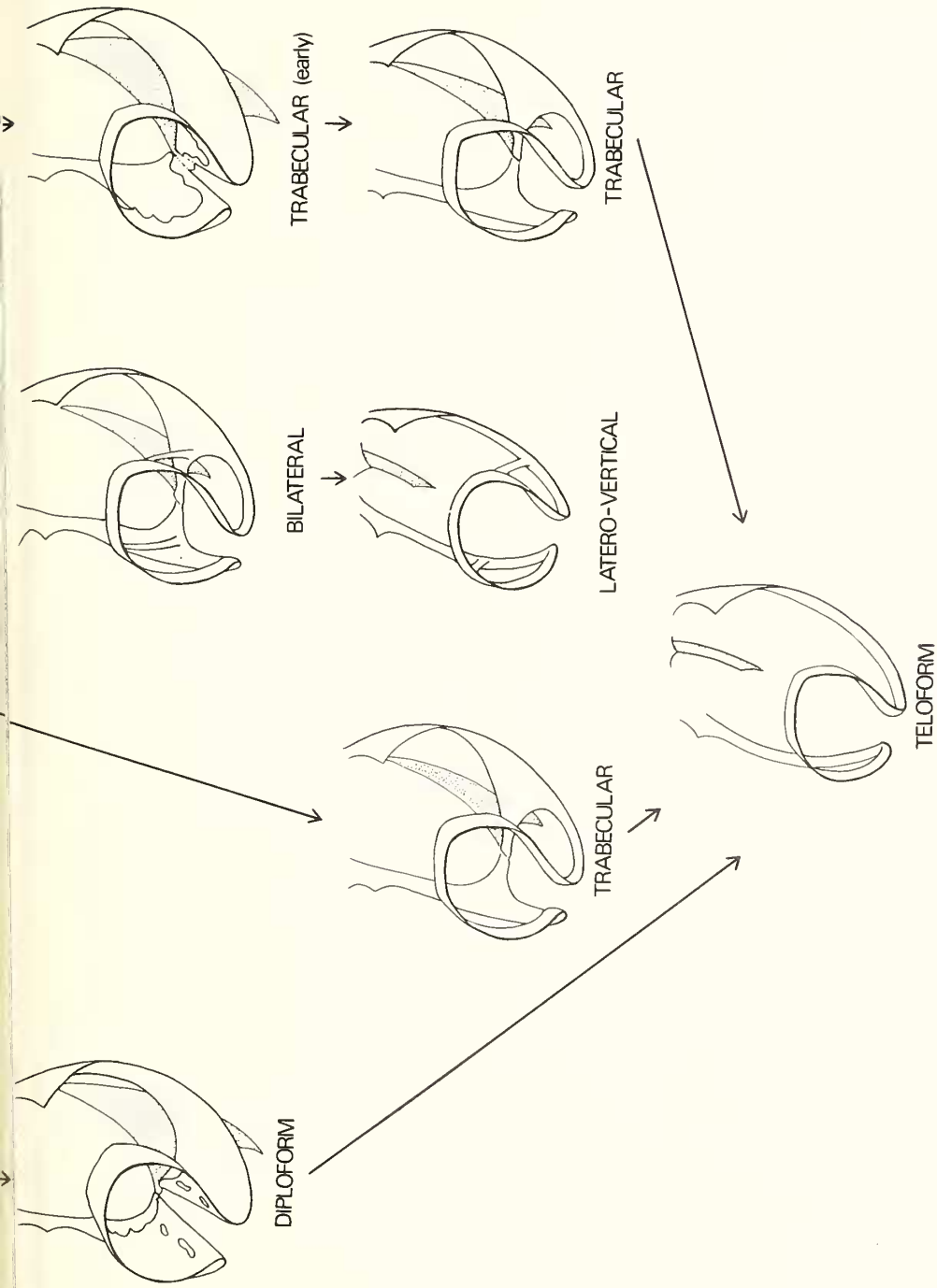
Since the publication of the Treatise the need for a reappraisal of the existing family boundaries has been indicated by some authors. Owen (1970) elevated the Cretaceous dallinid subfamily Kingeninae to family status and showed that relationships in loop structure existed between the members of this family, the Cainozoic genus *Frenulina*, and the laqueid genera *Laqueus* (Recent) and *Waconella* (Cretaceous). In 1973 both Cooper and I transferred the subfamily Frenulininae to the Laqueidae. Cooper's transference of this subfamily to the Laqueidae was based upon the study of growth phases of *Frenulina sanguinolenta* and upon a study of a new genus *Compsoria* with an adult loop pattern intermediate to that of *Frenulina* and *Laqueus*. The concurrent study of species of *Nipponithyris* indicated to Cooper that differences in loop development existed between the Frenulininae and the Nipponithyridinae stating that '*Frenulina* on the other hand in its final or frenuliniform stage has the hood so resorbed as to produce a window in the ascending elements, which is a trend towards the *Laqueus* loop. . . . In *Nipponithyris* the campagiform loop is resorbed anteriorly along the junction of the ascending and descending branches, thus trending towards the terebrataliiform loop stage which is its adult aspect' (Cooper 1973a, p. 20). My transfer of the Frenulininae (and the Kingenidae) to the Laqueidae was based also on an examination of the growth phases of the loop of *F. sanguinolenta* which showed

TEREBRATELLIDAE

LAQUEIDAE

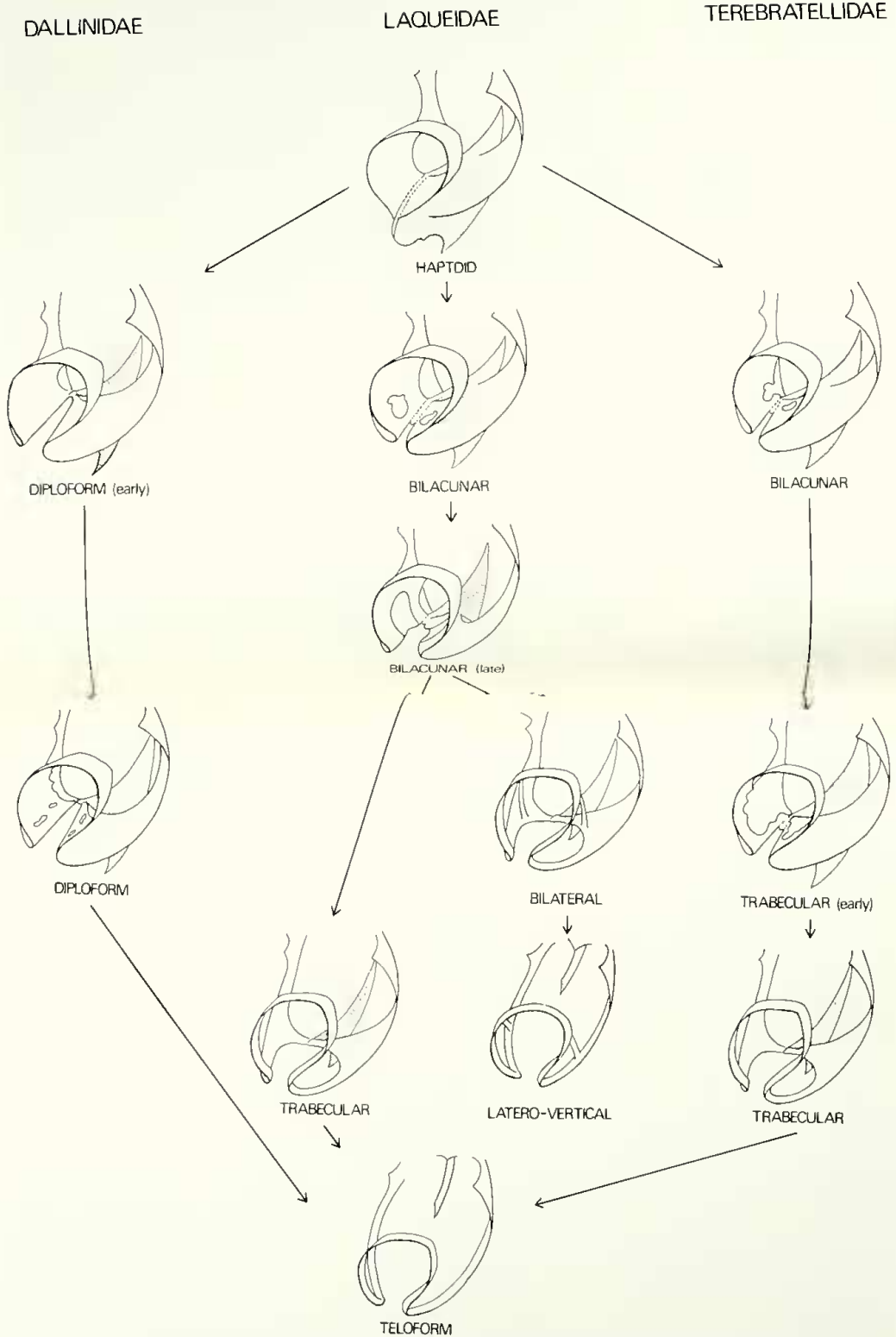
DALLINIDAE





TEXT-FIG. 3. Schematic representation of loop development in the families Dallimidae, Laqueidae, and Terebratellidae commencing with the haptoid loop pattern common to all and which precedes the intermediate loop patterns differentiating each family. This figure may be referred to in conjunction with Table 1.





TEXT-FIG. 3. Schematic representation of loop development in the families Dallinidae, Laqueidae, and Terebratellidae commencing with the haptoid loop pattern common to all and which precedes the intermediate loop patterns differentiating each family. This figure may be referred to in conjunction with Table 1.

relationships with the Tertiary genera *Aldingia* (previously attributed to the Kraussinidae) and *Paraldingia* and to *Kingena mesembrina* (Etheridge) from Australian Cretaceous beds. Cooper (1973b) created a new family the Macandreviidae for *Macandrevia* and *Notorygmia* on the basis of great differences in the cardinalia from other genera with supposed dallinid loop development.

The studies referred to above, either directly or indirectly, confirm the differences in loop development noted by Friele (1877) and thus emphasize the need to clarify and redefine patterns of loop development. This review has led to the redistribution of genera attributed previously to the Dallinidae, Laqueidae, and Macandreviidae. The bulk of the genera formerly included in the Dallinidae are transferred to the Laqueidae now regarded as synonymous with the Macandreviidae. With respect to attribution of genera the Terebratellidae remains unchanged but the diagnosis of the family together with the diagnoses of the Dallinidae and Laqueidae has been changed.

#### LOOP PATTERNS

*General.* The study of accounts of development of long-looped Mesozoic and Cainozoic brachiopods indicates that many similarities exist. The loop develops as the result of the growth and fusion of two structures, the descending branches and the ring. A median septum functions as a support until these processes of growth and fusion are completed when a loop independent of the septum is formed. In the earliest growth phases known the first structure to appear is the septum, the free border of which becomes grooved as a precursor to the development of a hood then a ring which envelops the crest of the septum. From the lateral walls of the septum lamellar structures arise, lengthen posteriorly, and meet extensions of the crura to form the descending branches (the descending branches arise from the crura alone in *Macandrevia cranium*). The attachments to the septum of the descending branches and the ring run parallel to each other. The fusion of these lines of attachment together with the resorption of parts of both the ring and the septum results in the adult loop pattern. The anterior and dorsal segments of the ring recurve from the descending branches to become the ascending branches which are united by the ventral segment of the ring now termed the transverse band.

Major differences existing between the families occur during intermediate stages of development (text-fig. 3). These differences arise as a result of the pattern and timing of resorption of portions of the ring and the stage at which it is freed from the septum. These factors, in turn, govern the distribution of segments of the ring to form portions of the loop (text-fig. 4). In each family the ventral segment of the ring forms the transverse band and the anterior sections of the lateral and dorsal segments form the ascending branches. The fate of the remaining segments of the ring (the dorsal and dorso-lateral segments posterior to the anterior sections forming the ascending branches) differs in each family. In the Dallinidae they provide ventral components to the anterior limbs of the descending branches; in the Terebratellidae these segments are resorbed; in the Laqueidae there is partial resorption only of the central areas, the posterior rim remaining as the vertical connecting bands.

Since early differences in patterns of dallinid and terebratellid loop development

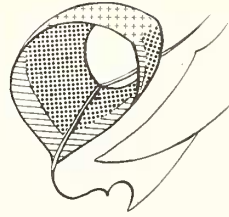


TEXT-FIG. 4. Diagrammatic representation of the haptoid loop phase showing the septum with the ring and part of the descending branch of one side. The shading of the ring differentiates the areas giving rise to parts of the loop.

The ventral segment (+shaded) becomes the transverse band in each family.

The anterior sections of the dorsal and lateral segments (hatched) become the ascending branches in each family.

The dorsal and dorso-lateral segments (dotted) provide ventral components to the descending branches in the Dallinidae; in the Laqueidae the central areas are resorbed, the posterior rim becoming the vertical connecting bands; in the Terebratellidae these segments are resorbed.



have been reviewed in previous sections only intermediate and later patterns of development are reviewed below for each family. Early phases of development cover the formation of the descending branches and of a ring, each structure being separately attached to the median septum. Intermediate loop patterns are defined as those patterns which commence with the anterior fusion of the attachments of the descending branches and the ring, and which incorporate those patterns developed before their complete detachment from the septum. Prior to the fusion of the attachments of the descending branches and the ring, the gross pattern of loop development is similar in each family. The intermediate patterns which differentiate the three families are described below.

At the end of each of the following three sections the studies on loop development appropriate to each family are recorded. These lists of studies include both comprehensive accounts and those which describe only isolated growth phases.

*Dallinid.* The final stage of early development in members of the Dallinidae shows that the attachments of the ring extend along the full length of the crest of the septum. Fusion of these attachments with the descending branches proceeds in an anterior to posterior direction until the full lengths of the attachments are fused and freed from the septum except for a short posterior section. These posterior segments of the fused attachments remaining connected to the septum are the lateral connecting bands. As a result of this fusion of attachments both the anterior limbs of the descending branches and the lateral connecting bands consist of doubled gutter-like structures, i.e. each has two components, a dorsal component derived from the anterior limbs of the descending branches and a ventral component from the dorsal segments of the ring. The remaining segments of the ring form the ascending branches and the transverse band.

Simultaneously with or shortly after fusion of the attachments lacunae perforate the ventral segments of the anterior limbs of the descending branches, i.e. the segments derived from the ring. This is the adult condition of the loop in *Campages*, in *Nipponithyris* (Pl. 44, figs. 5, 6), and in *Fallax*. This is also the stage represented in pl. 3, fig. 4 in Friele's (1877) account of the development of *Dallina septigera*. Atkins has commented upon the nature of the descending branches in the development of *Fallax dalliniformis* 'the gutter is formed not by the descending branch alone, but by the fused descending and ascending branches as in *Campages furcifera*' (1960a, p. 86). Cooper also states that in '*Nipponithyris* the campagiform loop is resorbed anteriorly along the junction of the ascending and descending branches, thus trending toward the terebrataliiform loop stage which is its adult aspect' (1973a, p. 20).

During the growth phases outlined above Friele and Atkins both noted spinosity in parts of the developing loop, namely the anterior border of the septum and the anterior and medial borders of the descending branches. In addition to resorption of areas of the septum anterior growth must also occur for, in most species of this family figured, the septum extends at least as far anteriorly as the loop.

The enlargement of the lacunae perforating the anterior limbs of the descending branches results in the resorption of their ventral components, i.e. the segments derived from the ring. The simultaneous resorption of the lateral connecting bands extending between the septum and the descending branches results in a loop entirely free of the septum and seen in adult specimens of *D. septigera*.

Studies of dallinid loop development: *D. septigera* by Friele 1877, Deslongchamps 1884, Fischer and Oehlert 1892, and Atkins 1960b. *F. dalliniformis* by Atkins 1960a. *Nipponothyris afra* by Cooper 1973a.

*Laqueid.* Early stages of development in the Laqueidae result in the formation of descending branches and of a ring enveloping the crest of the septum. As noted in *Frenulina sanguinolenta* (Richardson 1973a) there may be variation in the extent to which the ring envelops the crest of the septum, in other words the width of the band forming the ring may differ in comparable growth phases. Anterior fusion of the attachments of the ring and of the descending branches is either simultaneous with or is rapidly succeeded by the resorption of the anterior crest and border of the septum. While the attachments to the septum of the ring and the descending branches are still separated posteriorly, lacunae perforate the dorsal segments of the ring (text-fig. 3). The enlargement of these lacunae results in the separation of segments of the ring to form different parts of the loop. Those segments anterior to the lacunar borders (their attachments now fused with the descending branch attachments) form the ascending branches and the transverse band, those segments posterior to the lacunae form vertical bands, termed the medio-vertical connecting bands, extending from the septum to the transverse band. As noted above, those segments of the ring

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#### EXPLANATION OF PLATE 44

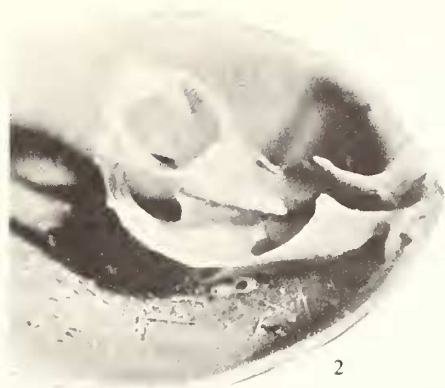
Photographs of the loop of three species from three different families illustrating the different patterns evident during intermediate loop phases.

Figs. 1, 2. *Frenulina sanguinolenta* (Gmelin) from Masthead Island, Queensland. Bilateral loop phase.

Shell length 8 mm, hypotype NMV H 184. 1, ventral view. 2, laterally tilted view to show vertical connecting band running from the transverse band to the septum and its descending branch attachment.

Figs. 3, 4. *Magellania flavescens* (Lamarck) from Kangaroo Island, South Australia. Early trabecular loop phase showing the appearance of the loop immediately after resorption of dorsal segments of the ring and before resorption of the anterior and medial regions of the descending branches. Parts of the ring remain as jagged edges on the anterior portions of the descending branches and the septum. Shell length 6 mm, hypotype NMV H 202. 3, ventral view. 4, laterally tilted view.

Figs. 5, 6. *Nipponothyris nipponensis*, Yabe and Hatai from Sôyô-maru Strait, Japan Sea. Diploform loop phase. Shell length 12 mm. Specimen from the collection of the late R. S. Allan in the Geology Department, University of Canterbury, Christchurch, New Zealand. 5, ventral view showing lateral connecting bands and descending branches both doubled, their ventral components being derived from the dorsal segments of the ring. Two lacunae may be seen in the ventral components of the descending branches, the enlargements of these lacunae leading to the resorption of these components. 6, laterally tilted view.



RICHARDSON, *terebratulacean loops*

(= ascending branches and transverse band) anterior to the lacunae are fused with the descending branch attachments. Posterior to the lacunae the attachments of the ring and of the descending branches do not fuse, the descending branch attachments forming the lateral connecting bands, the ring attachments forming the dorsal attachments (to the septum) of the vertical connecting bands. This pattern of loop is seen in adult members of *Aldingia*, *Paralidingia*, *Jolonica*, and *Kingena*. These genera all display a loop with two pairs of connecting bands (lateral and medio-vertical) although there are differences in the relative width of the bands going to make up the loop. This pattern is also seen in the developing loop of *Frenulina sanguinolenta* (Pl. 44, figs. 1, 2), *Macandrevia cranium*, *Laqueus californianus*, *Compsoria suffusa* Cooper, *Gemmarcula aurea*, *Dallinella obsoleta*, *Trigonosemus pulchellus*, and fleetingly in *Terebratalia transversa*. This pattern is commonly referred to as frenuliniform which, as Cooper (1973a) points out, is not the final stage of the loop of adult members of *Frenulina*.

During the next phases of development the processes of growth involved (simultaneous enlargement and resorption) change the position of the vertical bands relative to the septum so that they shift from medial to lateral regions of the loop. The ventral attachments of the vertical connecting bands remain fused to the transverse band but their dorsal attachments shift away from the septum to the areas of union of the descending branches and the lateral connecting bands. These bands are now called the latero-vertical connecting bands. This type of loop with the two pairs of connecting bands, lateral and latero-vertical, is seen in adult members of *Frenulina*, *Compsoria*, *Laqueus*, and *Waconella*. In the final loop pattern characteristic of *Pictothyris* the lateral connecting bands are resorbed so that only one pair of connecting bands, the latero-vertical bands, are retained. The two loop patterns described above are not characteristic of other genera referred to this family. The adult loops of *Gemmarcula*, *Terebratalia*, and *Dallinella* possess lateral connecting bands only, those of *Macandrevia* and *Notorygmia* are entirely free of the septum which is completely resorbed. These genera display the same pattern of development as other members of the family up to the formation of the lacunae and the delimitation of the medio-vertical connecting bands. From this loop phase two different lines of development may take place; in one the medio-vertical bands are not retained, in the other they are translated into latero-vertical connecting bands (*Frenulina*) which ultimately are retained rather than the lateral connecting bands (*Laqueus*). It is not absolutely clear in accounts of the development of *Macandrevia cranium* and of *Gemmarcula aurea* whether there is any shift in position of the vertical connecting bands prior to their resorption. However, it does seem likely that they skip the stage in which the vertical bands shift from a medial to a lateral position, so that these genera lose the vertical connecting bands before the lateral connecting bands.

The pattern of development outlined above is embellished by additional structures, the septal flanges, in some members of the Laqueidae. As noted on page 293 these flanges, originating as plates on the early septum, ultimately become transformed into horns projecting from the postero-lateral corners of the transverse band. This sequence of development has been described for *Frenulina sanguinolenta*, *Dallinella obsoleta*, *Gemmarcula aurea*, *Trigonosemus pulchellus*, and *Terebratalia transversa*.

Other modifications of the general pattern of development and seen only in some

members of the Laqueidae are the origin of the descending branches and the splitting of the septum, both topics being examined in detail in earlier sections. In *Macandrevia cranium* the descending branches arise from the crura alone, the only case known in which the descending branches do not have a double origin. *M. cranium* and *Laqueus californianus* are also described as possessing a median septum which is split anteriorly in early development. The crest of the septum in *Gemmarcula aurea* is described as being grooved with anterior divergences of the two sides.

The degree of spinosity displayed in the developing and adult loops of the Laqueidae is variable and seems to bear no simple relation to any other structure or condition of the loop. All members of the Terebratellacea display spinosity of the anterior border of the median septum during development. The developing loops of *M. cranium* and of *G. aurea* are described as showing spinosity not evident in the adult loops of these species. Apart from the anterior border of the septum neither the developing nor the adult loop of *Frenulina sanguinolenta* shows any spinosity. The adult loop of *Aldingia* is free of spines while spinous bands and branches characterize the adult loops of *Paraldingia woodsii* (Tate) and *Kingena mesembrina*, all with loops of the same pattern.

The loop development of *Terebratalia transversa* tends towards the pattern seen in members of the Terebratellidae in the brief duration of the identity of the lacunae so that vertical connecting bands are present only fleetingly. However, the rapidity with which the lacunae enlarge and breach the posterior walls of the ring is probably much greater in the Terebratellidae than in *T. transversa*. Atkins (1959b) in her study of the development of this species did not comment on any particular difficulty in finding this loop phase whereas hundreds of specimens of *Magellania flavescens* were opened before several examples suitable for the illustration of this phase were found.

Studies of laqueid loop development: *Compsoria suffusa* by Cooper 1973a. *Coptothyris grayi* by Hatai 1939. *Dallinella obsoleta* by Beecher 1895. *Frenulina cruenta* by Cooper 1973a. *Frenulina sanguinolenta* by Deslongchamps 1884; Cooper 1973a; and Richardson 1973a. *Gemmarcula arizonensis* by Cooper 1955. *Gemmarcula aurea* by Elliott 1947. *Gemmarcula humboldtii* by Steinich 1965. *Kingena mesembrina* by Elliott 1952. *Laqueus californianus* by Konjoukova 1948 and 1957. *Macandrevia cranium* by Friele 1877; Deslongchamps 1884; Fischer and Oehlert 1892; Elliott 1948; and Atkins 1959a. *Psilothyris occidentalis* by Cooper 1955. *Terebratalia transversa* by Atkins 1959b. *Trigonosemus pulchellus* by Steinich 1965.

*Terebratellid.* Members of the Terebratellidae follow a similar pattern in early intermediate growth phases to that described for the Laqueidae. In the first place the extent to which the ring occupies the crest of the septum may vary in a single species (Richardson, in press). Secondly, the anterior fusion of the attachments of the ring and of the descending branches may occur simultaneously with the anterior resorption of the septum or this fusion may occur while the septum, partition-like, separates each side of the loop. Finally, lacunae may arise in the dorsal segments of the ring at the same relative phase of development as they do in the Laqueidae, i.e. after the anterior fusion but before the posterior fusion of the ring and descending branch attachments. However, from this stage there are differences in development. In the terebratellid species examined there is a rapid enlargement of the lacunae so that the

posterior borders of the ring are breached (Pl. 44, figs. 3, 4). The rapidity with which these lacunae enlarge and break the borders of the ring probably accounts for the fact that they have not been described hitherto in terebratellid development (loc. cit.). It is also possible, as suggested in this paper, that lacunae may perforate the ring in some but not all terebratellid species or even individuals of one species. The width of the band forming the ring, a feature in which variation is apparent, may be such that the greater resorption required is aided by lacunae which perforate the ring and which enlarge rapidly to resorb its posterior segments. It is presumed that, in species with ring bands of narrower diameter, the gradual excavation of the posterior border is sufficient to reduce the width of the band. This is a process which is apparently continuous in all species, particularly later in development when the loop grows by the accretion of lamellae on its anterior borders as simultaneous resorption occurs of its posterior borders. In any case, whatever the amount of resorption required in different individuals the resulting loop pattern displays descending branches (still attached posteriorly to the septum) recurving into ascending branches united by a transverse band. Those portions of the descending branches remaining attached to the septum (and which are analogous with the resorbed dorsal segments of the ring) represent the lateral connecting bands. The resorption of these bands gives the adult loop free of any connection with the septum. Either of the two final loop patterns described above, i.e. with or without lateral connecting bands, are seen in the majority of terebratellid genera.

Studies of terebratellid loop development: *Aneboconcha obscura* by Cooper 1973b. *Diestothyris frontalis* by Konjoukova 1948. *Jaffaia jaffaensis* by Thomson 1916 and Richardson, in press. *Magas chitoniformis* by Steinich 1965. *Magellania flavescens* by Richardson, in press. *Magellania venosa* by Fischer and Oehlert 1892 and Cooper 1973b. *Neothyris lenticularis* by Douvillé 1879 and Richardson, in press. *Pirothyris vercoi* by Richardson, in press. *Terebratella dorsata* by Fischer and Oehlert 1892. *Waltonia inconspicua* by Thomson 1915 and Richardson, in press.

#### TERMINOLOGY

When Beecher (1895) established the subfamilies Dalliniinae and Magellaniinae on the basis of loop development he summarized and extended the practice of naming each different growth phase from the adult loop showing that particular pattern. Thus the Dalliniinae displayed platidiiform, ismeniiform, mühlfeldtiiform, terebrataliiform, and dalliniiform loop patterns and the Magellaniinae bouchardiiform, megerliniform, magadiform, magaselliiform, terebratelliiform, and magellaniiform patterns. As an inevitable result of the discovery of new genera and of increasing knowledge of brachiopod development, this nomenclature has had to be changed a great deal, a process which would be expected to continue. Like Atkins (1959a) it is felt that this type of nomenclature is confusing and that it would be more appropriate to use descriptive in place of generic adjectives to indicate different loop patterns. However, before extending this concept there are some changes made since the publication of the Treatise which should be noted and which are indirectly concerned with the terminology of loop patterns. Atkins (1959b) revised the existing state of knowledge of septal flanges (see p. 293) which were referred to later in the

Treatise as pre-campagiform flanges (p. H150). These flanges are not known to occur in *Campages* or its relatives and it is preferable to retain Atkins's term, septal flanges, for these structures. The use of the term vertical connecting bands, which may occupy either a medial or a lateral position, in place of the pre-frenuliniform, frenuliniform, laqueiform, or kingeniform connecting bands has also been recommended (Richardson 1973a). Baker suggested that succeeding loop patterns be termed phases rather than stages 'as this suggests the more real, cumulative growth pattern of the loop' (1972, p. 457). This recommendation is adopted but another suggestion of Baker's referring to the use of the term median septum presents difficulties which are discussed on page 293.

The Treatise describes the developing loops of members of the Terebratellidae as being characterized by a series of patterns labelled pre-magadiniform, magelliform, terebratelliform, and magellaniiform. This series of patterns conform with the various terebratellid growth series described in this and previous papers. However, the names applied to the series of patterns found in the Dallinidae (pre-campagiform, campagiform, frenuliniform, terebrataliiform, dalliniform) and the Laqueidae (pre-campagiform, campagiform, frenuliniform, laqueiform) are invalid for a variety of reasons. The use of the term frenuliniform with reference to one of the loop phases seen in the Dallinidae is the result of a misinterpretation, by various authors, of the growth series described by Friele (1877) for *Dallina septigera* (see p. 294). The frenuliniform loop phase is recognized as that stage which displays two pairs of connecting bands, the lateral and the latero-vertical bands. As noted previously vertical bands are delimited as the result of the presence, in the dorsal band of the ring, of two lacunae while the ring is attached posteriorly to the septum. In the Dallinidae resorption of segments of the ring occurs after the ring has lost any connection with the septum thus precluding the formation of vertical connecting bands.

Elliott (1947) proposed the terms pre-campagiform and campagiform to describe the early growth phases of the loop in the Dallinidae and the Laqueidae. Cooper has described the loop structure of adult members of *Campages* (1970) and immature and adult loops of the related genus *Nipponithyris* (1973a). The adult loop of *Campages* displays descending branches with double anterior limbs (the ventral components derived from the dorsal segments of the ring) a feature not observed in the developing or adult loop of any member of the Laqueidae or Terebratellidae. This loop pattern corresponds with that described by Friele (1877) for an intermediate loop phase of *D. septigera* and is the same as the adult pattern of *Fallax dalliniformis* described by Atkins (1960a). Succeeding developmental phases of *D. septigera* do not display vertical connecting bands and, as noted above, the fusion of the full lengths of the ring attachments with those of the descending branches precludes their formation. The loop pattern displayed by *Campages* is not followed by a frenuliniform phase but in ontogeny this pattern occurs at a comparable stage in the loop development of the Dallinidae to the frenuliniform stage in the Laqueidae. In addition as Cooper (1973a) has pointed out the form of the loop of *Frenulina* usually called the frenuliniform phase is not the final phase of the loop in this genus.

If we continue to follow the method of nomenclature used in the past, i.e. naming the loop patterns of a family from the adult genus showing that pattern, the only terms at present valid for each family are dalliniform for the Dallinidae and

terebrataliiform for the Laqueidae. Therefore new sets of terms are required for each of the two families, Dallinidae and Laqueidae. The need to provide new names for the loop patterns found in these families is questionable. In the first place no Cainozoic genus of the Dallinidae displays an adult loop pattern earlier than the so-called terebrataliiform phase, and in the Laqueidae no adult loop pattern is known prior to the pre-frenuliform phase. The second and more significant point is the wisdom of giving different names to similar structures which may follow a similar developmental pattern. Early loop patterns of all three families are similar; any differences which exist in these loop patterns at this stage seem to be differences in the width of the bands forming the descending branches and the ring. To adopt three different series of descriptive names for the loop patterns found in these families tends to give an entirely unjustified impression of separateness. It is desirable to attempt to indicate in their right perspective any similarities and differences which exist. For these reasons it is proposed that the former generic adjectives be replaced with purely descriptive terms some of which can be applied to each family. That such a change is needed is emphasized by Baker's (1972) work on the development of the Jurassic species *Zeilleria leckenbyi* which shows characteristics of both the dallinid and terebratellid loop patterns as then defined. In attempting to indicate these similarities Baker called the loop phases seen in this species pre-paramagadiniform, syncampagiform, frenuliform, terebrataliiform, dalliniform, zeilleriiform. The existing system could lead to even more formidable assemblages of names. However, Baker has had to base his interpretations of difficult material upon known patterns of development in Cainozoic brachiopods and to cope with such current misinterpretations as the belief that the campagiform precedes the frenuliform phases in ontogeny. Therefore the following terms are proposed to describe the loop phases which embrace:

1. The formation of the septum, the hood, and the rudiments of the descending branches—the *axial* phase.
2. The presence of a hood in place of a ring and complete descending branches, each structure being separately attached to the septum—*annular* phase.
3. The anterior fusion of the attachments of the ring and the descending branches—*haptoid* phase.
4. The presence of two lacunae in the dorsal segments of the band forming the ring—*bilacunar* phase.
5. The fusion of the attachments of the ring (completely free of the septum) with the descending branch attachments to form descending branches with doubled anterior limbs—*diploform* phase.
6. The presence of two pairs of connecting bands, lateral and latero-vertical—*bilateral* phase.
7. The presence of latero-vertical connecting bands only—*latero-vertical* phase.
8. The presence of lateral connecting bands only—*trabecular* phase.
9. The absence of any connecting bands so that the loop is free of the septum—*teliform* phase.

Thus to employ the proposed terminology terebratellid loop development is characterized by the following patterns: axial, annular, haptoid, bilacunar (thought to be optional), trabecular, teliform; laqueid loop development by axial, annular,



haptoid, bilacunar succeeded either by bilateral and latero-vertical or by trabecular and teloform phases; dallinid development by annular, haptoid, diploform, teloform. These terms are used for the principal morphological patterns evident and are employed without consideration of differences in dimensions of the bands in different genera. For example, the bilateral phase in laqueid development applies to the structure of the loop in *Frenulina*, *Compsoria*, and *Laqueus* although the bands forming the loop tend to be wider in *Frenulina* than in the other two genera. Also Baker (1972) refers to dalliniform and zeilleriiform phases both of which are regarded as teloform patterns since they differ only in the slender ribbon-like bands which replace the heavier structures of the earlier loop.

The following table sets out the new and old terminology together with the adult genera displaying the patterns named. In some cases one cannot provide exact equivalents, e.g. the adult loop of *Australiarcula* displays complete descending

TABLE 1. The adult genera of each family displaying the loop patterns defined with the new and the old (in parentheses) terminology.

Phase name	Genus with adult loop pattern
<b>DALLINIDAE</b>	
Axial (precampagiform)	Unknown
Annular (precampagiform)	Unknown
Haptoid (campagiform)	Unknown
Diploform	<i>Campages</i> , <i>Chathamithyris</i> , <i>Fallax</i> , <i>Nipponithyris</i> , ? <i>Glaciarcula</i>
Teloform (dalliniform)	<i>Dallina</i>
<b>LAQUEIDAE</b>	
Axial (precampagiform)	Unknown
Annular (precampagiform)	Unknown
Haptoid (campagiform)	Unknown
Bilacunar (frenuliniform)	<i>Aldingia</i> , <i>Jolonica</i> , <i>Kingena</i> , <i>Paraldingia</i>
Followed by either:	
1. Bilateral (laqueiform) and Latero-vertical (pictothyridiform) or	<i>Compsoria</i> , <i>Frenulina</i> , <i>Laqueus</i> , <i>Waconella</i> <i>Pictothyris</i>
2. Trabecular (terebrataliform)	<i>Dallinella</i> , <i>Diestothyris</i> , <i>Genmarcula</i> , <i>Pacifithyris</i> , <i>Terebratalia</i> , <i>Trigonosemus</i>
Teloform (dalliniform)	<i>Coptothyris</i> , <i>Macandrevia</i> , <i>Notorygmia</i>
<b>TEREBRATELLIDAE</b>	
Axial (premagadiniform)	<i>Neobouchardia</i> , <i>Australiarcula</i> , <i>Bouchardia</i> , <i>Bouchardiella</i> , <i>Malleia</i>
Annular (magadiniform)	<i>Magadina</i> , <i>Magas</i>
Haptoid (magelliform)	<i>Jaffaia</i> , <i>Magella</i> , <i>Pirothyris</i>
Bilacunar (or equivalent)	Unknown
Trabecular (terebratelliform)	<i>Aneboconcha</i> , <i>Gyrothyris</i> , <i>Magadinella</i> , <i>Magasella</i> , <i>Pachymagas</i> , <i>Terebratella</i> , <i>Waiparia</i> , <i>Waltonia</i>
Teloform (magellaniiform)	<i>Aerothyris</i> , <i>Austrothyris</i> , <i>Cudmorella</i> , <i>Iheringithyris</i> , <i>Magellania</i> , <i>Neothyris</i> , <i>Rhizothyris</i> , <i>Stethothyris</i> , <i>Victorithyris</i>

branches but no hood or ring while *Bouchardia* possesses a septal ring but no descending branches. In the list of terebratellid loop patterns the phase labelled bilacunar or equivalent means that a bilacunar phase is known in the development of some species but that it is presumed but not proven that there may be other methods of reducing the width of the band forming the ring in other species.

#### FAMILY AND SUBFAMILY DIAGNOSES

*Discussion.* The separation of terebratellacean genera according to patterns of ring resorption gives a more credible classification of the Dallinidae, Laqueidae, and Terebratellidae and one in which the relationships between the families are more explicit. The features used to distinguish the members of different families are either the presence of descending branches with double anterior limbs (Dallinidae), of vertical connecting bands (Laqueidae) or the absence of either of these structures in any loop phase (Terebratellidae). Supporting but less decisive distinguishing characters are dental plates, septal length, the width of the bands forming the loop, and cardinalia pattern. Dental plates are present in all members of the Laqueidae, in two of the eleven genera referred to the Dallinidae, and are not present in any member of the Terebratellidae. In general the septum of the Dallinidae is long (as long or longer than the adult loop) and of moderate length (approximately half the length of the loop) in the Terebratellidae; in the Laqueidae the septum appears to occupy the minimum area required to support the developing loop and may be entirely resorbed as soon as all connecting bands are resorbed. Before resorption occurs the descending branches and the ring are formed of bands of greater width in the Dallinidae than they are in the Laqueidae and the Terebratellidae. All members of the Dallinidae possess hinge plates which may be excavate or fused with the valve floor and they are always associated with the septum; the majority of terebratellid genera are similarly equipped (the exceptions being members of the Bouchardiinae in which hinge plates do not form parts of the swollen cardinalia) while the Laqueidae show a wide variation even within species in the condition of the hinge plates and their association or lack of it with the septum. The cardinal process is always prominent in the Terebratellidae; in most members of the Laqueidae and the Dallinidae it is small or absent although one subfamily in each family (each of which includes only Japanese genera) shows a well-developed cardinal process.

Two genera, *Terebratalia* and *Jaffaia*, give some picture of the relationships which may exist between members of different families. The pattern of ring resorption in *Terebratalia transversa* (p. 303) is intermediate in type to that described as characteristic of the Terebratellidae and the Laqueidae. *Terebratalia* is also noted for the variability of the cardinalia and some of its external characters (Atkins 1959*b* and Paine 1969) however the presence of dental plates together with the absence of hinge plates anchor the genus in the Laqueidae. *Jaffaia* has no such determinant characters and remains a linking form between the Dallinidae and the Terebratellidae. In its ontogeny *Jaffaia* does not proceed to the intermediate developmental loop phases considered to be of diagnostic value and the adult loop is of late haptoid pattern. However, the bands forming the ring and the descending branches are as wide as these structures in comparable growth phases of members of the Dallinidae. Further

development of the loop in *Jaffaia* could follow either a dallinid or a terebratellid pattern. The absence of dental plates and the nature of the cardinalia form no bar to inclusion in the Dallinidae as it is constituted at present.

Family DALLINIDAE Beecher, 1893. Emend. nov.

*Diagnosis.* Loop passing through all or part of axial, annular, haptoid, diploform, and teloform growth phases.

*Comments.* The existing subfamilies Dallininae and Nipponithyrinae are retained for two groups of genera differing in cardinalia pattern. The erection of a third subfamily to embrace those genera with dental plates, namely *Fallax* and *Glaciarcula*, would be quite unwarranted at this stage of our knowledge of these and related genera. *Fallax*, apart from the presence of dental plates, is closely allied with *Dallina* and *Campages*. However, the affinities of *Glaciarcula* are less clear. *Glaciarcula* is allied with *Fallax* in the presence of dental plates and its type of cardinalia and with *Aneboconcha* (subfamily Terebratellinae) in its external features. Friele (1877) commented on the resemblances apparent in the developing loop of *Dallina septigera* and of *Glaciarcula spitzbergensis* and figured two specimens of the latter species in which the anterior limbs of the descending branches appear to be doubled, i.e. at the diploform phase. However, Elliott (1956) states that the loop is terebratelliform while Cooper describes it as 'terebrataliform, much stouter than that of the austral shell *Aneboconcha* and with short, thick attachments to the median septum' (1973*b*, p. 28).

The allocation of Cainozoic genera to dallinid subfamilies and their diagnoses is as follows:

Subfamily DALLININAE Beecher, 1893. Emend. nov.

Dallinidae with adult diploform or teloform loop patterns; without dental plates; with excavate hinge plates fused medially with septum, a small cardinal process if present.

Genera included: *Dallina*, *Campages*, *Pegmathyris*, *Chathamithyris*.

Subfamily NIPPONITHYRINAE Hatai, 1938. Emend. nov.

Dallinidae with adult diploform loop pattern; without dental plates; with hinge plates thickened and fused with valve floor, cardinal process well defined.

Genera included: *Nipponithyris*, *Isumithyris*, *Miyakothyris*, *Yabeithyris*, *Tanakura*.

Subfamily uncertain: *Fallax*, *Glaciarcula*.

Family LAQUEIDAE Thomson, 1927. Emend. nov.

*Diagnosis.* Loop passing through axial, annular, and haptoid phases to a bilacunar loop pattern; bilacunar pattern may be the adult loop pattern or be followed either by bilateral and latero-vertical phases or by trabecular and teloform phases; dental plates present.

*Comments.* The simplest method of classifying this family would be to adopt the twofold division evident when only loop developmental patterns are taken into account. The members of this family would then be differentiated on whether vertical

connecting bands are retained through later development stages (*Laqueus*, *Waconella*, *Kingena*, *Zittelina*, *Belothyris*, *Frenulina*, *Compsoria*, *Aldingia*, *Paralidingia*, *Jolonica*, *Pictothyris*) or whether the vertical bands are lost before the lateral (horizontal) connecting bands (*Terebratalia*, *Dallinella*, *Trigonosemus*, *Macandrevia*). The features used, other than adult loop patterns, to distinguish the subfamilies (cardinalia type and the presence of septal flanges during development) may prove to be of little diagnostic value within the family Laqueidae. However, further studies of loop development and in particular the study of Mesozoic genera should indicate if such a division would be a better method of classification than that outlined below.

In the previous section on the Dallinidae only Cainozoic genera were redistributed amongst the two subfamilies retained. A number of Mesozoic genera are included in this family. The relationships between *Kingena mesembrina* (Australian Cretaceous) and the Australian Cainozoic genera *Aldingia*, *Paralidingia*, and *Frenulina* have been described previously (Richardson 1973b). The European members of *Kingena* and its relatives were reviewed by Owen (1970) who commented also on similarities between these genera and the Recent *Frenulina* and *Laqueus*. The Mesozoic genera discussed in these two papers are included in this reallocation of genera. Steinich (1965) in describing faunas from the Lower Maastricht Chalk of Rügen recorded the loop development of *Trigonosemus pulchellus*. The clarity of Steinich's illustrations and descriptions of this developmental sequence leave little doubt that *T. pulchellus* should be included in the Laqueidae and it appears to be related to members of the Terebrataliinae.

Subfamily KINGENINAE Elliott, 1948. Emend. nov.

Laqueidae with adult bilacunar or bilateral loop patterns, with septal flanges in early loop phases; hinge plates excavate or solid, fused medially or discrete or fused with valve floor, cardinal process small if present.

Genera included: *Laqueus*, *Waconella*, *Kingena*, *Zittelina*, *Belothyris*, *Frenulina*, *Compsoria*, *Aldingia*, *Paralidingia*, *Jolonica*.

Subfamily PICTOTHYRINAE Yabe and Hatai, 1941. Emend. nov.

Laqueidae with adult latero-vertical loop pattern; cardinalia thick, heavy, with prominent cardinal process.

Genera included: *Pictothyris*, *Kikaithyris*, ?*Kamoica*.

Subfamily MACANDREVIINAE Cooper, 1973. Nom. transl. Emend. nov.

Laqueidae with adult trabecular or teloform loop patterns with median septum not associated with cardinalia in trabecular patterns and lost in teloform patterns; hinge plates excavate and fused medially and separately with valve floor, cardinal process small if present.

Genera included: *Macandrevia*, *Notorgymia*, *Diestothyris*.

Subfamily TEREBRATALIINAE n. subf.

Laqueidae with adult trabecular or teloform loop patterns, with septal flanges in early loop phases; hinge plates commonly absent, cardinal process variable in size.

Genera included: *Terebratalia*, *Dallinella*, *Coptothyris*, *Pacifithyris*.

Subfamily uncertain: *Kurakithyris*.

Family TEREBRATELLIDAE King, 1850. Emend. nov.

*Diagnosis.* Loop passing through all or part of axial, annular, haptoid, bilacunar (fleeting and never represented in adult genera), trabecular, and teloform growth phases; dental plates and spicules absent.

*Comments.* Since the publication of the Treatise the only change made in this family is the emendation of the diagnosis of the subfamily Bouchardiinae to include *Malleia* (Richardson 1973c).

#### GENERAL DISCUSSION

In place of the two patterns (dallinid and terebratellid) previously described this study indicates that three patterns of loop development are evident in the long-looped brachiopods of the Cainozoic. The key factors determining differences in loop development are not the presence of lacunae, hoods, rings, divided septa, or the origin of the descending branches but are the manner of resorption of parts of the ring (a factor noted by Friele in 1877 but subsequently ignored) and the stage at which the ring is freed from the septum. As a direct result of these factors the developing loop of the Laqueidae displays vertical connecting bands while that of the Dallinidae displays descending branches with double anterior limbs; neither of these structures are present in the developing loop of the Terebratellidae.

Thus the presence either of vertical connecting bands or of doubled descending branches, in intermediate or adult loop phases, provide the key to the type of development characteristic of the Dallinidae or of the Laqueidae. Subsequent resorption of these structures in these two families results in the formation of an adult loop similar to that of the Terebratellidae.

Such an adult loop pattern is also seen as the teloform phase in the development of some Palaeozoic and Mesozoic genera. Differences in the development of these comparable adult structures seem to be centred around the emergence of a septal pillar to carry the future ascending elements. In Palaeozoic genera (Cooper 1955) all parts of the loop develop from the crura, i.e. the descending elements grow forward and fuse medially thus forming a structure which gives rise to the ascending elements. In Mesozoic and Cainozoic genera the descending and ascending elements arise concurrently, the posterior segments of the descending branches from the crura, the ascending elements and the anterior segments of the descending branches from the septal pillar.

The development of a septal pillar may be one device to achieve an adult loop and therefore an adult lophophore more rapidly, a factor which Elliott (1948, 1953, 1957) considers to be of paramount importance in the evolution of brachiopods. I can make no comment on this theory or upon Baker's suggestion (1972) that the presence of spinose branches of the loop may be of greater significance than the absence of a median septum. However, these studies have clarified a number of areas which complement Baker's recent studies on the loop development of the Jurassic

species *Zeilleria leckenbyi*. Baker noted that early phases of development are terebratellid in aspect while later phases are dallinid but that, in the possession of spines, the greater part of the development of the zeilleriid loop resembles dallinid development. Baker also showed that the median septum *sensu lato* is derived from two sources, an early septal pillar and a later downgrowth from the cardinalia. In those Cainozoic brachiopods studied by the author the adult septum is also the result of the fusion of two components, and as is the case for *Z. leckenbyi*, the future ascending elements of the loop arise only from the septal pillar. It has also been shown that the early and late developmental phases of the Terebratellidae, Dallinidae, and Laqueidae are similar and that they differ in intermediate phases only in methods of ring resorption. Consequently there is no need to divide the development of *Z. leckenbyi* into dallinid and terebratellid aspects. There are differences in the form of the septal pillar and in the formation of the hood in this Jurassic species and in the Cainozoic genera studied which show a similar but apparently simplified developmental process. If the patterns of loop development in Cainozoic genera have been interpreted correctly then *Zeilleria* is allied to the Laqueidae in the presence of a bilacunar loop phase and of dental plates, the cardinalia being similar to these structures in some members of the laqueid subfamily Kingeninae. The spines so characteristic of *Zeilleria* seem to be vanishing features in the Cainozoic members of the Terebratellacea. Spines appear only sporadically although they tend to be associated more frequently with the loops of the Laqueidae than with those of the other families. The Laqueidae is characterized by much greater fluidity in many morphological characters than are the other families and it is possible that in the Laqueidae one sees the type of archaic reservoir from which diverse groups may spring. Many morphological overlaps can be seen in this family. For example the development of *Terebratalia* leads directly to the terebratellid pattern although other features of this genus anchor it in the Laqueidae. The members of the family also display most of the types of cardinalia which may develop in the other two families. The anterior bifurcation of the septal pillar of *Macandrevia* while not characteristic of Cainozoic genera appears to be present in all Mesozoic genera whose development is known.

It is doubtful whether the families reviewed here should be regarded as of equal taxonomic status with the other four families attributed to the Terebratellacea. The development of the loop, if any, in these families is different in many respects from that of the Dallinidae, Laqueidae, and Terebratellidae so that by comparison these three families appear as a closely related group. The Thaumatosiidae (Cooper 1973*b*), Megathyrididae, Platidiidae, and Kraussinidae vary according to whether ascending or descending elements take precedence in loop development, in addition other factors related to the cardinalia and foramen separate them from the Dallinidae, Laqueidae, and Terebratellidae. Whether the similarities between the former families are sufficient to associate them together as a group distinct from the dallinid-laqueid-terebratellid group is a matter requiring further study.

At present the suborder Terebratellidina contains two superfamilies, the Zeilleriacea and the Terebratellacea. As Baker (1972) has pointed out, his own work on *Zeilleria* and that of Babanova (1965) on another Jurassic genus *Aulacothyris* suggests that typical zeilleriids may need to be removed from the Zeilleriacea to the Terebratellacea. The studies together with those of Owen (1970) on Cretaceous genera also suggest