PHOTONEGATIVE YOUNG IN THE TRIASSIC LAMELLIBRANCH *LIMA LINEATA* (SCHLOTHEIM)

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ABSTRACT. The occurrence of young specimens of *Lima lineata* (Schlotheim) within the lunules of adults of this German Triassic species is held to be due to photonegative habits and points to a possible origin of nest-building in the Limidae. The non-occurrence of this feature in some parts of Germany and its abundance in other parts is believed to depend on whether or not the adult was byssally attached.

IN the deeply excavated lunules of double-valved specimens of *Lima lineata* (Schlotheim) from the Wellenkalk (Middle Triassic), near Heidelberg and Würzburg, it is common to find one or two double-valved specimens of young of the same species. Two things show that this association is not accidental; firstly the young are nearly always at the extreme anterior end of the lunule—of thirty-nine young observed thirty-two were anterior, six were median (including four which were members of a pair and which were as anterior as the other member of the pair would allow), and only one was posterior; secondly the young nearly always have their lunules pressed close to the floor of the adult lunule (twenty-nine out of thirty-seven determinable cases). The purpose of this note is to discuss this phenomenon.

Seilacher (1954) has shown, from mode of crushing and orientation of attached epizoa, that double-valved specimens of *Lima lineata* were usually embedded with the commissure vertical and resting on the antero-dorsal margin (Pl. 59, fig. 7). This orientation, which I have seen in two specimens *in situ* at Lengfurt, near Würzburg, was the life-orientation of the species. This is shown by the fact that modern Limidae normally rest in the same position (Studnitz 1931), except when lying at random in the nest, and by the fact that the byssal gape, which is fairly large in *Lima lineata* (Pl. 59, fig. 4), is on the antero-dorsal side.

The elongate antero-dorsal margin of the Limidae is an adaptation to this mode of life and has led to the markedly posterior position of Limid umbones. The antero-dorsal side of *Lima lineata*, in particular, makes a very firm base to rest upon; it is a broad, heart-shaped area (Pl. 59, figs. 1–6) consisting of the excavate, cordate lunule bordered to right and left by rather flat anterior umbonal ridges which have specially coarse radial ribs. When resting on the sea-floor in the position described these anterior umbonal ridges would be the only parts of the shell actually touching the floor and their coarse ornament would help to prevent slipping at the contact. In 1910 Douvillé (p. 645) had already noticed the adaptive significance of the flattened antero-dorsal surface in *Plagiostoma*, in which subgenus *L. lineata* should probably be placed (Philippi 1900, p. 621).

Hence *Lima lineata* rested in life with the lunule downwards. Communication between the sea and the lunule was, nevertheless, possible through the gap between the prominent umbones. It was doubtless through this gap that the young specimens entered. They could scarcely have found their way so commonly into such a small gap, however,

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unless they were photonegative with a definite tendency to enter small crannies. And in this connexion it is interesting to find the same photonegative tendency in Recent *Lima* (Crozier 1921). The actual position which the young adopted at the extreme anterior end of the lunule (Pl. 59, figs. 1–5) may also, with light coming from above, have been the darkest place inside the lunule. At least it was clearly the farthest point from the source of illumination. The orientation which the young adopted, with their lunules pressed to the floor (or 'ceiling') of the adult lunule, meant that their relationship with their substratum was the same as that of the adults to the sea-floor and suggests that they were byssally attached.

Before proceeding farther a digression on the habits of Recent Limids is necessary. These fall morphologically into three groups which Pelseneer (1911, p. 32) called *Mantellum*, *Limatula*, and *Radula*. In nomenclature these groups are unsound (*Mantellum* Bolten 1798 = *Lima* Bruguière 1792 (same type species) and *Radula* Klein 1753 is pre-Linnaean (Arkell 1931, p. 128)). From the present standpoint, however, nomenclature is unimportant since the three groups seem to have real existence. '*Mantellum*' (e.g. *Lima hians*) includes forms with extensive gapes round the whole shell margin (except the hinge line); they have the interesting habit of using the byssus to form a sort of nest, usually under stones or inside empty shells. MacGinitie and MacGinitie (1949, p. 346) say of the American species *Lima dehiscens* that it 'builds nests *in cavities* by spinning byssus threads and attaching them to the surrounding rocks in a scattered formation. The completed nest is suggestive of the nest that certain spiders build and in which they wait for their prey.' (My italics.) Studnitz (1931, p. 301) gave a very similar account of nest-building in the European *Lima hians* which usually makes its nest inside empty *Mytilus* or *Cardium* shells. There seems to be no fixational byssus in '*Mantellum*', for Pelseneer contrasts these 'Limes nidificatrices' with the 'Limes à byssus fixateur' represented by '*Radula*'. Pelseneer's second group, *Limatula*, consists of small equilateral forms with a fairly wide byssal gape but no gape round the rest of the shell margin. Little is known of the habits of this group, but there is no evidence of nest-building in the British species *L. subauriculata* (C. M. Yonge, personal communication). Pelseneer's third group, '*Radula*', includes very large species (e.g. *Lima excavata*) with a flattened or excavate antero-dorsal margin and no gape but the byssal gape, with a fixational byssus and without the nest-building habit. '*Mantellum*' can swim by clapping its valves (Studnitz 1931; MacGinitie and MacGinitie 1949) and it is possible that *Limatula* and '*Radula*' can also do so though the habit does not seem to have been recorded.

Now '*Radula*' is very like *Plagiostoma* and, indeed, there is no clear distinction between them apart from age (Philippi 1900, p. 621). By the same token it is '*Radula*', of all Pelseneer's three Recent groups, which *Lima lineata* most nearly resembles. It is similar in its large size, excavate lunule, and absence of any gape except the byssal gape; and this comparison suggests that *L. lineata* was not a nest-builder.

There is more direct evidence to the same effect. Seilacher (1954, p. 167) stressed the fact that double-valved *Lima lineata*, which had evidently been buried with commissure vertical, nevertheless had their valves closed. He concluded from this that they must have been buried shortly after death, for on death the ligament would have opened the valves automatically if the shell had been lying free on the sea-floor. This deduction does not seem to go far enough, however, for on death the valves would open at once. To produce fossils with their valves closed burial would therefore have to be simul-

taneous with death or slightly precede it. In fact it seems likely that double-valved *Lima lineata* found in the life-position with their valves closed were nearly always killed by burial. The same conclusion would not, of course, apply to valves buried with commissure horizontal for these would be closed by weight of sediment.

From this argument it follows that the attached animals on *Lima lineata* (or at least those found on the lower half or two-thirds of an animal killed by only partial burial) must have been attached during the life of the *Lima*. This is confirmed by the presence on one specimen of *L. lineata* (Pl. 59, fig. 7*a*) of a *Lopha sp.* which is truncated against a growth-line of the 'host' and so must have lived when this growth-line represented the edge of the valve. Now attachment of epizoa in such abundance as is usual could scarcely have happened if the *Lima* had been surrounded in life by a nest of byssal threads. The occurrence of *Lopha sp.* in the Muschelkalk has been previously noticed by Seilacher (1954) and Cox (1932).

Furthermore, there is evidence of a fixational byssus in *Lima lineata*, which, as pointed out above, probably does not occur in Recent nest-builders. Seilacher (1954, p. 176) noticed that small, single-valved shells of various species were often present in the lunules of his specimens (cf. Pl. 59, fig. 6). Near Freudenstadt (text-fig. 1), from which most of Seilacher's material came, this phenomenon was quite regular (about 30% of specimens). It is clearly different from the attachment of double-valved young in the lunule, for the fact that the shells are single-valved and of many different species proves that they became associated with the *L. lineata* only after their death. Seilacher's explanation, that they represent debris attached to the byssus of the *Lima*, seems the only reasonable one.

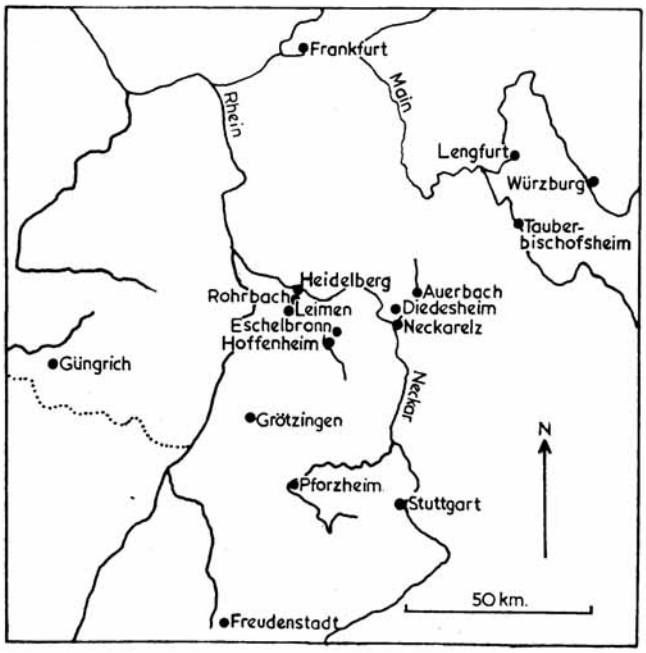
EXPLANATION OF PLATE 59

Figs. 1–7. *Lima lineata* (Schlotheim). 1, Antero-dorsal aspect. ×1. Diedesheim. Heidelberg University collection. Note young specimen at extreme anterior end of the adult lunule, oriented with its lunule to the floor of that of the adult. 2, Antero-dorsal aspect. ×0·75. Leimen. Heidelberg University collection. Remarks as for fig. 1. 3, Oblique antero-dorsal aspect. ×0·75. Rohrbach. Heidelberg University collection. Remarks as for fig. 1. 4, Antero-dorsal aspect. ×0·75. Lengfurt. British Museum no. LL8481. This specimen was found *in situ* in the quarry with the antero-dorsal margin downwards. The particularly coarse costation of the anterior umbonal ridges and the byssal gape between the two halves of the lunule are clearly visible. Of the two young individuals in the lunule, one is at the extreme anterior end and the other is as anterior as the first member of the pair would allow. Both have the lunule pressed close to the floor of the adult lunule. 5, Antero-dorsal aspect. ×0·75. Leimen. Heidelberg University collection. Remarks as for fig. 1. 6, Oblique antero-dorsal aspect. ×0·75. Güngrich near Pirmasens. Heidelberg University collection. Note the presence of abundant byssally attached debris at the posterior end of the lunule, and the shallowness of the lunule, possibly due to the persistence of the byssus in the adult. The debris includes two valves of a young *Lima lineata* (at *a*) and a small gastropod *b* as well as other material. The specimen of *Anodontophora fassaensis* (Wissmann) at *c* was probably part of the byssally attached debris but has been displaced by compaction of the sediment. 7, Oblique lateral aspect. ×0·75. Lengfurt. British Museum no. LL8482. This figure shows the specimen resting on the antero-dorsal margin in the orientation in which it was found *in situ*. The epizoa are *Placunopsis plana* (Giebel), *Lopha sp.* and small bryozoa.

Fig. 7*a*. *Lopha sp.* ×2·25. Enlarged view of specimen also visible in fig. 7. Note the truncation against a growth-line of the 'host' which proves that the *Lopha* must have lived when the 'host' was of the size represented by the growth line.

Figs. 1–3 and 5 are by Dr. A. Seilacher and figs. 4 and 6–7*a* are by J. Pope.

However, though *L. lineata* was probably not a nest-builder, its young had a habit of entering crannies and fixing themselves inside and it was probably from this that the Limid habit of building nests inside cavities arose. This is not to suggest, of course, that *Lima lineata* was the direct ancestor of nest-building Limidae; but if *L. lineata* was photonegative the ancestor of '*Mantellum*' may also have been so.



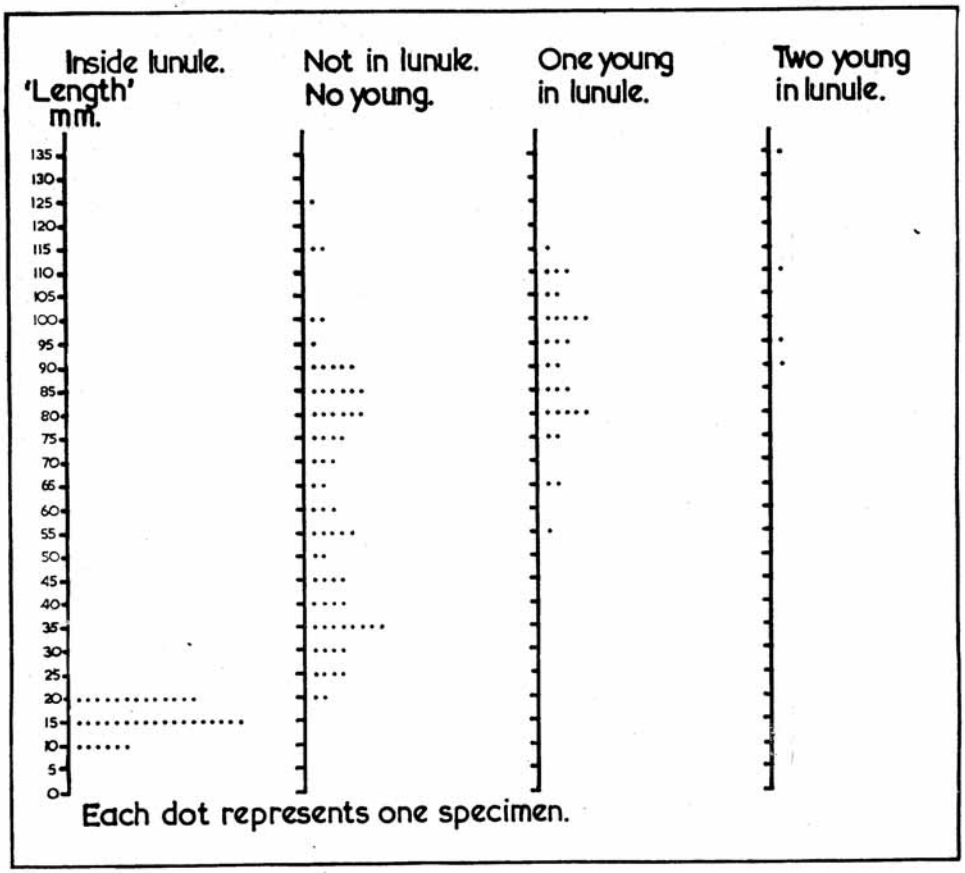
TEXT-FIG. 1. Locality map. Young inside the lunule are abundant near Heidelberg and Würzburg but apparently absent near Freudenstadt. Byssally attached debris, on the other hand, is abundant near Freudenstadt but rare near Heidelberg and Würzburg.

Text-fig. 2 shows the relation between habit and 'length' in *Lima lineata* from the Wellenkalk, near Heidelberg and Würzburg, 'length' being the largest dimension parallel to the antero-dorsal margin. One hundred and one specimens have been used in the construction of the figure (not counting young specimens inside the lunules of other specimens) and their localities of origin are as follows:

(i) Lengfurt near Würzburg, 3 specimens (collected by the author, British Museum numbers LL8481–3).

(ii) Leimen, 54 specimens; Diedesheim, 35; Auerbach, 4; and 1 specimen each from Tauberbischofsheim, Neckarelz, Rohrbach, Eschelbronn, and Hoffenheim (in the Heidelberg University collection).

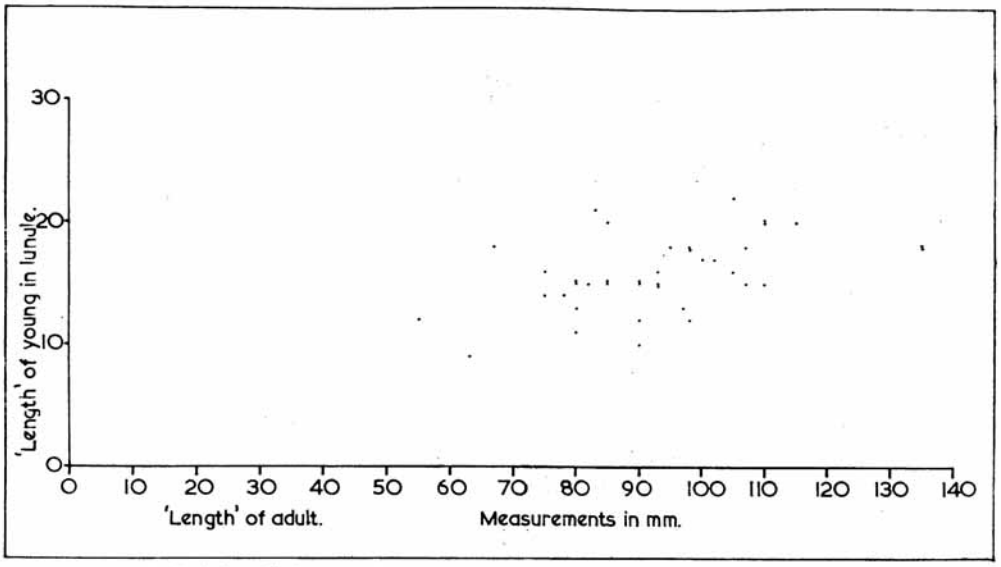
The sample presented in text-fig. 2, as pointed out above, is part of a population which died suddenly. For this reason the age and size distribution of the sample, apart



TEXT-FIG. 2. Distribution of habit with 'length' in *Lima lineata* from the Wellenkalk near Heidelberg and Würzburg. 'Length' is the greatest dimension parallel to the antero-dorsal margin and is plotted to the nearest 5 mm.

from the considerable vagaries of preservation and collection, should be the same as in a living population of the species. It therefore seems legitimate to conclude that in the Heidelberg–Würzburg area a young *Lima lineata* did not try to enter an adult lunule until it was about 7 mm. long. Perhaps below this size it was not photonegative. Although in the figure almost 100% of the specimens between 5 and 20 mm. long are found inside lunules, the percentage was probably very much less in life. Unprotected individuals of this size would probably have been disarticulated after death and so would not have been included in the sample which was purposely restricted to double-valved specimens. Also it is clear that small Limas inside adult lunules would be much more easily

trapped by sudden deposition of sediment than would similar individuals living outside. At about 20 mm. the young left the lunules, which had presumably become uncomfortably small. Then, at a length of about 55 mm. or greater, the animals started in their turn to serve as 'host' to young, and this continued till death.



TEXT-FIG. 3. Relationship between 'length' of young in lunule and 'length' of 'host' adult, based on all observed specimens with young in the lunule from the Wellenkalk. 'Length' is the greatest dimension parallel to the antero-dorsal margin.

Text-fig. 3, which is based on all observed specimens from the Wellenkalk with young in the lunule, includes two specimens from Güngrich near Pirmasens besides those used in the construction of text-fig. 2. It shows that the size of a young specimen was related to the size of the 'host', i.e. roughly speaking the adult was six times as large as the associated young. At first this might suggest that a young *Lima* in the lunule of a large 'host' had attached itself when the 'host' was smaller and grown *pari passu* with it. This is probably not the correct explanation, however, for the percentage linear growth-rates of the adults would probably be negligible by comparison with those of the young. It seems more likely that young Limas were capable of leaving a lunule they had outgrown, and that then they either lived free, or found more spacious accommodation.

The fact that Seilacher did not find double-valved young inside the lunules of his specimens from near Freudenstadt proves that they must be very rare there. On the other hand, text-fig. 2 shows that near Heidelberg and Würzburg thirty-three specimens out of a total of seventy-three longer than 50 mm. had one or two young inside the lunule. This is probably linked with the fact that, as mentioned above, 30% of Freudenstadt specimens had byssal debris in the lunule while stray fragments which might

represent such debris were present in only four of the seventy-three specimens from near Heidelberg and Würzburg. Even though such debris will often have been removed during preparation the difference is probably significant. It suggests that perhaps the typical adult near Heidelberg lay free on the sea-floor, whereas the typical adult near Freudenstadt was byssally fixed. This is not improbable, for the Wellenkalk near Freudenstadt is of more marginal facies and only half as thick as near Heidelberg and Würzburg (55 m. as opposed to 98 m. (Schmidt 1928, opp. p. 24)) and so the sea near Freudenstadt was probably shallower and more turbulent.

Persistent byssal attachment in the adult might affect the young in two ways. Firstly there would be a mass of byssus and byssally attached debris blocking the gap between the umbones of the adult and making it difficult for the young to enter the lunule. Secondly there was probably a tendency for byssal fixation to be correlated with a very shallow lunule. Thus the specimen from Güngrich shown in Pl. 59, fig. 6, has byssal debris and a much shallower lunule than is usual near Heidelberg (cf. Pl. 59, figs. 1–5) and the same also seems true of the specimens with byssal debris from near Freudenstadt of which Seilacher has published drawings (1954, fig. 7, p. 177). These shallow lunules, which doubtless resulted from the pull of the byssus on the lunular mantle edge, would probably not have provided adequate space for a young *Lima* even if it had succeeded in entering.

Byssal attachment persisted in the Heidelberg–Würzburg area at least up to a length of 30 mm. This is shown by two specimens of this size in the Heidelberg collection from Diedesheim which are pressed lunule downwards against the inner concave side of a large valve of *Lima lineata*. It is at least possible that byssal attachment persisted up to a length of about 55 mm., at which length the first young are found in the lunule (text-fig. 2).

Before leaving this subject, however, it is as well to note that one specimen in the Heidelberg collection from Diedesheim has both a young in the normal position in the lunule and a shell fragment which might represent byssal debris. On the other hand, it is quite possible that the position of this particular fragment is quite accidental.

The southern boundary of the area in which young occur in the lunule is not at present clear. However, single specimens in the Heidelberg collection from Grötzingen and Pforzheim (text-fig. 1) were without young.

Young specimens do not occur in the lunules of *Lima striata* (Schlotheim) in the Heidelberg collection. The lunule of this Upper Muschelkalk species was shallower than is usual in *L. lineata* and this perhaps suggests permanent byssal attachment. The Wellenkalk species *L. radiata* Goldfuss sometimes has young in the same position and orientation as *L. lineata*.

The conclusions of this paper can be summarized as follows:

1. The occurrence of young in the lunules of *Lima lineata* is not accidental since their positions and orientations are almost constant.

2. In life *L. lineata* rested with the lunule on the sea-floor but the lunule was open to the sea by the gap between the umbones. The young could only have entered the lunule with such frequency if they had been photonegative with a tendency to enter crannies.

3. *L. lineata* was not a nest builder since it resembles Recent non-nest-building Limidae, had a fixational byssus, and was usually covered with epizoa which attached during the *Lima*'s lifetime and could not have penetrated a nest of byssal threads.

4. Nevertheless, the nest-building habit could well have evolved from the habit of byssal attachment inside crannies shown by young *L. lineata*, for Limid nests are preferentially made inside cavities.

5. In the Heidelberg area young Limas inside lunules are 10–20 mm. long. A substantial proportion of individuals more than 55 mm. long acted as 'host'. And the young was usually about one-sixth the length of the associated adult.

6. Adult *L. lineata* in south Germany were probably byssally attached. In consequence the lunule was shallow and the gap between the umbones was blocked by byssus and byssal debris so that young could not enter the lunule. Farther north the adults were not byssally attached and so the young could enter.

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JEFFERIES, *Lima lineata* (Schlotheim) and *Lopha sp.*