THE TYPE SPECIES OF THE BRACHIOPOD *YUNNANELLINA* FROM THE DEVONIAN OF SOUTH CHINA

by MA XUEPING

ABSTRACT. *Yunnanellina hanburyi*, the type species of the genus, is widely distributed in South China. Study of the external and internal features of abundant specimens from three sections in central Hunan indicates that other previously described nominal species and subspecies of *Yunnanellina* from the Upper Devonian of South China, are junior synonyms of the type species. *Y. hanburyi* is very varied in both external form and internal structures. Internally, the septalium may be open, or covered anteriorly by a connectivum. This connectivum shows a systematic change with time and, on this basis, three morphotypes have been established which comprise the *Y. hanburyi* lineage. The stratigraphical range of the lineage can be correlated with the upper *crepida* Zone (Early Famennian).

RHYNCHONELLA hanburyi Davidson, 1853, the type species of *Yunnanellina* Grabau, 1931, is widely distributed in South China. Davidson's original material includes only five specimens, four of which possess two plications in the sulcus, with one, a juvenile, too immature to have developed a sulcus or fold. Kayser (1883) noticed some uniplicate specimens and correctly assigned them to Davidson's species as a varietal form. But since 1931, more species and subspecies, some of which have been introduced in the literature as mutations or varieties, have been described from the Upper Devonian of South China. These are *Yunnanellina hanburyi* mut. *lata* Grabau, 1931; *Y. uniplicata* Grabau, 1931; *Y. triplicata* Grabau, 1931; *Y. hanburyi* mut. *sublata* Tien, 1938; *Y. triplicata* var. *latiformis* Tien, 1938; *Y. obesa* Tien, 1938; *Y. heyuanzhaiensis* Fang *in* Fang and Zhu, 1974 (= *Y. xintianensis* Zhao *in Yang et al.* 1977); *Y. uniplicata mesosulcata* Liu *in* Liu *et al.* 1982 and *Y. undatussulcus* Li, 1987. All the above nominal species or subspecies were established solely on different external features, especially the number of sinal plications and general outline. The validity of these taxa has not as yet been tested. Nevertheless, the binomials *Yunnanellina hanburyi*, *Y. uniplicata* and *Y. triplicata* have frequently appeared in the Chinese literature.

Sartenaer (1971) gave a fairly thorough treatment of *Yunnanellina* and discussed forms labelled *Yunnanellina* from most parts of the world. He redescribed the type species based chiefly on the type material deposited in the Natural History Museum in London, and material in the United States National Museum in Washington, D.C. This redescription was largely based on external characters. Regarding the internal structure, Sartenaer pointed out (p. 204) that the 'septalium [was] short, deep, wide, amphora-shaped and uncovered'. This description was based on only one sectioned specimen and as such can not be taken as definitive.

Xu (1979) discussed the stratigraphical distribution of the genus and gave a Famennian age for the *Yunnanellina–Yunnanella* fauna. The present study is an attempt to clarify the taxonomy of *Yunnanellina hanburyi* and related forms from South China and to demonstrate its intraspecific and stratigraphical variations in internal morphology.

MATERIAL AND METHODS

Yunnanellina is very abundant in Hunan, especially in the centre of the province, where Upper Devonian strata with abundant benthic fossils are well developed, making it the most important

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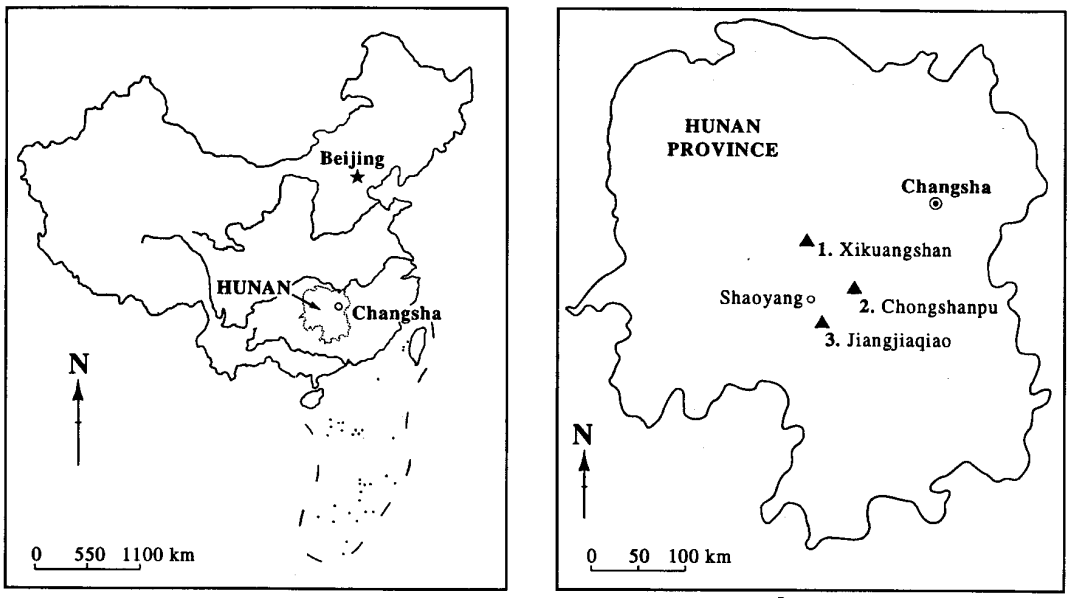


TEXT-FIG. 1. Location map of the study area. 1, Xikuangshan section (samples beginning with the letter L). 2, Chongshanpu section (T). 3, Jiangjiaqiao section (C).

area for research into the Upper Devonian of China. Numerous specimens of *Yunnanellina*, most of which are well preserved, have been collected from three sections in central Hunan (Text-fig. 1). Thirty-six specimens were sectioned, of which twenty-two have been serially sectioned to reveal the systematic change in internal structure. Most of the sections were recorded as acetate peels. The distance between each adjacent peel was usually taken at *c.* 0·3 mm. Detailed microstructure was added to the camera lucida drawings of the outline of the internal structure through examination of the peels under a microscope. The illustrated acetate peels were selected to show significant changes in the internal structure. The thirty-six sectioned specimens include twelve of '*Y. uniplicata*', eighteen of '*Y. hanburyi*', and six of '*Y. triplicata*'. In the following text, these three 'species' are expressed as uniplicate, biplicate and triplicate forms, respectively. All specimens illustrated in the text-figures and plates are deposited in the Department of Geology, Peking University.

TAXONOMIC DISCUSSION OF *YUNNANELLINA* FROM SOUTH CHINA

Ten species and subspecies of *Yunnanellina* have been described from the Upper Devonian of South China. The following list gives the features by which they were distinguished.

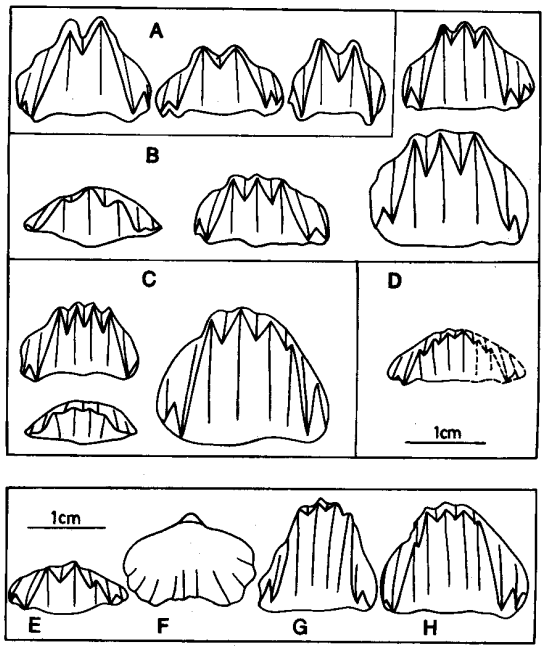
1. *Y. hanburyi* (Davidson, 1853): with two plications in the sulcus.
2. *Y. h.* mut. *lata* Grabau, 1931: with flatter shell than *Y. hanburyi.*
3. *Y. h.* mut. *sublata* Tien, 1938: similar to *Y. h.* mut. *lata*, but smaller.
4. *Y. uniplicata* Grabau, 1931: one plication in the sulcus.
5. *Y. u. mesosulcata* Liu *in* Liu *et al.*, 1982: with a furrow on the sinal plica and correspondingly a small median plica present in the interspace on the fold.
6. *Y. triplicata* Grabau, 1931: with three plications in the sulcus.
7. *Y. t.* var. *latiformis* Tien, 1938: with a flatter shell than *Y. triplicata.*
8. *Y. obesa* Tien, 1938: a rather broader obese form with three plications in the sulcus.

9. *Y. heyuanzhaiensis* Fang *in* Fang and Zhu, 1974 (= *Y. xintianensis* Zhao *in* Yang *et al.* 1977?): with four plications in the sulcus.
10. *Y. undatussulcus* Li, 1987: with two or three plications in the sulcus, which is concave in the middle part.

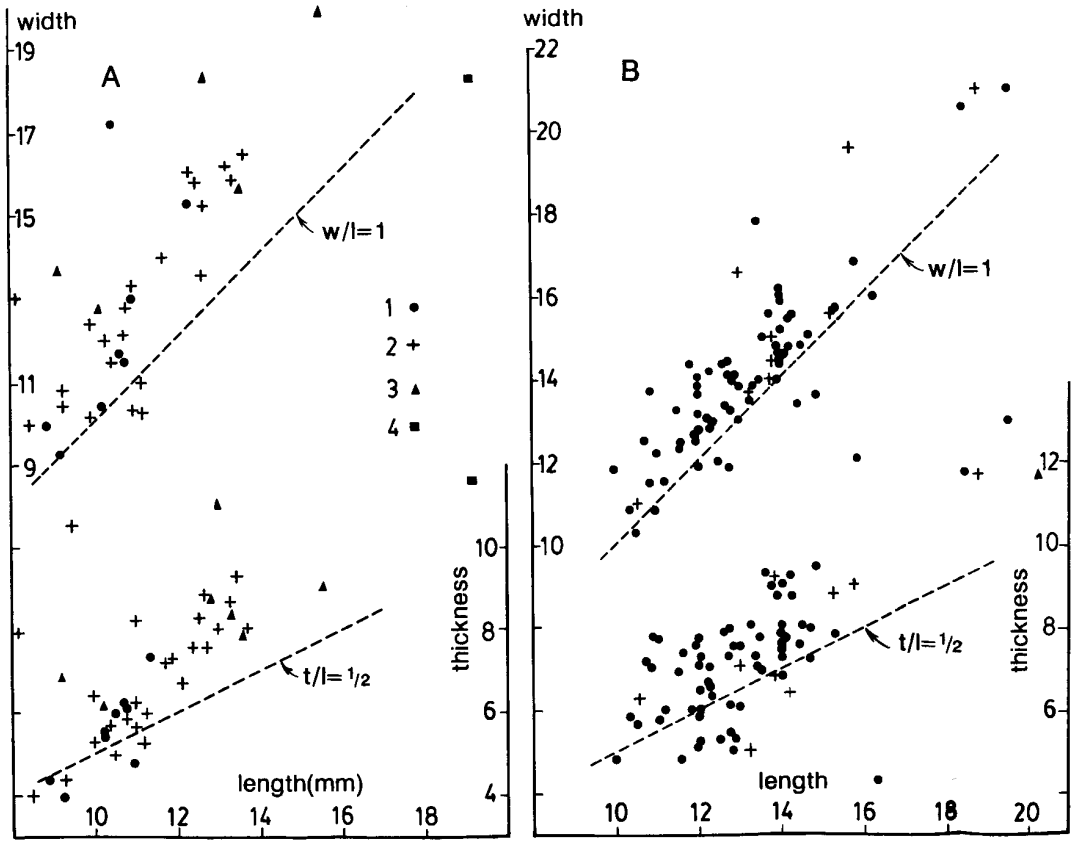
Most of the above species or subspecies were originally defined on the basis of only a few or even a single specimen. Davidson's original material was purchased from a Chinese drugstore, and the original locality and stratum can not be determined. It is questionable that the material is from Guangxi Province. Grabau's material, which also has questionable provenance, was used by him to establish two new species and a subspecies chiefly based on differences in the number of the sinal plications. Most subsequent Chinese workers followed this example and named species and subspecies based on minor differences in external morphology.

The present study shows that all the above species and subspecies belong to the type species, *Y. hanburyi*. However, this idea is not new. Kayser (1883) included his uniplicate form in *Y. hanburyi* (Davidson). Tien (1938, p. 46) considered that his *Y.* cf. *triplicata* Grabau (based on one specimen) 'is not only a direct derivative of the biplicate form – *Y. hanburyi*, but also foreshadows the quardriplicate form. If we could prove this in the future when more materials are available, I would prefer to regard all them as varieties of *Y. hanburyi* because they are all essentially identical, apart from the number of the plicae in the sinus and on the fold' (quoted from Tien's original English text). Sartenaer (1971) did not consider the species *Y. triplicata* and *Y. uniplicata* to be valid as they entered the range of variability of *Y. hanburyi*, but this was not discussed in depth. I have the following evidence to reject the other species and subspecies.

1. Specimens from the same sample show different shapes and possess different numbers of plications in the sulcus. If the number of sinal plications and general shape of a shell is taken as the most important criterion for species recognition, this would lead to many 'species' and 'subspecies' in a given sample, which is unlikely according to modern concepts in biology. This is demonstrated by sample C–C, for example (Text-fig. 2A–D). Uniplicate, biplicate and triplicate forms are present, and one specimen shows five plications in the sulcus. This would require the erection of four



TEXT-FIG. 2. Variation in external morphology. A–D, sample C–C; all anterior views of uniplicate (A), biplicate (B), triplicate (C) and pentaplicate (D) specimens (PUM92032–42). E, sample C–D; PUM92043, showing a parietal plica on the right slope. F–G, sample L–D3xt; showing transverse shell (PUM92044) and high sinal tongue (PUM92045). H, sample L17; PUM92046, with two strong central plicae and a faint plica on each side, of which the plica on the left may be considered as a parietal one.



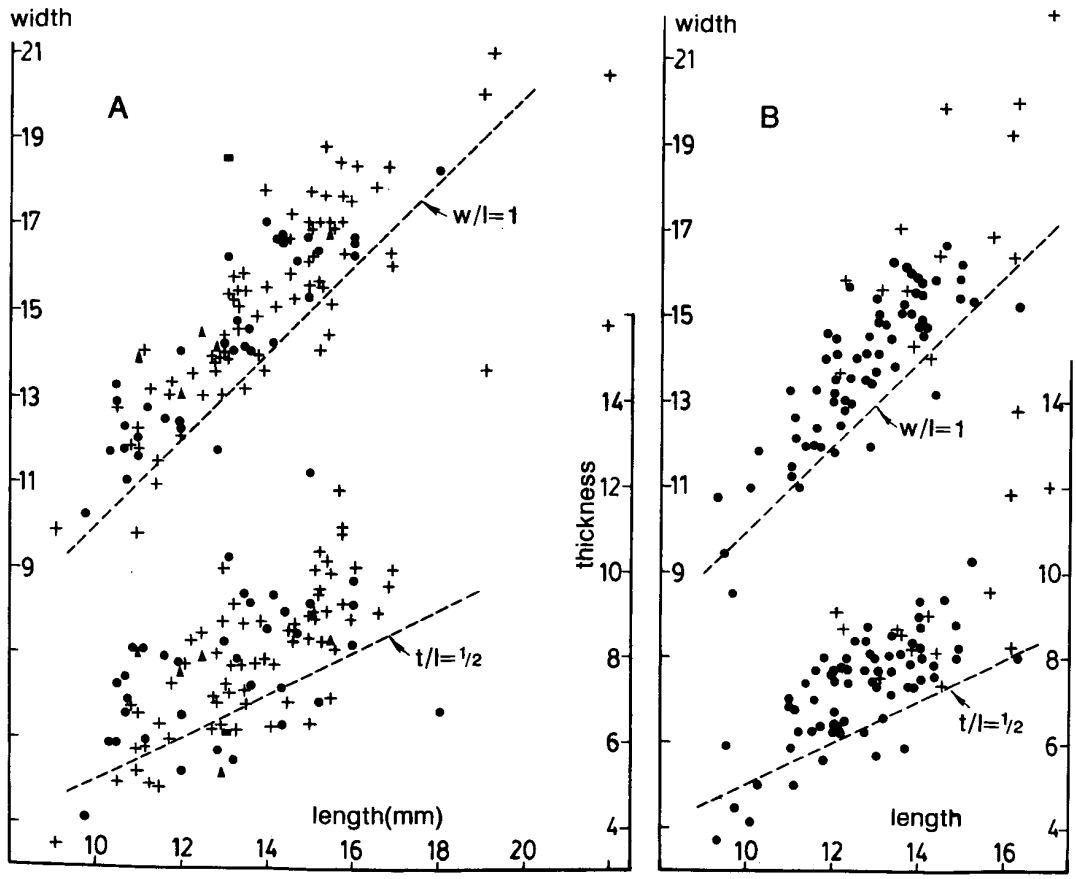
TEXT-FIG. 3. Scatter diagram showing length-width and length-thickness relationship. Legends 1–4 refer to uniplicate, biplicate, triplicate and quadriplicate specimens, respectively. Reference lines (dashed) are drawn for comparison of different samples. A, sample L17. B, sample C–H.

'species' on account of the number of sinal plications. But, only the rarity of specimens would preclude the quadriplicate or pentaplicate forms from being a separate species because they are basically identical with the uni-, bi- and triplicate forms. Secondly, different shapes are present in the uni-, bi-, and triplicate forms. In the biplicate form, '*Y. hanburyi*', '*Y. h.* mut. *lata*' and '*Y. h.* mut. *sublata*' can be recognized; in addition, there is still a globose form similar to '*Y. obesa*' in general shape, but different from it in the number of sinal plications (this again would be a new 'species'). A similar case is for the triplicate form including '*Y. triplicata*', '*Y. t.* var. *latiformis*' and '*Y. obesa*'. Actually flat forms ('*lata*', '*sublata*' and '*latiformis*') are composed of most immature specimens. Certainly, some flat specimens could be adults because their frontal commissure is highly elevated by plications, a feature of maturation (see section on General Morphology).

2. Occasionally in a sample, one or two specimens of bizarre morphology may be present. I have observed specimens with the sulcus protruding to a high tongue, or with a transverse or very globose shell, or with parietal plications, which are normally absent (Text-fig 2E–H). Several more examples of abnormal growth are shown in Plate 1, figures 7–8, 21–22. The specimens in Plate 1, figures 7–8 would represent '*Y. uniplicata mesosulcata*' Liu with a furrow on the strong sinal plica and, correspondingly, a small median plica present in the interspace on the fold. The specimens in Plate

1, figures 21–22 show a similar case with, in addition, the right plica on the fold (or left plica in sulcus) bifurcating anteriorly.

3. The growth curve shows basically the same pattern for specimens of uniplicate, biplicate and triplicate forms in the same sample (Text-figs 3–4).



TEXT-FIG. 4. Scatter diagram showing L–W and L–T relationship. Legend as for Text-figure 3. A, sample C–C. B, sample C–D.

4. Like external features, internal structures also vary between specimens in a single sample, e.g. sample C–H. In this sample in the uniplicate form, the connectivum (i.e. cover plate over the septalium; see Sartenaer 1969) may appear when the septalium disappears in some specimens; in others it may cover the septalium and persist in front of the septalium; other specimens may not have a connectivum or may just possess a semiconnectivum (see below). In the biplicate form, the connectivum is not present. The internal characters, like the external morphology, are therefore quite varied. These internal variations apparently do not represent separate species or subspecies, otherwise the uniplicate form with similar general shape in one sample (as in sample C–H) would have to be further subdivided into 'species' or 'subspecies'.

In conclusion, the *Yunnanellina* specimens from the Upper Devonian of South China appear to belong in the same species *Y. hanburyi*. Such species as *Pugnax utah* (Marcou), *P. postmodica-*

formis, *P. hunanensis* and *P. chaoi* described from Shaoyang by Ozaki (1939) probably also belong to the type species. This is especially the case if Ozaki's (1939) specimens are confirmed to be Famennian in age, rather than Visean as was originally reported (see Yang *et al.* 1977, p. 389).

GENERAL MORPHOLOGY OF *YUNNANELLINA HANBURYI*

External morphology

The external structure of *Yunnanellina hanburyi* has been extensively described by many previous workers (Grabau 1931; Tien 1938; Wang *et al.* 1964; Sartenaer 1971). However, these authors have concentrated chiefly in describing the ornament. Here I present a brief description of other aspects.

Shape and growth. Y. hanburyi is usually dorsibiconvex, but the ventral valve is more convex at the umbo. The general outline is triangular. Width, length and thickness dimensions of *Yunnanellina* are characterized by simple linear growth (Text-figs 3–4). In young shells width and length are seen to be nearly equal. When the shell is very small, length is even greater than width, but in adult forms width increased more rapidly than length. The greatest thickness is at the frontal commissure because it is highly elevated there by plications. This feature is a reflection of growth stage (Text-fig. 5). In the young stage, the shell is much flatter; the plications are not present, with only numerous striae covering the whole shell surface; the greatest thickness is not at the frontal commissure, but near the mid-length. Because of the influence of the growth pattern, the thickness of specimens in a sample is very variable, making this character poorly correlated with length or width.

Beak and pedicle opening. Yunnanellina hanburyi possesses deltidial plates and a small palintrope (Text-fig. 6). The pedicle opening is oval. The beak is usually slightly incurved.

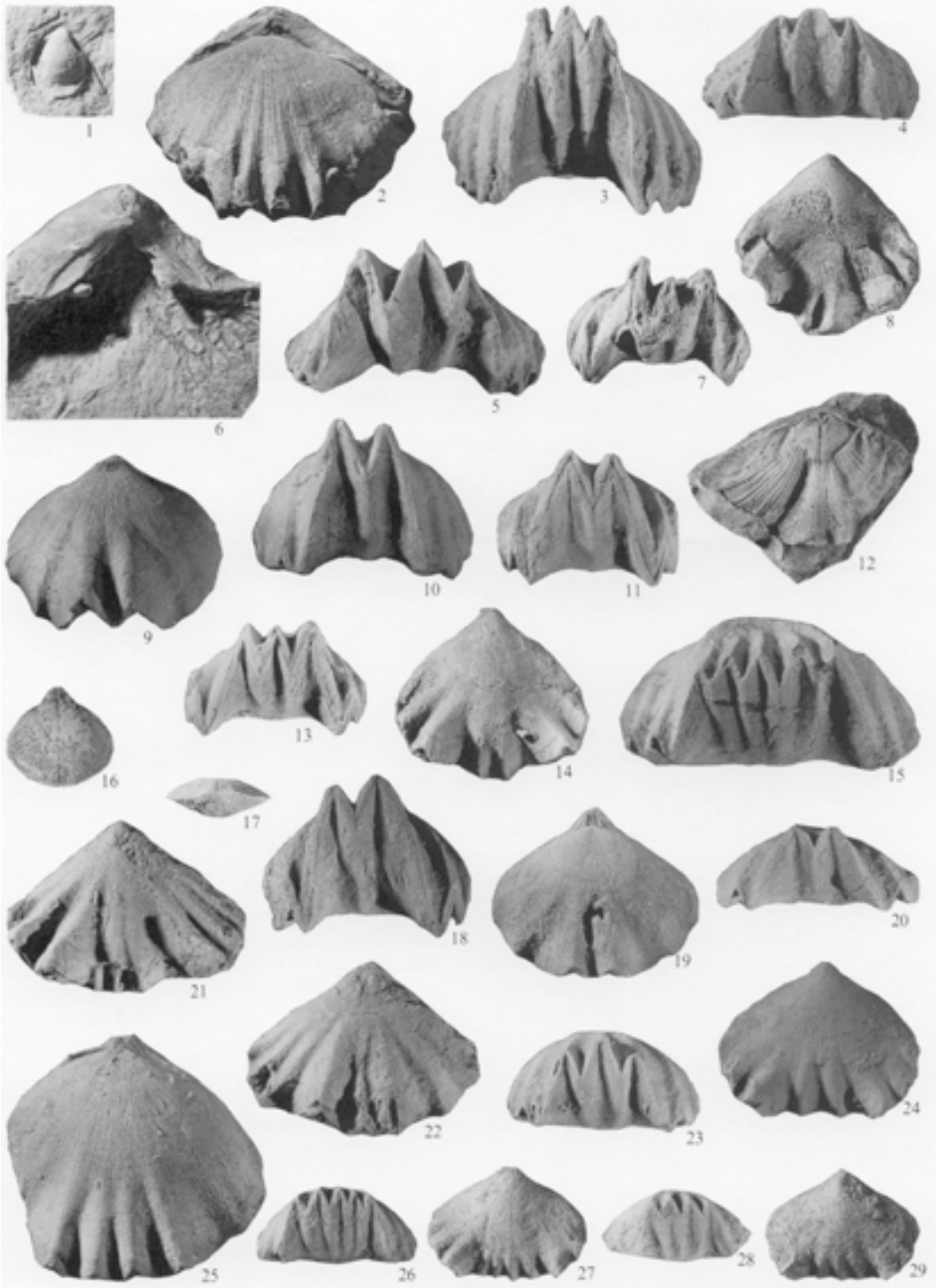
EXPLANATION OF PLATE 1

Figs 1–15. *Yunnanellina hanburyi* Morphotype 1. 1, sample L12/0·7–0·8; ventral view of a juvenile specimen (PUM92080) showing greater length than width. 2–5, sample L12/0–0·1; dorsal view of a triplicate specimen (PUM92063), anterior views of biplicate specimens (PUM92081–83); note the variation. 6, sample L12/0·4–0·5; showing teeth of a biplicate specimen (PUM92084). 7–8, sample C–H; anterior and ventral views of PUM92085 showing the presence of a small central plication on the fold and corresponding anterior furrow on the sinal plication. 9–10, sample L12/0·7–0·8; dorsal and anterior views of a uniplicate specimen (PUM92086). 11, sample C–H; anterior view of a uniplicate specimen (PUM92087). 12, sample L12/0·7–0·8; internal mould of brachial valve of a uniplicate specimen (PUM92088) showing adductor muscle scars. 13–14, sample C–H; anterior and ventral views of biplicate specimen (PUM92089). 15, sample C7–2; anterior view of a large quardriplicate speciment (PUM92090).

Figs 16–25. *Yunnanellina hanburyi* Morphotype 2. 16–17, sample C–E; dorsal and anterior views of a juvenile specimen (PUM92091). 18, sample C–C; anterior view of PUM92092. 19–20, sample C–D; dorsal and anterior views of immature specimen (PUM92093). 21–22, sample C–G, PUM92094; ventral and dorsal views showing abnormal growth of sinal plications; note a faint median furrow present in the sulcus and small median plica in the interspace on the fold; one lateral plica bifurcates at the front into two weak ones. 23–24, sample L19/0; anterior and ventral views of a biplicate specimen (PUM92095). 25, sample L19/0; dorsal view of a triplicate specimen (PUM92096) showing pattern of striation.

Figs 26–29. *Yunnanellina hanburyi* Morphotype 3. Sample L–D3xt; anterior and ventral views of quadriplicate and triplicate specimens (PUM92097–98).

All figures ×2, except fig. 1, ×3 and fig. 6, ×4.



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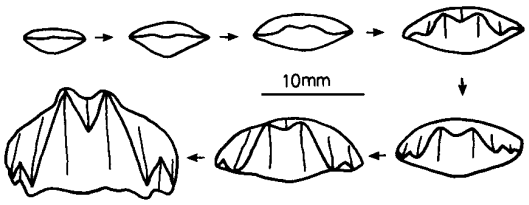
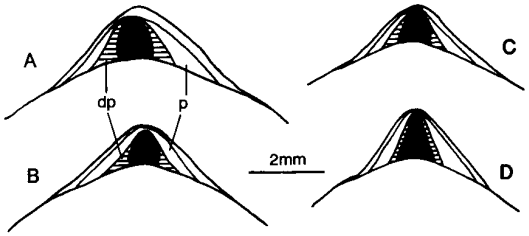


TEXT-FIG. 5. Growth stages as reflected by the outline of the frontal commissure. Drawn from specimens PUM92047–53 from the same sample (C–D).



TEXT-FIG. 6. Pedicle opening and related structures from juvenile (D) to adult (A) stages. dp = deltidial plate; p = palintrope. A, sample C–E, PUM92054. B, sample L17, PUM92055. C, sample C–C, PUM92056. D, sample C–D, PUM92057. Specimens of A and B uniplicate, whereas in the latter two, the sulcus has not developed and sinal plication cannot be defined.

TABLE 1. Relative proportion of various forms of *Y. hanburyi* in different samples (arranged in stratigraphical order).

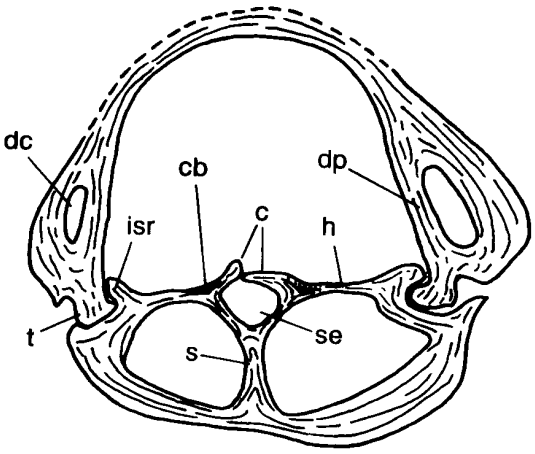
		Uniplicate		Biplicate		Triplicate		
Sample	N	N_1	%	N_2	%	N_3	%	Morphotypes
L–D3xt	20	—	—	6	30·0	13	65·0	Morphotype 3
C–A	11	—	—	7	63·6	4	36·4	
C–C	116	35	30·2	75	64·7	5	4·3	Morphotype 2
C–D	83	67	80·7	16	19·3	—	—	
C–E	63	53	84·1	9	14·3	—	—	
L17	45	10	22·2	26	57·8	8	17·8	
C–G	18	7	38·9	9	50·0	2	11·1	
C–H	76	65	85·5	10	13·2	1	1·3	Morphotype 1

Plications. One to five plications may be present in the sulcus of *Yunnanellina hanburyi*. Specimens with one to three sinal plications are most common. However, in a given sample, usually only one of the three forms is predominant (Table 1). Specimens with four or five sinal plications are very rare. There are, on average, two plications on each side in the uniplicate, biplicate, or triplicate form. This character does not seem to vary stratigraphically.

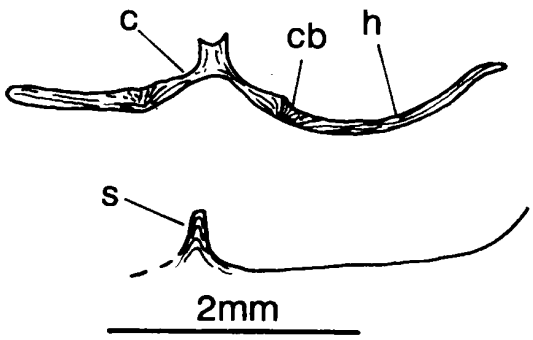
Internal structure

Nomenclature used for the description of the internal structure in serial sections is shown in Text-figure 7.

Cardinalia. Teeth are supported by a pair of dental plates. The dental cavity is variable in size. This feature does not show any systematic change with time, but in '*Y. uniplicata*', the dental plates seem nearly consolidated with the shell wall. The inner socket ridge is more prominent than the outer.



TEXT-FIG. 7. Nomenclature for the internal structure in transverse serial sections. cb = crural base; c = connectivum; dc = dental cavity; dp = dental plate; h = hinge plate; isr = inner socket ridge; s = septum; se = septalium; t = tooth.

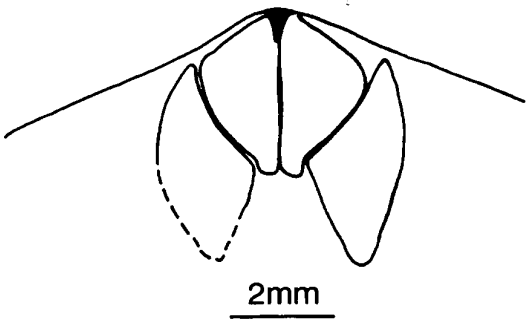


TEXT-FIG. 8. The herringbone-shaped connectivum with a divided crest. See also Plate 2, figure 8.

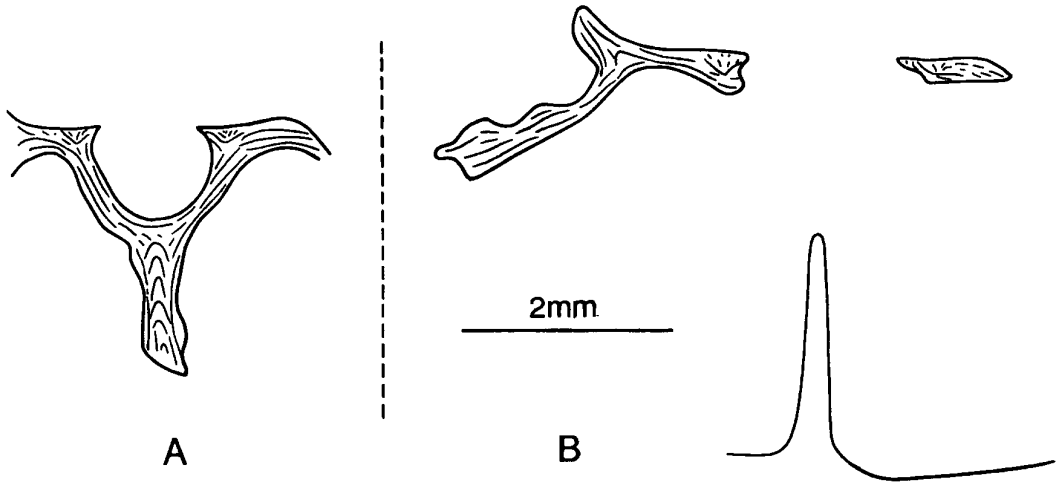
The latter is low, its inner face being crenulated. The hinge plates are horizontal, divided by the septalium. The septalium may be wide or narrow. Stratigraphically lower specimens usually show a wide septalium, while those from upper levels have a narrow one. The septalium is usually open posteriorly, being uncovered or covered anteriorly by a connectivum. This is the first record of a connectivum in *Yunnanellina*. In some specimens this structure may be just an extension halfway to the midline from each of the hinge plates, here called a *semiconnectivum*; in others, it may not be present. The connectivum is actually a joint plate resulting from further development of the semiconnectivum. The unification makes it appear slightly concave, planar, or herringbone-shaped. In the latter form, a divided crest may exist (Text-fig. 8).

Lophophore support. Crural bases are located at the junction of the hinge plates and the septalium. They begin at the posterior end of the hinge plates, and extend anteriorly giving rise to the freely projecting crura. Crural bases, which are usually clearly defined, are triangular, point downward, and have, in cross-section, a tail extended horizontally outward.

Muscle attachment. Yunnanellina does not possess a cardinal process. Adductor muscle scars in the brachial valve are well impressed in a mould specimen (Text-fig. 9). Posterior adductors are heart-shaped, separated by a low, rounded septum. Anterior adductors are horn-shaped.



TEXT-FIG. 9. Adductor muscle scars in the brachial valve (see Pl. 1, fig. 12).



TEXT-FIG. 10. Transverse peels of *Y. hanburyi* Morphotype 1, showing broad septalium (A) and the absence of connectivum (B). Sample T12, a biplicate specimen (PUM92058).

SYSTEMATIC PALAEONTOLOGY

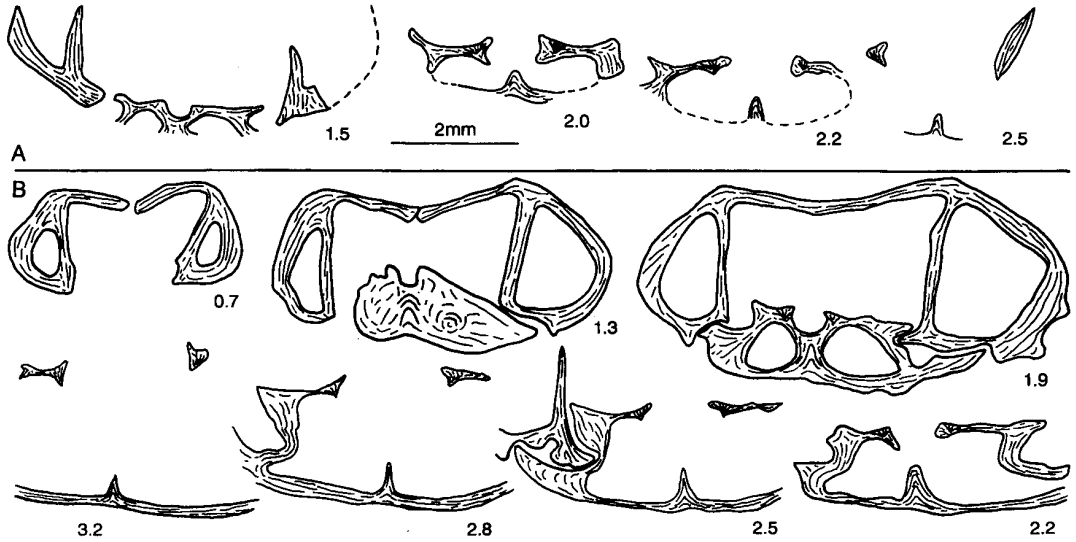
Order RHYNCHONELLIDA Kuhn, 1949
Family YUNNANELLIDAE Rzhonsnitskaya, 1956
Genus YUNNANELLINA Grabau, 1931

Type species. Rhynchonella hanburyi Davidson, 1853, p. 356, pl. 15, figs 10–11.

Range. Famennian. Rare occurrences of Frasnian (Yang *et al.* 1977) and Visean (Ozaki 1939) ages have been reported, but these need confirmation.

Distribution. South China (abundant), Northwest China (rare), ?Kazakhstan, ?Novaya Zemlya (Russia).

Remarks. The combination *Yunnanella hanburyi* was first utilized by Grabau (1923–24, p. 195). However, the genus *Yunnanella* was neither described nor given a type species in this paper (contrary to Tien 1938, p. 48). It was only in 1931 that Grabau thoroughly described the genus



TEXT-FIG. 11. Transverse serial sections of biplicate *Y. hanburyi* Morphotype 1. Numbers refer to distance in mm from ventral apex. A, sample C–H, PUM92059. B, sample L12/0–0·1, PUM92060 (shell compressed).

Yunnanella and designated *Y. synplicata* Grabau as the type species of *Yunnanella*. *Yunnanellina* was proposed as a subgenus of *Yunnanella*, with *Rhynchonella hanburyi* Davidson as the type species (Grabau 1931). Subsequently both *Yunnanella* and *Yunnanellina* have become two well-used names in the Chinese literature, because they are very abundant and good markers of Famennian strata in South China. However, in the *Treatise* (McLaren *in* Moore 1965) *Yunnanella* and *Yunnanellina* are listed as junior synonyms of *Nayunnella* Sartenaer, 1961 and *Yunnanella* Grabau, 1923, respectively, a proposal which I do not support.

Yunnanellina Grabau, 1931 can be easily distinguished on superficial evidence from *Yunnanella* Grabau, 1931 by the presence of its finer striae arising independently and continuing over the plications. In the latter, the plicae are formed anteriorly by a single enlarged strica, or two or more united striae. In addition, the striae of *Yunnanellina* increase in number chiefly by multibifurcations and cover more densely the shell surface. In *Yunnanella*, however, the shell surface is covered by relatively coarse and sparse striae characterized by both bifurcation and intercalation. The internal structure of the latter needs detailed study before comparisons can be made with the former.

Stratigraphically this species can be divided into three chronological morphotypes based on the variation pattern of the connectivum, especially in the biplicate form, and in the septalium.

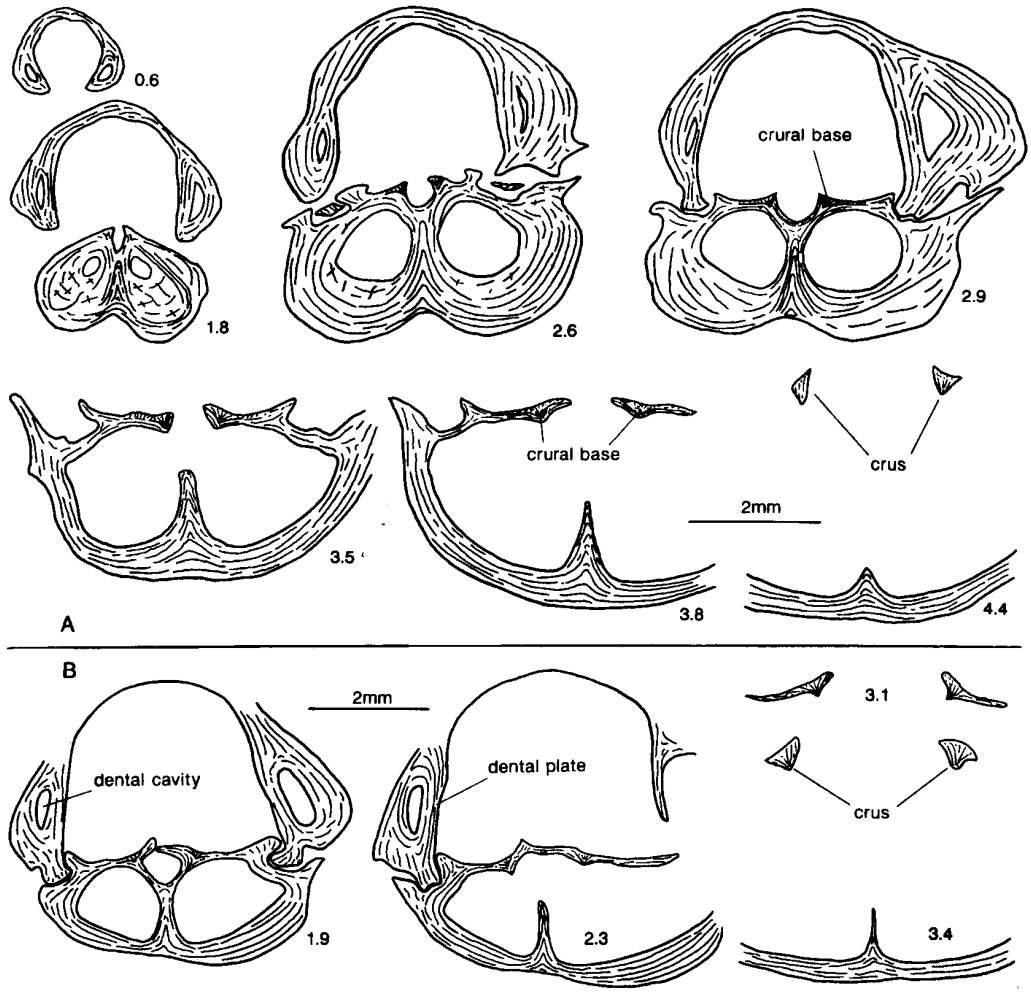
Yunnanellina hanburyi Morphotype 1

Plate 1, figures 1–15; Plate 2, figures 1–3, 7; Text-figures 10–13

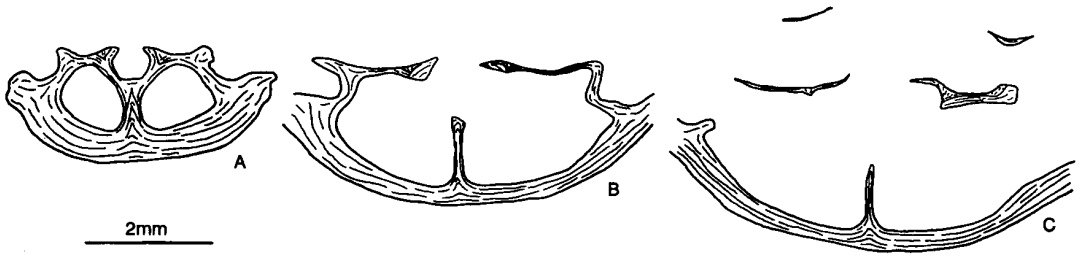
Diagnosis. Specimens of *Yunnanellina hanburyi* in which the biplicate form does not possess a connectivum. The septalium of all specimens is broad and rounded.

Description. In the biplicate form, dental plates are well developed. Dental cavities are large, oval in shape. In the brachial valve, hinge plates are usually horizontal, separated by the septalium. Crural bases are small, not well-defined. The most important feature is the absence of a connectivum anteriorly over the septalium.

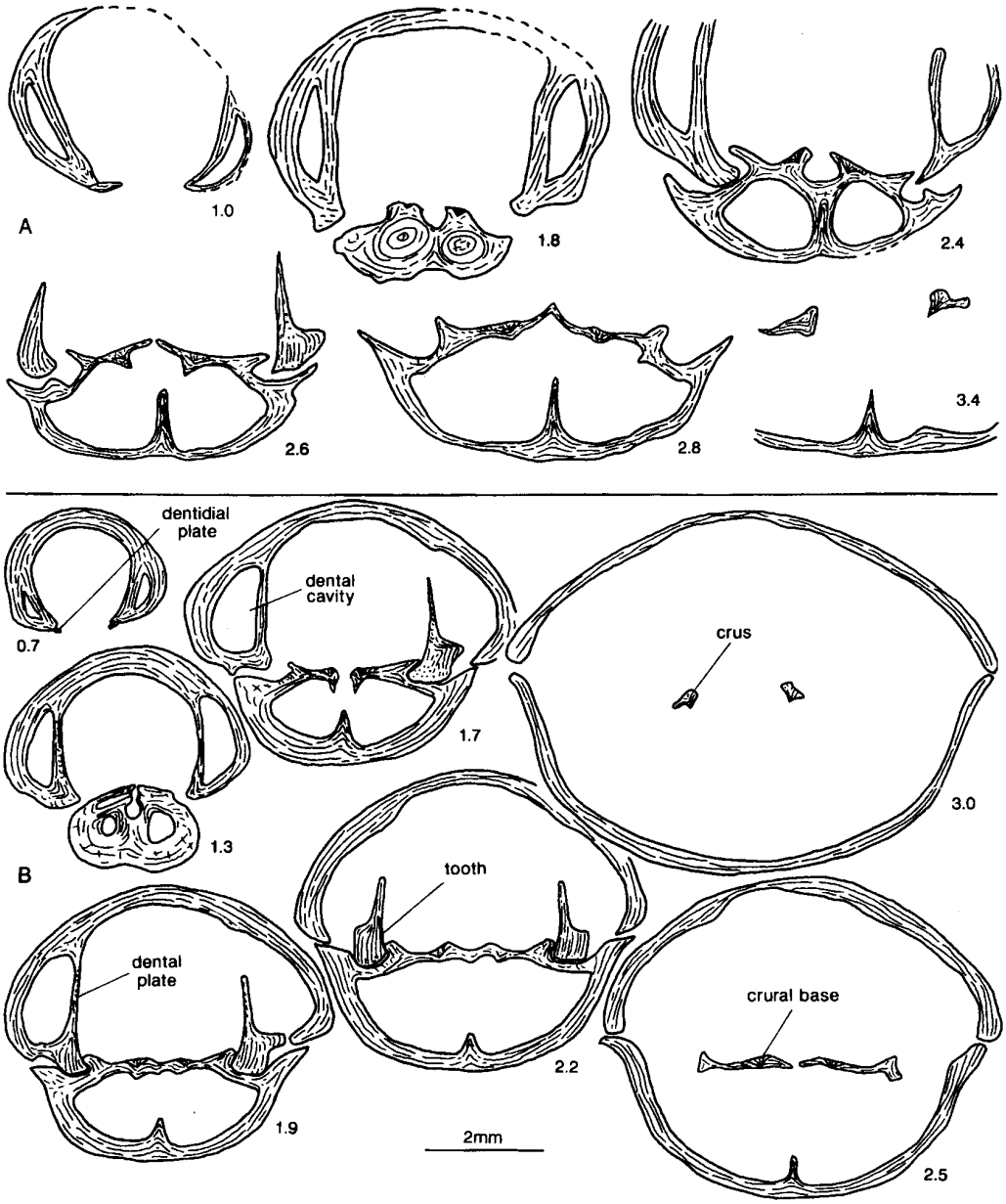
In the uniplicate form, the shell is strong. Dental plates are thick, more or less consolidated with the shell wall, leaving the dental cavities very narrow, small, or even slit-like. The septalium is still broad and rounded, but posteriorly it becomes very narrow. Crural bases are usually well-defined; in some specimens, they may



TEXT-FIG. 12. Transverse serial sections of uniplicate *Y. hanburyi* Morphotype 1. Note the small size of the dental cavity. Sample C–H. A, PUM92061. B, PUM92062. Compare with Plate 2, figure 7.



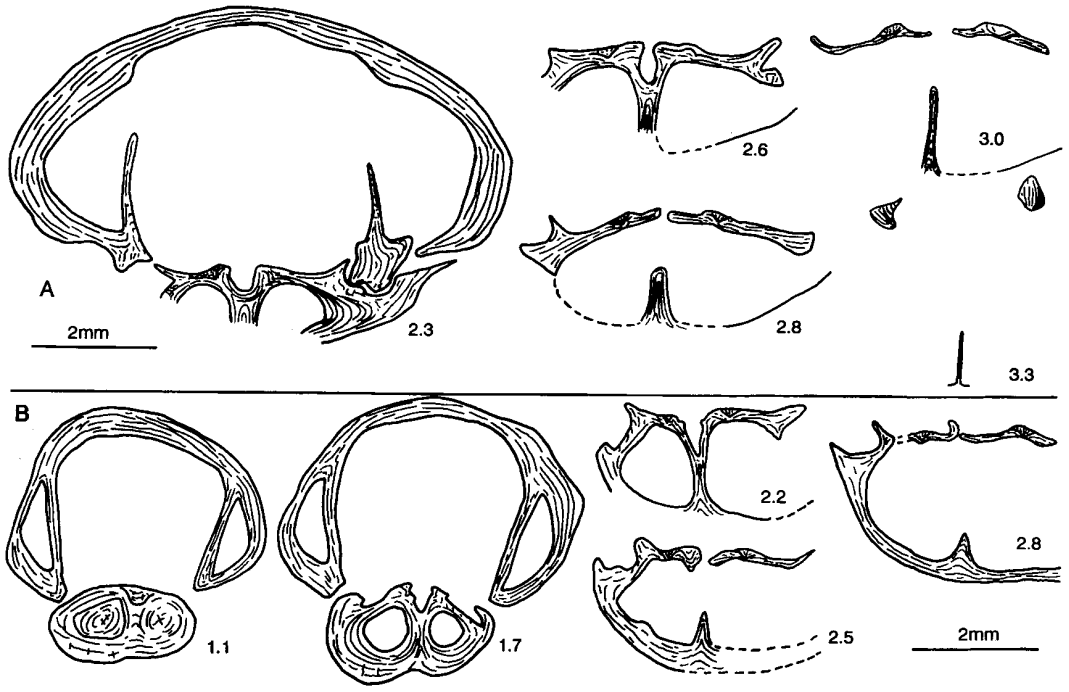
TEXT-FIG. 13. Three serial sections of triplicate *Y. hanburyi* Morphotype 1. Sample L12/0–0·1, PUM92063. (Also shown in Pl. 1, fig. 2; Pl. 2, fig. 2).



TEXT-FIG. 14. Transverse serial sections of uniplicate *Y. hanburyi* Morphotype 2. A, sample C–C, PUM92064. B sample L19/0, PUM92065.

extend for a short distance laterally. The connectivum is present in some specimens, but in others it may be just a semiconnectivum. The connectivum may cover the septalium exactly or stretch farther forward than the septalium. The crus is triangular, point down in cross section, pointing ventrally and slightly anteriorly.

In the triplicate form, a semiconnectivum is present. It seems that the end of the crura are curved ventroposteriorly so that the crura and the hinge plates with crural bases are shown in the same section.



TEXT-FIG. 15. Transverse serial sections of biplicate *Y. hanburyi* Morphotype 2. Note the narrowness of the septalium. A, sample C–C, PUM92066. B, sample L19/0·2–0·4, PUM92067.

Material. Over 145 specimens: from the middle part of the Chang lungchieh Shale, near Laojiangchong village, Xikuangshan area: L10/7·9 (one specimen); L11 (fragments); L12 (1·7 m thick, over fifty specimens, some of which are in good state of preservation; the biplicate form is predominant); from the lower part of the Famennian, near Tingziling, about 4 km east of Chongshanpu: T12 (two specimens); T13 (two specimens); from the lower part of the Famennian, near Chenjiayuan, about 4 km east of Jiangjiaqiao: C7–2 (two specimens); C–H (eighty-five specimens).

EXPLANATION OF PLATE 2

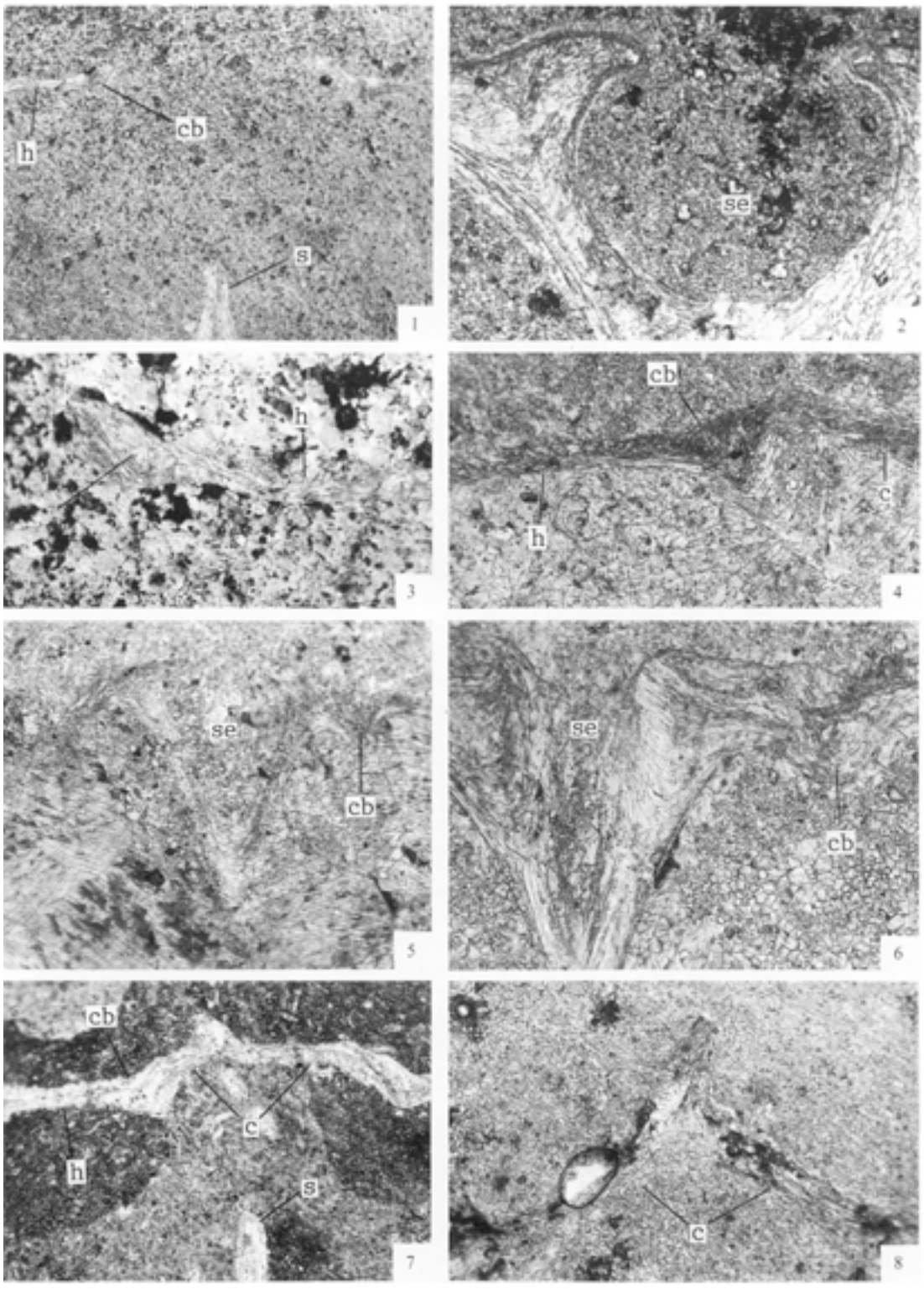
Figs 1–3, 7. *Yunnanellina hanburyi* Morphotype 1. 1, sample L12/0–0·1; showing the absence of connectivum of a biplicate specimen (PUM92060). 2, same specimen as Pl. 1, fig. 2; showing broad and rounded septalium. 3, sample L12/0·6; a biplicate specimen (PUM92077) showing right hand hinge plate and crural base, but without connectivum medially (towards the left on photograph). 7, sample C–H; showing a uniplicate specimen (PUM92062) with connectivum.

Figs 4, 6, 8. *Yunnanellina hanburyi* Morphotype 2, 4, sample C–D; showing a biplicate specimen (PUM92078) with the connectivum. 6, sample L17; showing a triplicate specimen (PUM92072) with very narrow septalium; note that the position of the crural base is on the hinge plate and not at the junction of the hinge plate and the septalium. 8, sample C–E; showing a uniplicate specimen (PUM92079) with a herringbone-shaped connectivum; note the divided crest.

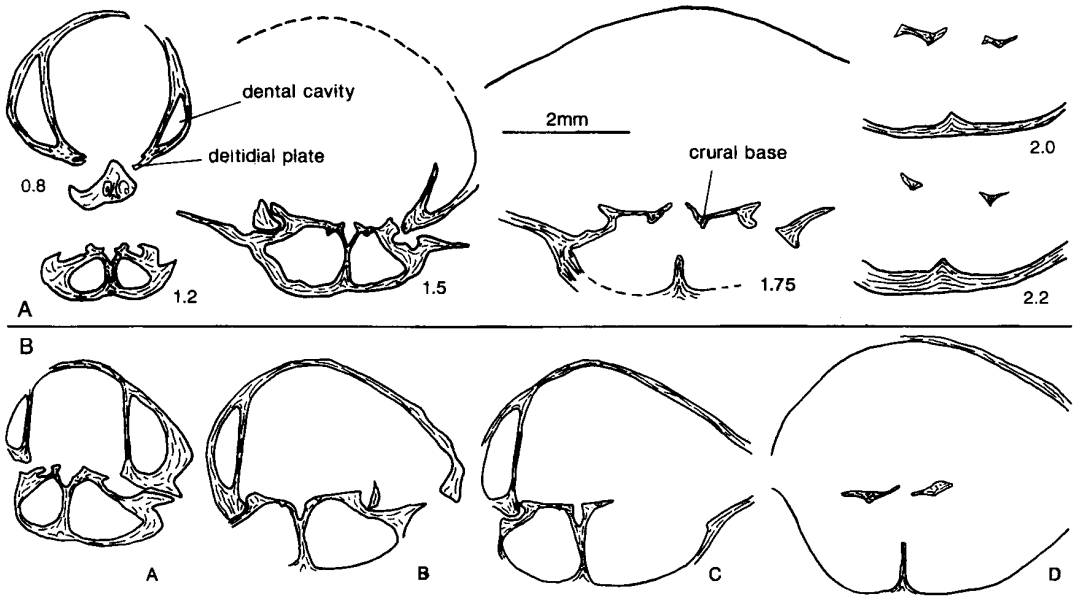
Fig. 5. *Yunnanellina hanburyi* Morphotype 3. Sample L–D3xt; a triplicate specimen (PUM92068) with V-shaped septalium and outward disposition of the crural base.

All figures × 75, except figs 1 and 7, × 30; c = connectivum; cb = crural base; h = hinge plate; s = septum; se = septalium.

PLATE 2



MA XUEPING, *Yunnanellina*



TEXT-FIG. 16. Transverse serial sections of triplicate (A) and biplicate (B) *Y. hanburyi* Morphotype 3. Sample L–D3xt. A, PUM92068, also partly shown in Plate 2, figure 5. B, PUM92069.

Yunnanellina hanburyi Morphotype 2

Plate 1, figures 16–25; Plate 2, figures 4, 6, 8; Text-figures 14–15

Diagnosis. Yunnanellina in which all specimens possess a connectivum. A narrow and deep septalium is common.

Description. In this morphotype, the uni- and biplicate specimens are predominant. In the uniplicate form, the dental cavity is larger than that in Morphotype 1. Dental plates are well developed in all forms. The septalium is usually narrow and deep, V-shaped or vase-shaped. In this case, crural bases are usually not located at the junction of the septalium and the hinge plates but lie outward in the hinge plates. Some specimens from sample C–C may show a broad and rounded septalium.

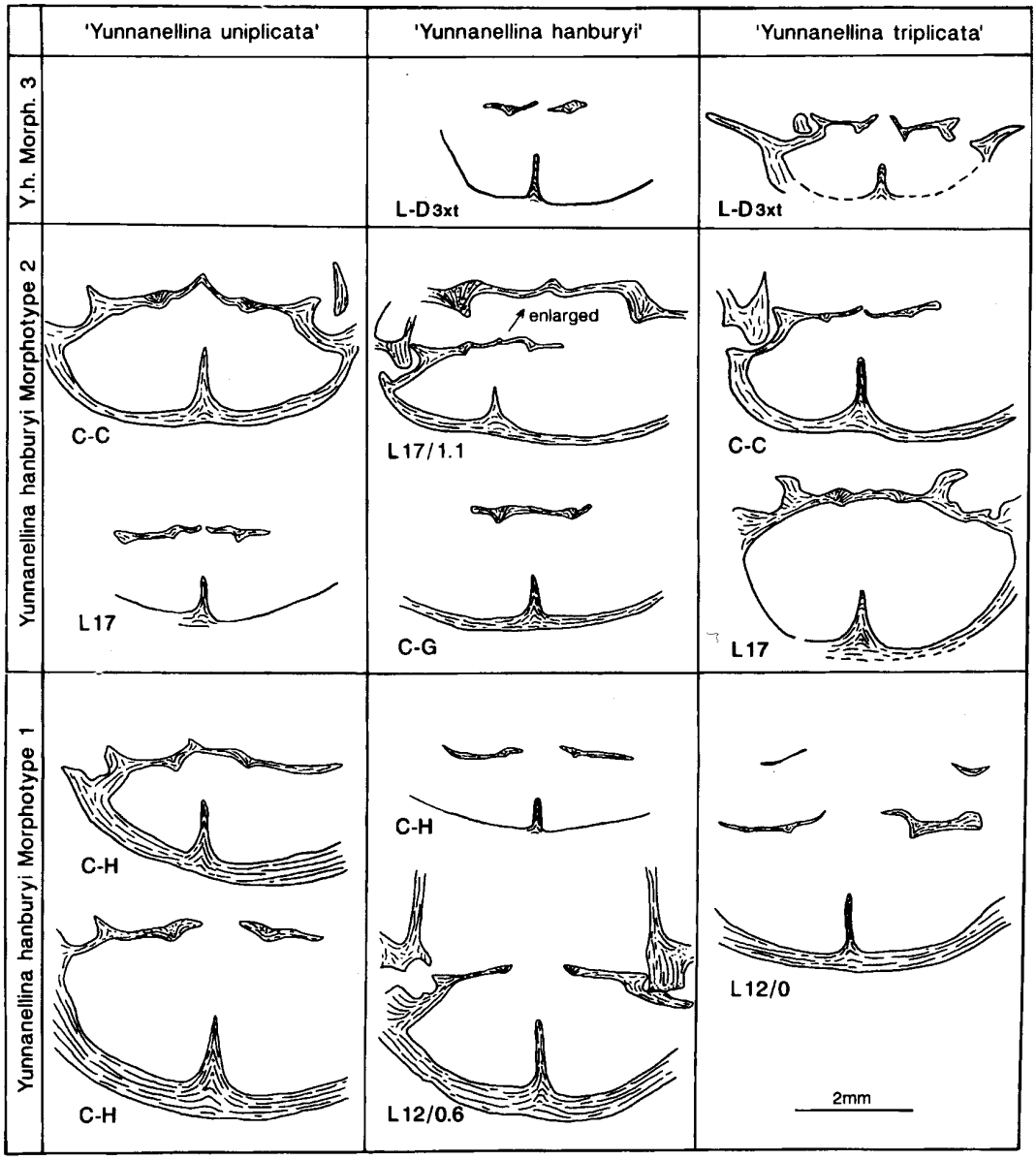
A connectivum is present in all forms. In the uniplicate form, the connectivum may be herringbone-shaped in stratigraphically higher specimens; it may be plane or slightly concave in stratigraphically lower specimens.

Material. In total about 400 specimens, most of which are in a good state of preservation: upper part of the Changlungchieh Shale, near Laojiangchong village: L15/0·55 (one specimen); L15/1·7 (three specimens); L17 (about forty specimens); L17/1·1 (about ten specimens on slab); L19/0 (seventeen specimens); L19/0–0·2 (nine specimens); L19/0·2–0·4 (thirty specimens); L19/0·35 (three specimens); L19/0·4–0·6 (three specimens); L20/1·7–2·0 (two specimens); near Chenjiayuan village: C–G (eighteen specimens); C–E (sixty-eight specimens); C–D (ninety specimens); C–C (one hundred and twenty specimens).

Yunnanellina hanburyi Morphotype 3

Plate 1, figures 26–29; Plate 2, figure 5; Text-figure 16

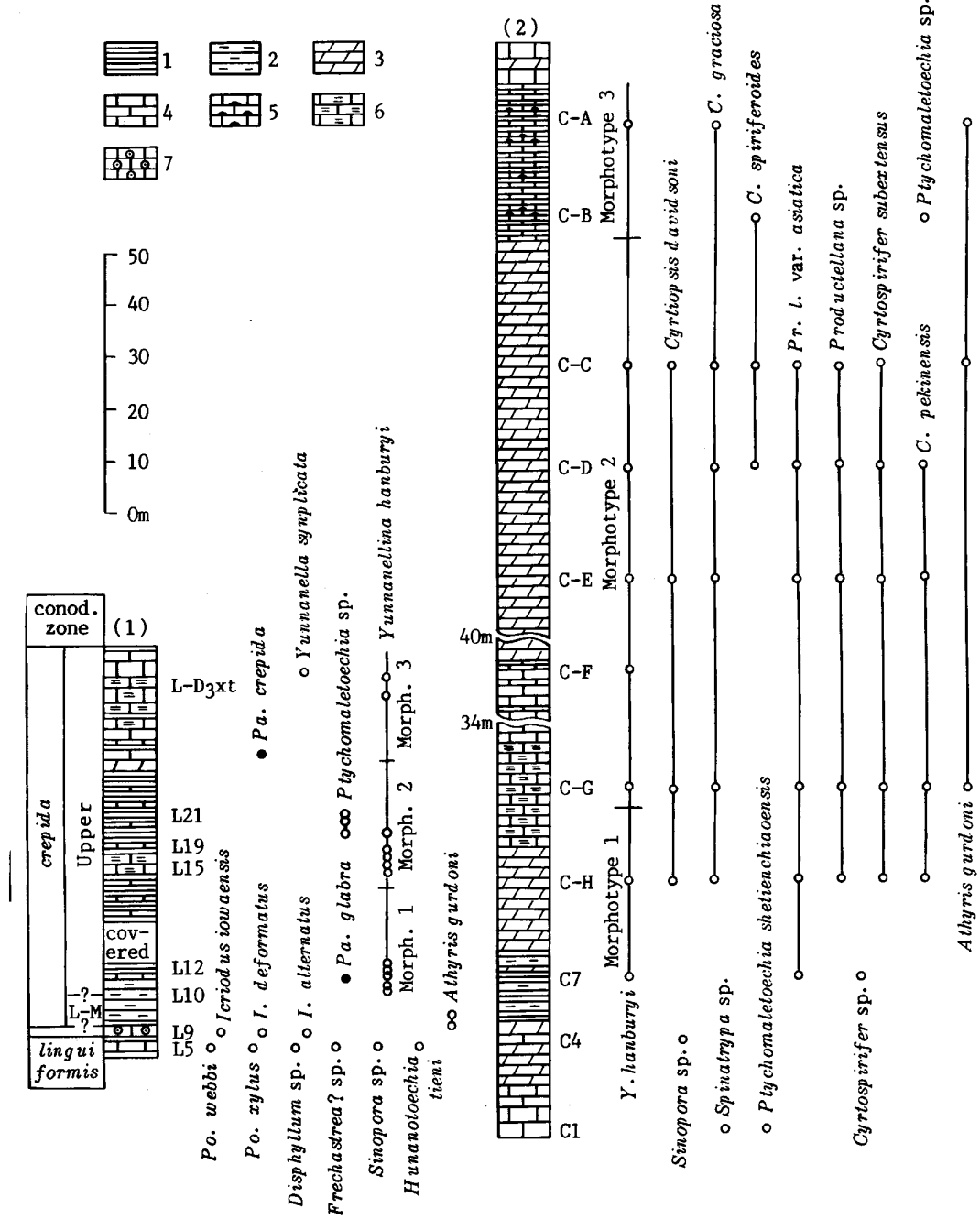
1938 *Yunnanellina hanbruyi* mut. *sublata* Tien, pp. 45–46, pl. 6, figs 3–5.
1938 *Yunnanellina* cf. *triplicata* Grabau; Tien, p. 46, pl. 6, fig. 8.
1938 *Yunnanellina triplicata* var. *latiformis* Tien, p. 47, pl. 6, fig. 6.
1938 *Yunnanellina obesa* Tien, p. 48, pl. 6, fig. 7.



TEXT-FIG. 17. Variation of connectivum in the brachial valve of *Y. hanburyi* with time. Most line drawings are selected from text-figures and plates of serial sections of different specimens shown in the text. Others are from L17, uniplicate (PUM92070) and triplicate (PUM92071); L17/1·1 (PUM92073); C–G (PUM92074); C–H, biplicate (PUM92075) and C–C, triplicate (PUM92076).

Diagnosis. Specimens of *Y. hanburyi* with a semiconnectivum and usually a narrow and deep septalium.

Description. Shell usually small. All specimens so far found are bi- and triplicate. Internal structure is weak. Dental plates are well developed. Septalium is usually narrow and deep. A semiconnectivum is present in all forms.



TEXT-FIG. 18. Stratigraphical distribution of *Y. hanburyi* and correlation of the Xikuangshan (1) and Jiangjiaqiao (2) sections. Data of black dots are adopted from Hou *et al.* (1988). Legend: 1, shale; 2, mudstone; 3, marl; 4, limestone; 5, nodular limestone; 6, limestone with argillaceous bands; 7, oolitic limestone.

Material. Thirty-one specimens from the Tutzutang Member, near Laojiangchong village: L–D3xt (twenty specimens); and from near Chenjiayuan village: C–A (eleven specimens).

VARIATION IN THE CONNECTIVUM AND SEPTALIUM WITH TIME

Morphotype 1. In the biplicate form, the connectivum is not present, or it occurs as a very short inward extension from the hinge-plate. This has been verified in the five sectioned specimens from the three stratigraphical sections (Text-fig. 17). In the uniplicate form, the connectivum is very varied, as discussed above for sample C–H. The only sectioned triplicate specimen possesses a semiconnectivum. The septalium in all the forms is broad and rounded.

Morphotype 2. The connectivum is present in all the specimens. It is usually planar in the biplicate and triplicate forms. The uniplicate form of this morphotype may be further subdivided into two varieties. The stratigraphically lower variety is characterized by a planar connectivum as seen in specimens from both the Xikuangshan and Chongshanpu sections. The stratigraphically higher variety is characterized by a herringbone-shaped connectivum. The septalium of this morphotype is usually narrow and deep in the lower part, but becomes broader higher up the stratigraphical section.

Morphotype 3. This morphotype possesses a semiconnectivum. The septalium is variable in shape, usually V- to U-shaped in cross-section.

STRATIGRAPHY AND DISTRIBUTION OF *Y. HANBURYI*

In central Hunan, the Upper Devonian includes the Shetianqiao and the Xikuangshan formations. The Xikuangshan Formation is composed of three members (Tien 1938). The lower member is the Chang lungchieh Shale, about 100 m thick, which consists of grey-green shales, thinly-bedded marls and minor limestones. The lower part possesses abundant corals and a common rhynchonellid, *Hunanotoechia tieni* (Ma, 1993), of late Frasnian age. The upper part (about 50 m thick) hosts abundant *Yunnanellina hanburyi* and cyrtospiriferids. The overlying member is the Tutzutang Limestone (about 20–40 m thick), in which *Y. hanburyi* is present in its lower part. The uppermost member is the Makunao Limestone (about 200 m thick), which is rich in brachiopods, including cyrtospiriferids and *Yunnanella.* It is separated from the Tutzutang Limestone by the thin Nitangli iron ore bed (1–2 m thick).

Yunnanellina hanburyi first occurs about ten metres above the Frasnian/Famennian boundary as found in the Xikuangshan, Jiangjiaqiao and Chongshanpu sections (Text-fig. 18). The boundary can be recognized from the first occurrence of *Icriodus deformatus* Han, a conodont which is present in the lower *triangularis* Zone in South China (Jia *et al.* 1988). But, at the Xikuangshan section, it is associated with *I. iowaensis*, a species beginning to occur in the middle *triangularis* Zone in South China (Bai Shunliang, oral communication). The occurrence of *Palmatolepis glabra* in bed L11 (Hou *et al.* 1988) may indicate the upper *crepida* Zone. The upper occurrence of *Y. hanburyi* probably still lies within the upper *crepida* Zone because of the presence of this zonal species at the base of the Tutzutang Member (Hou *et al.* 1988). This is further supported by data from the Qidong section in Hunan Province, where the *Yunnanellina* fauna is displaced by the *Yunnanella* fauna at the top of the *crepida* Zone (Wang and Bai 1988). Therefore, the entire range of *Y. hanburyi* may well coincide with the upper *crepida* Zone.

At the Jiangjiaqiao section, no conodont data are available, but there are abundant brachiopods, including *Y. hanburyi*, cyrtospiriferids and productids. Using the three morphotypes of *Y. hanburyi*, it is possible to correlate this section with the Xikuangshan section. Obviously, the rate of sedimentation in the Jiangjiaqiao area was much higher than that in the Xikuangshan area because the former sequence is much thicker.

CONCLUSIONS

The variations in both external and internal structures of *Yunnanellina hanburyi* (Davidson, 1853) have been thoroughly described based on abundant specimens collected from central Hunan. It is concluded that the other nominal species and subspecies founded later from South China are all junior synonyms of *Y. hanburyi*. This demonstrates that care must be taken in using external features alone to establish new species, especially when few specimens are to hand. Internal structure is usually considered to be reliable feature for taxonomy, but some species, like *Yunnanellina hanburyi*, may show a wide range of variations in the internal structure, even in specimens from the same sample. Better understanding of this kind of species (variable in both external and internal structure) can only be achieved through the study of numerous specimens whose locality and stratum are clearly known. When the morphology of a brachiopod is well understood, it could, potentially, enable finer subdivision of its stratigraphical range.

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