PHYLOGENY OF *ORBIRHYNCHIA* PETTITT, 1954 (BRACHIOPODA: RHYNCHONELLIDA)

by NEALE MONKS *and* ELLIS OWEN

ABSTRACT. A computer-based parsimony analysis of the brachiopod genus *Orbirhynchia* (Late Albian–Middle Campanian) is described. The resulting cladogram indicates that the genus divided into two distinct lineages soon after its appearance in the Late Albian. One group is known only from marly and sandy facies of Cenomanian age, while the second, more diverse, group appeared later in the Cenomanian but persisted into the Campanian. These two groups exhibit distinct morphological trends which may be related to different ecological niches, perhaps with respect to local sedimentary environment.

KEY WORDS: brachiopod, *Orbirhynchia*, Cretaceous, phylogeny, palaeoecology.

BRACHIOPODA form a comparatively minor component of Cretaceous marine faunas, but some taxa are widespread and distinctive, making them useful biostratigraphical markers. The rhynchonellid genus *Orbirhynchia* ranges from the Upper Albian to the Upper Coniacian, and species occur in a wide variety of sediments throughout north-west Europe, from shallow water sandy facies to deeper water chalks. The appearance of particular species of *Orbirhynchia* at certain levels is well known. Examples include the bands of *O. mantelliana* in the Middle Chalk of southern England described by Kennedy (1969) and others, and the appearance of *O. weisti* in the Plenus Marls (Jefferies 1962). Owen (1978) and Holdaway (1982) discussed the ecological tolerances of the mid Cretaceous brachiopods, and observed that most species are restricted to particular lithologies, implying that environmental conditions may have been important in controlling the occurrence of brachiopod species.

PHYLOGENETIC ANALYSIS

Description of genus

Orbirhynchia incorporates acutely biconvex to orbicular rhynchonellids; dorsal fold usually very slight, anterior commissure with low arcuate uniplication rarely asymmetrical. Numerous rounded to slightly angular costae. Umbonal characters vary from short, pointed, with suberect beak and small rounded or oval foramen to more elongate with exposed deltidial plates and foramen. Internal characters with falciform crura. A representative selection of *Orbirhynchia* species is shown in Plate 1.

Investigated taxa

All known species of *Orbirhynchia* were included in the analysis except for *O. parva*, which we consider to be small *O. mantelliana*, and are listed in Table 1. All material used for this analysis is from the Department of Palaeontology, The Natural History Museum (NHM), London; the principal specimens used for character determination are listed in Table 1, together with their stratigraphical age. Some characters, for example internal features, were determined from the literature, primarily Pettitt (1954) and Owen (1988).

Outgroup taxon

Orbirhynchia belongs to the subfamily Lacunosellinae together with a few other, mostly Jurassic, genera. The subfamily is characterised by the presence of falciform crura and a weak or absent dorsal septum

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(Ager *et al.* 1965). The type species of *Lacunosella* was used as the outgroup, namely *Lacunosella arolica*, a Late Jurassic European species.

Characters

The potential sources for an analysis are the valves of the shell, the umbo, and the lophophore supports. The Appendix lists the characters used in this analysis with the different states exhibited by the analysed taxa of these characters. The data matrix based on these characters is also presented in the Appendix. This was compiled in MacClade (Maddisson and Maddisson 1992). In some cases species are polymorphic with respect to given characters, and these are entered as such in the matrix (i.e. with all observed states separated by a forward slash).

Analytical methods

The data matrix was processed using the parsimony analysis program PAUP (Swofford 1993). The optimality criterion used was that of maximum parsimony. All characters were unordered and initially given equal weight. After the first run, the data set was re-weighted using the rescaled consistency index to determine the most consistent characters (successive re-weighting; see Farris 1969, 1989). Searching was done by using the 'branch and bound' option which guarantees to find the most parsimonious trees. Searching was performed twice, once using the accelerated transformation optimisation (ACCTRAN) and then again using the delayed transformation (DELTRAN).

EXPLANATION OF PLATE 1

Figs 1–3. *Lacunosella arolica* (Oppel,1866), Upper Jurassic, Birmensdorfer-Schichten, Switzerland; NHM B 37034; ×1.

Figs 4–6. *Orbirhynchia praedispansa* Pettitt, 1954, Middle Chalk, Lower Turonian, Dover, Kent; NHM B 80024; ×1·5.

Figs 7–9. *Orbirhynchia dispansa* Pettitt, 1954, Middle Chalk, Upper Turonian, Planus Zone, Borstal Manor Pit, Rochester, Kent; NHM B 80113, holotype; ×1·5.

Figs 10–12. *Orbirhynchia wiesti* (Quenstedt, 1871), Lower Chalk, Upper Cenomanian, Chardstock, Devon, ×1·5, NHM BB 12396.

Figs 13-15. *Orbirhynchia bella* Pettitt, 1954, Upper Chalk, Lower Campanian, Quadratus Zone, East Harnham, Wiltshire; NHM BB 12394, holotype; ×1·5.

Figs 16–18. *Orbirhynchia obscura* Pettitt, 1954, Lower Chalk, Cenomanian, Folkestone, Kent; NHM BB 12397, holotype; ×1·5.

Figs 19–21. *Orbirhynchia pisiformis* Pettitt, 1954, Upper Chalk, Coranguinum Zone, Quidhampton, near Salisbury, Wiltshire; NHM B 92580, holotype; ×1·5.

Figs 22–24. *Orbirhynchia reedensis* (Etheridge, 1881), Upper Chalk, Upper Santonian, Marsupites Zone, Foreness Point, Margate, Kent; NHM B 79890; ×1·5.

Figs 25–27. *Orbirhynchia compta* Pettitt,1954, Middle Chalk, Turonian, Labiatus Zone, Branscombe Cliff, Devon; NHM BB 12398, holotype; ×1·5.

Figs 28–30. *Orbirhynchia granum* Pettitt, 1954, Upper Chalk, Middle Campanian, East Harnham, Wiltshire; NHM BB 12393, holotype; ×1·5.

Figs 31–33. *Orbirhynchia wilmingtonensis* Owen, 1988, Lower Chalk, Lower Cenomanian, Mantelli Zone, Wilmington, Devon; NHM BB 82132; holotype; ×1·5.

Figs 34–36. *Orbirhynchia boussensis* Owen, 1988, Upper Cenomanian, Sables de Bousse, Bousse, Sarthe, France; NHM BB 82131, holotype; ×1·5.

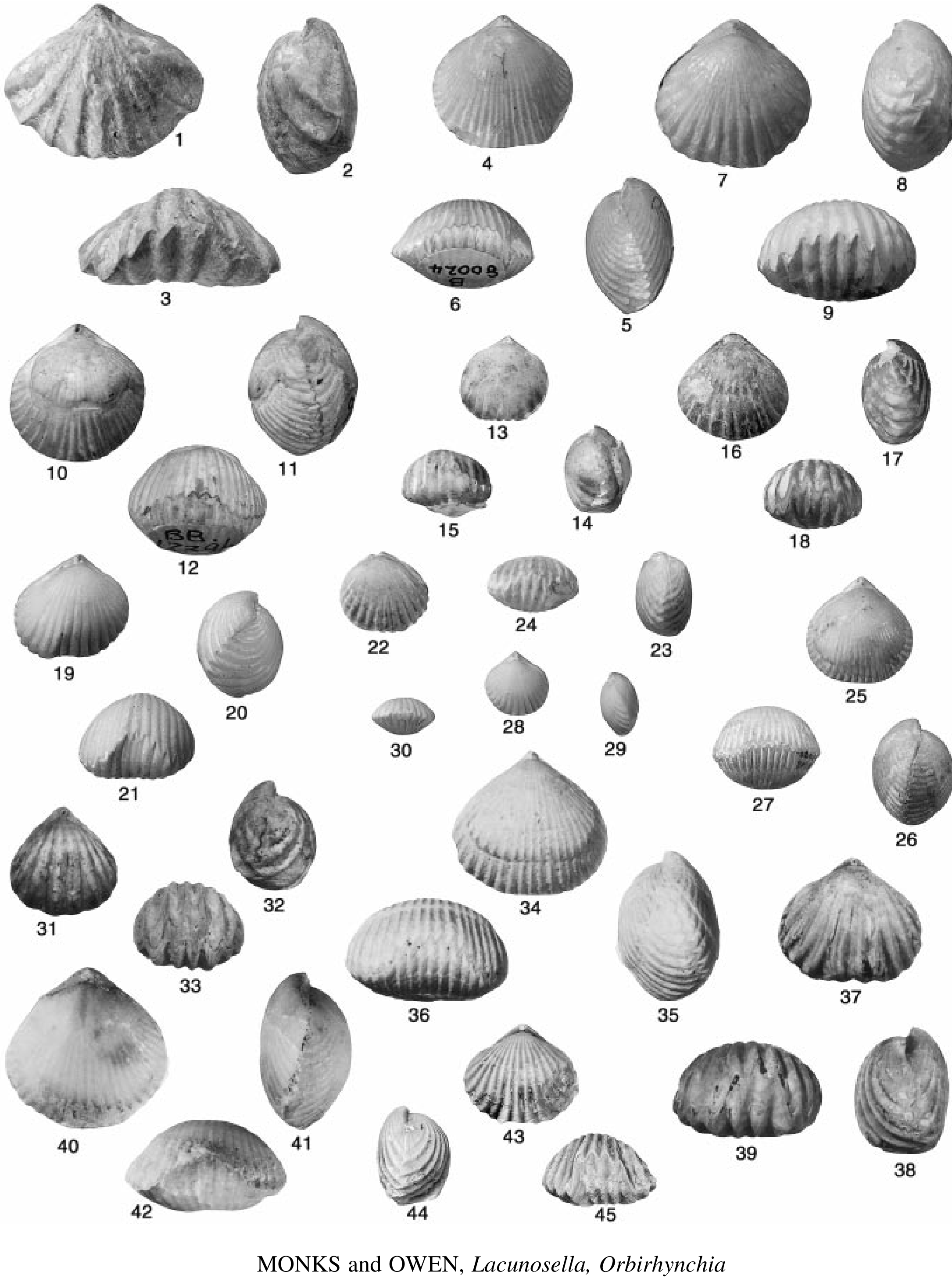
Figs 37–39. *Orbirhynchia mantelliana* (J. de C. Sowerby, 1826), Lower Chalk, Totternhoe Stone, Barrington, Cambridge; NHM BB 81020; ×1·5.

Figs 40–42. *Orbirhynchia multicostata* Pettitt, 1954, Lower Chalk, Upper Cenomanian, South Ferriby, Yorkshire; NHM BB82342; ×1·5.

Figs 43–45. *Orbirhynchia obscura* Pettitt, 1954, Lower Chalk, Lower Cenomanian, Folkestone, Kent; NHM B 29725; ×1·5.

Views of all specimens are consecutively dorsal, lateral and anterior; NHM, The Natural History Museum, London.

PLATE 1



MONKS and OWEN, *Lacunosella, Orbirhynchia*

TABLE 1. Species of *Orbirhynchia* included in this analysis.

Species	Material studied	Stratigraphical range of species
O. parkinsoni Owen	Holotype, BB. 39276	Upper Albian, Cambridge Greensand
O. mantelliana (J. de C. Sowerby)	BB. 82841-66	Lower Cenomanian, Chalk Marl
O. obscura Pettitt	Holotype, BB. 12397	Lower Cenomanian, Lower Chalk
O. wilmingtonensis Owen	Holotype BB. 82132	Lower Cenomanian, Upper Greensand
O. multicostata Pettitt	BB. 76357-66	Middle Cenomanian, Lower Chalk
O. boussensis Owen	Holotype BB. 82131	Upper Cenomanian, Sable de Bousse
O. wiesti (Quenstedt)	BB. 83277-83	Upper Cenomanian and Lower Turonian, Lower and Middle Chalk
O. compta Pettitt	Holotype, BB. 12398	Lower Turonian, Middle Chalk
O. cuvieri (d'Orbigny)	B. 85944	Lower Turonian, Middle Chalk
O. orbignyi (Pettitt)	B. 8166	Middle Turonian, Middle Chalk
O. praedispansa Pettitt	B. 80024	Lower Turonian, Middle Chalk
O. dispansa Pettitt	Holotype, BB. 80113	Upper Turonian, Middle Chalk
O. reedensis Pettitt	B. 79890	Upper Turonian to Upper Santonian, Middle Chalk
O. pisiformis Pettitt	B. 92580	Upper Coniacian to Lower Campanian, Upper Chalk
O. bella Pettitt	Holotype, BB. 12394	Lower and Middle Campanian, Upper Chalk
O. granum Pettitt	Holotype, BB. 12393	Lower and Middle Campanian, Upper Chalk

Results

Since there are no missing characters, ACCTRAN and DELTRAN optimisation result in identical trees. The first runs, using equal character weightings, produced seven trees. The strict consensus is given in Text-figure 1A. After the characters were re-weighted only a single tree was produced (Text-fig. 1B) which is the one used for the subsequent discussion herein. This tree has a consistency index of 0·51 and a retention index of 0·75.

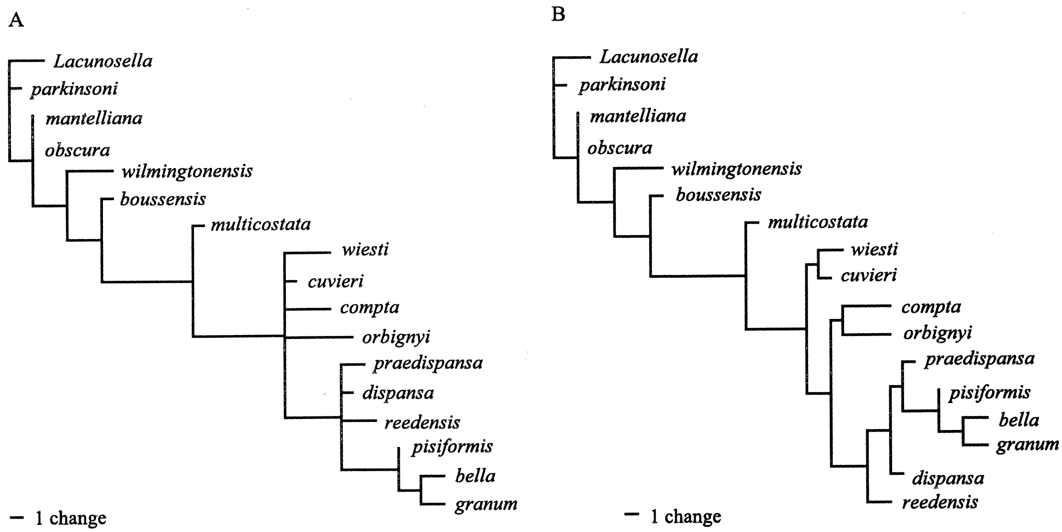
RESULTS

Bootstrap and Bremer support

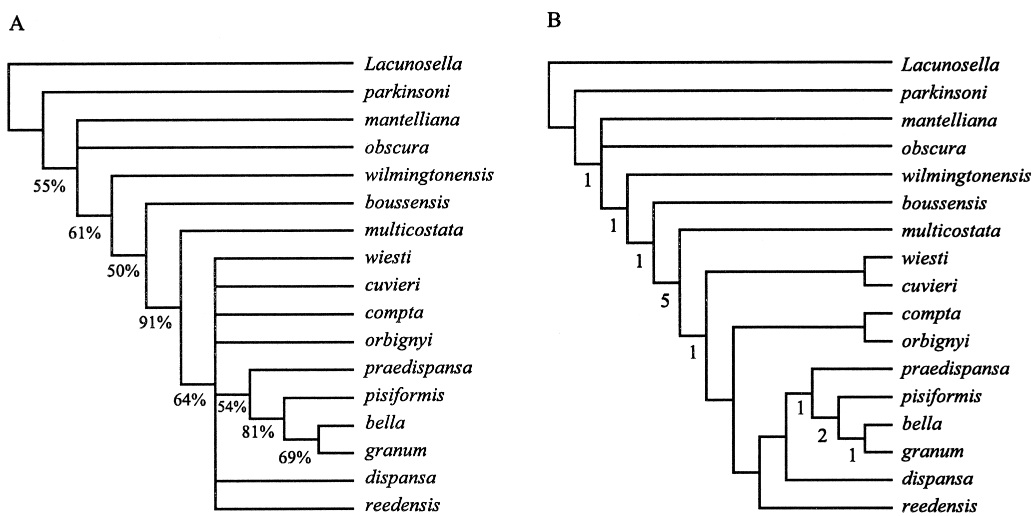
Bootstrapping is a conservative test of the robustness of the tree topology (Felsenstein 1985). It was performed using PAUP on one hundred replicates. The results are given in Text-figure 2A as the percentage of bootstrap trees of which the labelled branches are found. Bremer or branch decay support is another test of tree robustness, determining the number of extra steps above the length of the most parsimonious trees at which a given branch collapses. The Bremer support values are given in Text-figure 2B.

Topology and pattern of character distribution

Tree topology is broadly pectinate, though with a distinct division between the basal taxa with generally few characters distinguishing them (*O. parkinsoni*–*O. wilmingtonensis*) and an in-group defined by six, unambiguous character state changes (*O. multicostata* upwards). The high bootstrap and Bremer decay values corroborate the distinctiveness of this in-group. Text-figure 3 illustrates the pattern of character distribution across the tree. Character transitions are labelled (see Appendix for explanations of characters and their observed states). Of particular note are unique character transformations (i.e., have a consistency index of 1).



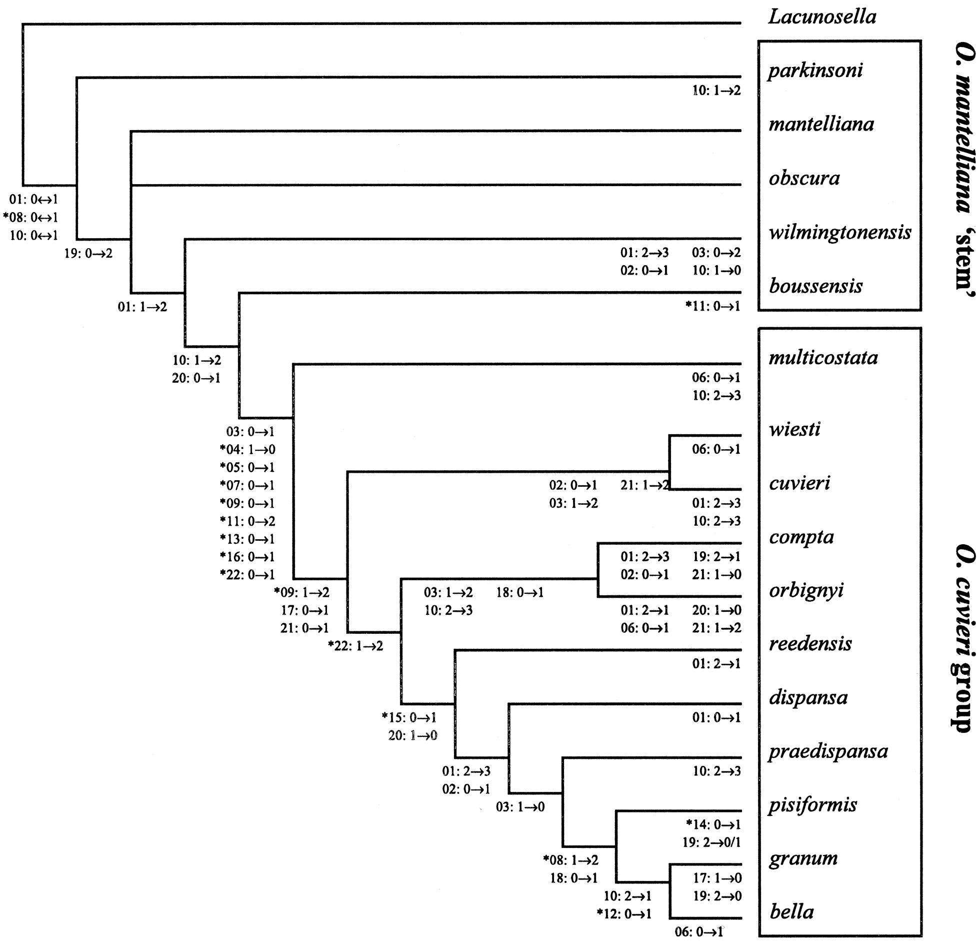
TEXT-FIG. 1. A, strict consensus of seven trees. Length of branches is proportional to the number of characters which support that branch. B, after re-weighting only a single tree was produced. Tree length = 65 steps; CI = 0·51; RI = 0·75. Length of branches is proportional to the number of characters which support that branch.



TEXT-FIG. 2. A, 50 per cent majority rule consensus tree of one hundred replicates of the data matrix. Numbers indicate the percentage of bootstrap trees within which that branch occurs. Length of branches is proportional to the number of characters which support that branch. B, selected tree with Bremer support values labelled. Note that, by definition, branches not in the strict consensus tree (Text-fig. 1A) have a Bremer support value of 0.

DISCUSSION

Although Pettitt (1954) suggested ways in which some species of *Orbirhynchia* could have arisen from others, Owen (1988) postulated phylogenetic relationships within the genus based upon morphological rather than stratigraphical grounds, and identified two species groups. One of these included *O. cuvieri* plus species that were probably or possibly conspecific, namely *O. compta*, *O. multicostata*, *O. orbignyi*

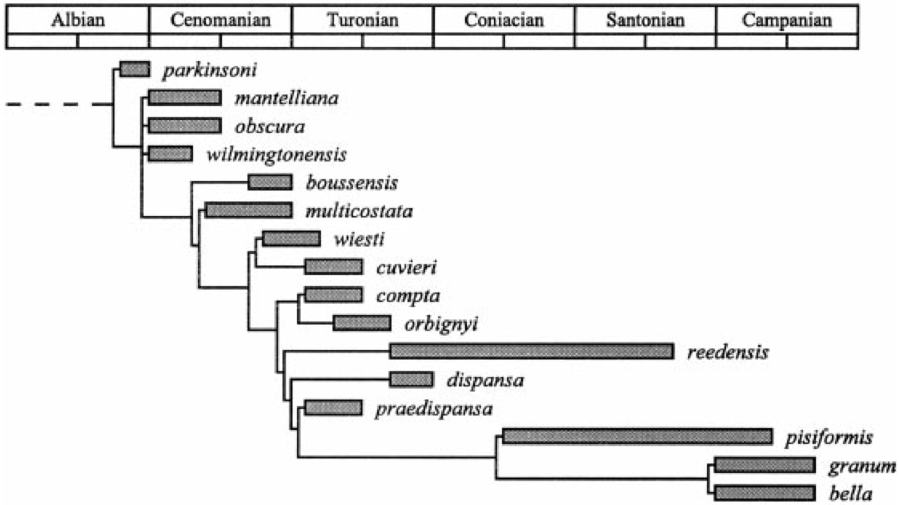


TEXT-FIG. 3. Selected tree with character state changes labelled below the branch to which they refer (see Appendix for details of characters and potential states). Characters with a consistency index of 1 are denoted with an asterisk.

and *O. wiesti*. The second group included *O. mantelliana* and species that were either conspecific (*O. obscura*, *O. parva*), subspecies (*O. dispansa*), or closely related (*O. boussensis*, *O. wilmingtonensis*). This division describes the lower part of the cladogram (Text-figure 3), with the exception of the position of *O. dispansa*. The *O. mantelliana* group is the 'stem' part of the cladogram while the *O. cuvieri* group is the more crownward in-group.

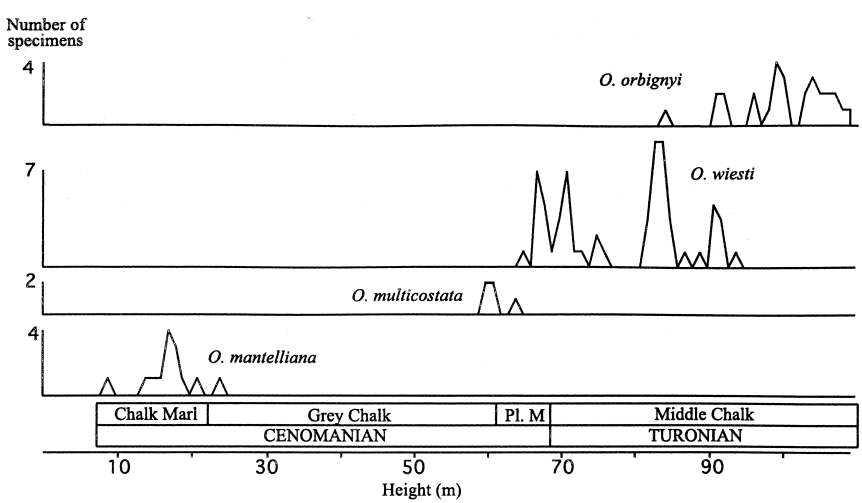
A useful test of any phylogeny is its congruence with stratigraphy. Text-figure 4 is a phylogenetic tree based on the analysis described here following the methods described by Smith (1994). Overall, the match is good, with the most derived species being towards the crown of the tree. It is evident that the *O. mantelliana* group is confined to the Cenomanian, while the *O. cuvieri* group has a much greater range, from the Cenomanian to Campanian.

The distribution of *Orbirhynchia* spp. within the Chalk is distinctly patchy. One of us (NM), in collaboration with A. S. Gale and A. B. Smith, has been involved in a detailed study of the macrofossils from the most complete and thickest Cenomanian and Lower Turonian section in the Anglo-Paris Basin. Over a hundred specimens of *O. mantelliana*, *O. multicostata*, *O. orbignyi*, and *O. wiesti* from the Lower and Middle Chalk at Folkestone, Eastbourne, and Beachy Head have been collected and logged at 10 cm intervals, the separate localities being tightly correlated using biostratigraphical and Milankovich cycle



TEXT-FIG. 4. Phylostratigraphy of the genus *Orbirhynchia* based on the analysis described in the text. The method is that described in detail in Smith (1994). 'Ghost ranges' link taxa at the highest time horizon at which their implied common ancestor could have occurred. Taxa that are not characterised by unique, derived characters may be ancestor grades, and are treated here as such, giving rise directly to other taxa.

data (Gale *et al.* 2000). Text-figure 5 plots the distribution of *Orbirhynchia* through this section. *O. mantelliana* is confined to a relatively small part of the succession, a series of bands in the Chalk Marl and the very base of the Grey Chalk. According to Kennedy (1969), these bands may be observed elsewhere in southern England. Similarly, *O. multicostata* is limited in its distribution, occurring in the lower part of the Plenus Marls (Jefferies 1962). While it is tempting to relate the apparent environmental preferences of each of these species (see Holdaway 1982; Owen 1988) with the evolution of the genus,



TEXT-FIG. 5. Distribution of *Orbirhynchia* spp. from the Lower and Middle Chalk at Eastbourne, Sussex. Pl. M., Plenus Marls.

without detailed information on the functional morphology and ecology of these brachiopods it is not possible to come to any substantive conclusions on this point.

CONCLUSION

The first *Orbirhynchia* appeared during the Late Albian and flourished during the Cenomanian, apparently adapted to the marly or sandy conditions which existed in certain areas of the Anglo-Paris Basin at that time. These species tend towards a subpentagonal dorsal profile, relatively coarse ribbing and often asymmetrical gapes, and correspond to the *O. mantelliana* group of Owen (1988). A distinct clade appeared in the Middle Cenomanian and lasted until the Campanian. These species are found in finer, less clay-rich sediments. This clade, the *O. cuvieri* group of Owen (1988), is characterised by a weakly ornamented, compact-rounded shape, a short umbo with a small foramen, and internally by small and thin lophophore supports.

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APPENDIX

Characters used in cladistic analysis

Character	Feature	States
1	Dorsal outline	Triangular (0); subpentagonal (1); oval with flat anterior (2) or approximately circular (3)
2	Anterior outline	Approximately biconvex but with distinct dorsal valve flattening (0) or globose, strongly biconvex (1)
3	Lenticularity	Strongly (0); slight, most noticeably on small specimens (1) or absent (0)
4	Commissure	Arcuate (0) or trapezoidal (1)
5	Sulcus asymmetry	Sulcus variable, inconsistently symmetrical (0) or symmetrical on all specimens (1)
6	Sulcus depth	Weak, imperceptible (0) or moderately strong (1)
7	Linguiform extension	Long (0) or short (1)
8	Overall size	Large (over 2 cm); medium (around 1·5 cm) or very small (1 cm)
9	Shell thickness	Shell robust and thickened throughout (0); thick initially thinning towards the aperture (1), or rather thin and delicate throughout (2)
10	Costation	Few (12 or less); moderate (around 18); numerous (around 24) or very numerous (over 30)
11	Costae shape	Angular and elevated (0); subangular to rounded (1) or very rounded (2)
12	Persistence of costae	From the umbo to the aperture (0) or the umbonal region lacks costae (1)
13	Depth of costae	Deeply incised (0) or weak (1)
14	Umbo	Suberect (0) or erect (1)
15	Umbo produced	Umbo short, deltidium obscured (0) or umbo produced with exposed deltidium (1)
16	Dental lamellae	Relatively weakly developed, restricted to near hinge (0) or robust extending into mantle cavity (1)
17	Beak shape	Sharp (0) or rounded (1)
18	Foramen shape	Circular (0), pyriform (1) or oval (2)
19	Foramen size	Large (0), medium (1) or small (2)
20	Apical angle	Obtuse (0) or acute (1)
21	Deltidial plates	Conjunct but simple (0); produced into a lip (1) or a tube (2)
22	Crura	Thick falciform (0); deflected dorsally (1), or thin (2)

Data matrix

	Characters																					
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Lacunosella	0	0	0	1	0/1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
parkinsoni	1	0	0	1	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0
mantelliana	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2	0	0	0
obscura	1	0	0	1	0	0	0	1	0	1	0	0	0	0/1	0	0	0	0	2	0	0	0
wilmingtonensis	3	1	2	1	0/1	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0
boussensis	2	0	0	1	0/1	0	0	1	0	2	1	0	0	0	0	0	0	0	2	1	0	0
multicostata	2	0	1	0	1	1	1	1	1	3	2	0	1	0	0	1	0	0	2	1	0	1
wiesti	2	1	2	0	1	1	1	1	2	2	2	0	1	0	0	1	1	0	2	1	2	1
cuvieri	3	1	2	0	1	0	1	1	2	3	2	0	1	0	0	1	1	0	2	1	2	1
compta	3	1	2	0	1	0	1	1	2	3	2	0	1	0	0	1	1	1	1	1	0	2
orbignyi	1	0	2	0	1	1	1	1	2	3	2	0	1	0	0	1	1	1	2	0	2	2
praedispansa	3	1	0	0	1	0	1	1	2	3	2	0	1	0/1	1	1	1	0	2	0	1	2
dispansa	3	1	1	0	1	1	1	1	2	2	2	0	1	0/1	1	1	1	0	2	0	1	2
reedensis	1	0	1	0	1	0	1	1	2	2	2	0	1	0	1	1	1	0/1	2	0	1	2
pisiformis	3	1	0	0	1	0	1	2	2	2	2	0	1	1	1	1	1	1/2	0/1	0	1	2
bella	3	1	0	0	1	1	1	2	2	1	2	1	1	0/1	1	1	1	1/2	2	0	1	2
granum	3	1	0	0	1	0	1	2	2	1	2	1	1	0/1	1	1	0	1	0	0	1	2