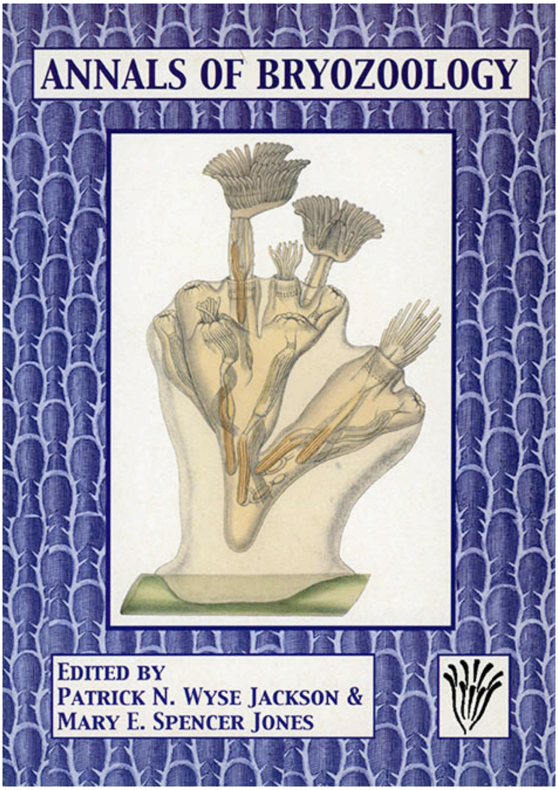

Paper in:

Patrick N. Wyse Jackson & Mary E. Spencer Jones (eds) (2002) *Annals of Bryozoology: aspects of the history of research on bryozoans*. International Bryozoology Association, Dublin, pp. viii+381.

W.D. Lang, orthogenesis and the evolution of Cretaceous cribrimorph Bryozoa

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1. Introduction

Peter Bowler, in his aptly named book *The Eclipse of Darwinism*,[1] described the widespread scepticism around the beginning of the 20th Century among biologists who, although accepting the fact of evolution, questioned natural selection as the driving mechanism responsible for evolutionary change. Four alternatives to natural selection were identified by Bowler as being popular at this time: Theistic Evolution, Lamarckism, Orthogenesis, and the Mutation Theory. Orthogenesis was championed mainly by palaeontologists who perceived numerous apparent instances in the fossil record of parallel evolution following particular pathways (trends) that often led to morphologies which seemed to be of an increasingly non-adaptive nature and culminated in lineage extinction. Much of the evidence for orthogenesis came from the occurrence of fossils with grossly enlarged, thickened or elaborated shells and bones, features for which it was difficult to imagine any advantage to the organisms possessing them. Among the most complete theories proposed at the time to account for such 'overdevelopment' was that offered by W.D. Lang, an invertebrate palaeontologist working at the British Museum (Natural History) [BM(NH)]. Lang's theory sprang from his detailed morphological and systematic studies of Cretaceous cribrimorph bryozoans. His arguments, couched in emotive prose - lineages being 'doomed to extinction' as a result of individuals building their own 'tombs' through excessive calcification - are for the most part untenable in the light of our current understanding of evolutionary biology. Indeed, even at the time of publication Lang failed to attract significant numbers of followers who were willing to proselytise his theories.[2] Nevertheless, Lang's theories did find their way into student textbooks[3] still in use over half a century later.

With renewed interest in evolutionary trends,[4] it is opportune to review Lang's work on cribrimorph bryozoan evolution, not merely because it represents an imaginative attempt to interpret the fossil record, but also to highlight the fact that subsequent research on Cretaceous cribrimorphs has been so scant that we still lack the empirical data and phylogenetic framework needed to evaluate the pattern of cribrimorph evolution and test certain aspects of Lang's theories. After a biographical sketch of Lang, I discuss his thesis of cribrimorph evolution and assess his work in the context of modern evolutionary theory and advances in bryozoology. In addition to the primary literature, I have had access to 17 octavo fileboxes containing Lang's correspondence, official and personal, over a period of more than fifty years.[5]

2. W.D. Lang

William Dickson Lang was born on 29th December 1878 in the Punjab, India, where his father was a civil engineer working on the construction of the Jumna Canal.[6] The Lang family were firmly rooted in the Victorian upper middle-classes, with the army, the clergy[7] and the Indian Civil Service figuring prominently among the professions traditionally practised by his relatives and ancestors. Lang's father Edward endured worsening health while in India and retired from the Indian service the year after his son's birth, settling in Harrow in the northern suburbs of London with his family in 1879; however, he survived for only a year, leaving his widow Hebe to bring up William and the other children. W.D. Lang received his early education at Christ's Hospital, Hertford, before becoming a day pupil at Harrow, a leading bastion, then as now, of the English Public School tradition. An early interest in natural history was fuelled by family holidays to the coasts of Dorset, Yorkshire, Devon, Lincolnshire and North Wales. In later life, Lang subscribed to the idea that there are born naturalists,[8] of which he considered himself to be an example.[9] His leanings towards natural history were scarcely satisfied at Harrow where the emphasis was on the Classics. However, in 1898 he entered Pembroke College, Cambridge as a scholar to read the Natural Sciences Tripos with Zoology.

It was during 1898 that Lang first visited Charmouth in Dorset, a place he was to revisit almost annually thereafter in connection with his work on Jurassic biostratigraphy,[10] and which was to be his home[11] upon retirement 40 years later. Errol White[12] attributed Lang's failure to graduate from Cambridge with a First to a lack of supervision: there was only one science don at Pembroke and very few of Lang's fellow students read Natural Sciences. Lang's teachers at Cambridge included Sidney Harmer, destined to become Director of the British Museum (Natural History) and a leading authority on Recent Polyzoa (= Bryozoa), and Henry Woods, perhaps best known for his textbook on

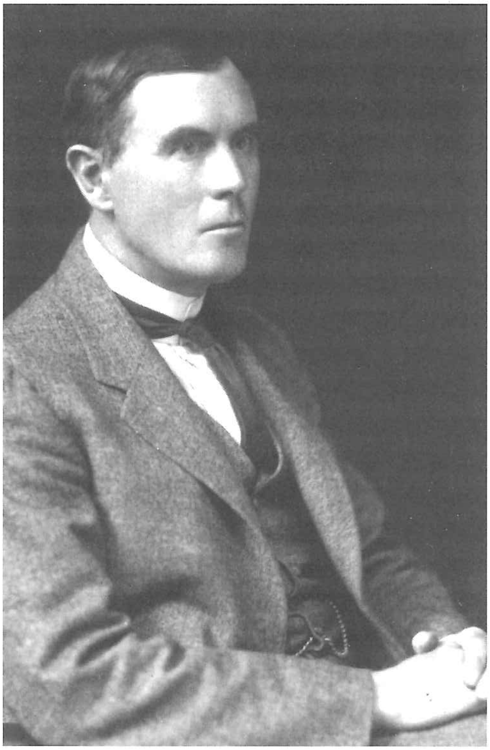

Figure 1. An undated photograph of W.D. Lang taken sometime during the period of his employment at the British Museum (Natural History).

invertebrate palaeontology,[13] then in its second edition, and who encouraged Lang to apply for a position at the British Museum (Natural History). This post had become vacant on the retirement of Henry Woodward in 1901. Lang (Figure 1) was appointed in the face of strong competition and, on 1st October 1902, he entered the Department of Geology at the BM(NH) where he was to spend all of his working life. His remit covered fossil Protozoa, Coelenterata, Porifera, Polyzoa (Bryozoa) and miscellaneous smaller groups. Previously under the care of J.W. Gregory, these collections were in a poor curatorial condition when Lang arrived.

Most of Lang's efforts during his first few years at the BM(NH) were directed towards the registration and labelling of specimens - his diligence in carrying out this task is obvious from the large number of handwritten entries he made in the accession registers. The Keeper in these early years was Arthur Smith Woodward, a distinguished ichthyologist who, unfortunately, was later to be drawn into the Piltdown forgery. Lang's immediate superior was the echinoderm specialist Francis Arthur Bather who succeeded Smith Woodward as Keeper in 1924. Lang and Bather had very different personalities and backgrounds; they disagreed about various matters,[14] and Bather was a major critic[15] of his colleague's orthogenetic theories. Lang's career at the BM(NH) followed a common pattern: curation giving way to research which in turn was replaced by administration when Lang himself became Keeper in 1928, following a year's apprenticeship as Deputy Keeper. Stearn[16] remarked on the unusual working hours adopted by Lang who started very early in the morning and finished long before most of his colleagues, a regime which severely restricted any participation in scientific societies, made yet more difficult by his perceived physical weaknesses.[17] As Keeper, he ran the Department of Palaeontology along traditional and very formal lines, and is reputed[18] to have had a particular abhorrence of newspaper reporters who frequently arrived in search of a story.

The first[19] of Lang's papers devoted wholly or principally to bryozoans appeared in 1904. All of his early papers concerned Jurassic and Cretaceous cyclostomes, but within ten years his focus of interest had shifted to Cretaceous cheilostomes.[20] The most substantial of his publications on bryozoans were the two volumes of the *Catalogue of the fossil Bryozoa (Polyzoa) in the Department of Geology, British Museum (Natural History)*.[21] Following on from three volumes published previously by J.W. Gregory, Lang's Catalogues dealt entirely with Cretaceous cribrimorph cheilostomes and went far beyond a simple listing of individual specimens present in the BM(NH) collection. Instead, they attempted a full monographic treatment of this group of bryozoans and included lengthy discussions of their morphology and evolution. Lang's final paper on bryozoans was published as early as 1925,[22] after which corals and Dorset geology dominated his scientific interests.[23]

In 1929 Lang was elected a Fellow of the Royal Society, but it is evident from the correspondence in his archives at The Natural History Museum (= BM(NH)) that he had been unsuccessfully proposed for election on several previous occasions.[24] He retired in 1938 on his 60th birthday and bade farewell to the BM(NH), never to return during the 28 years that remained of his life. His retirement was spent almost entirely in Charmouth where he was extremely active in various aspects of local natural history. For example, he became an authority on the Victorian fossil collector Mary Anning,[25] and wrote annual reports on natural history for the *Proceedings of the Dorset Natural History and Archaeological Society*. He was clearly held in great esteem as an expert in diverse areas of natural history, not only geology but also botany, entomology, ornithology and marine biology.

3. Orthogenesis

Bowler[26] provides a succinct history and philosophy of orthogenesis on which the brief account below is largely based. The term orthogenesis means 'linear evolution'. It was introduced by Wilhelm Haacke[27] who believed that the 'germ plasm' was structured in such a way that it predisposed variation to occur in particular directions, leading to linear patterns of evolution. The principal popularizer of orthogenesis was Theodor Eimer[28].

Eimer's studies of parallel evolution of colour patterns in butterflies,[29] which he believed had no function, led him to abandon an earlier belief in Lamarckism in favour of orthogenesis, a form of evolution which, in contrast to both Lamarckism and Darwinism, did not necessarily involve adaptation. Eimer went as far as to claim that "Orthogenesis is a universal law".[30]

Whereas Eimer and other biologists derived their evidence for non-adaptive parallel evolutionary trends entirely from living organisms without recourse to the fossil record, palaeontologists entering the fray had the advantage of being able to offer a time dimension to orthogenesis.

According to Gould:[31]

> The theory of orthogenesis became a touchstone for anti-Darwinian paleontologists, for it claimed that evolution proceeded in straight lines that natural selection could not regulate. Certain trends, once started, could not be stopped even if they led to extinction.

A recurrent theme among palaeontologists advocating orthogenesis was that the evolution of lineages ran in close parallel to the ontogeny of individuals: just as an ageing individual develops senile features and dies, so an ageing lineage evolves senile features and becomes extinct.[32] Alpheus Hyatt believed this to be the case for ammonoids, a group in which the appearance of supposedly senile species in the Cretaceous heralded their final extinction.[33] Two popular examples were commonly quoted in the palaeontological literature of orthogenetic evolution culminating in the appearance of morphological characters ultimately fatal to the lineage. The first was the progressive tightening of the coiling in shells of the Jurassic oyster *Gryphaea*, leading to individuals which could scarcely open their shells. The second was the evolution of gigantic antlers in *Megaloceros*, the Giant Irish 'Elk' of the Pleistocene.

Another widely cited instance of orthogenesis, the evolution of the horse, is very different from either *Gryphaea* or *Megaloceros* in that it does not involve the evolution of seemingly maladaptive features. This contrast illustrates just one of the many variations in the way that the term orthogenesis was applied. George Gaylord Simpson[34] remarked that orthogenesis:

> is usually employed not simply as the name of a phenomenon but also as the designation of some theory purporting to explain it.

The distinction made explicit in Simpson's statement is a particularly fundamental one between an evolutionary pattern and an evolutionary process.[35]

Orthogenesis in its various guises was given very serious consideration by palaeontologists during the early years of the 20th Century. Lull,[36] for example, regarded orthogenesis as an evolutionary theory worth entertaining either in opposition to natural selection or supplementary to it. He pointed out several lines of evidence for orthogenesis, particularly the widespread occurrence of parallel evolution, the incidence of 'over-specializations', and the apparent constitutional limitations on variation similar to those found by plant and animal breeders. As to the causes of orthogenesis, Lull noted that predetermination had been explained either by the existence of an intangible and unknown force within the organism or by the laws of organic growth.

Orthogenesis was discarded by most scientists, especially zoologists, as early as 1940. The following passage was written in 1937 by the President of the British Association for the Advancement of Science E.B. Poulton:[37]

> The appeal to Orthogenesis, or internal developmental force, as the motive cause of evolutionary progress has often been made – generally by palaeontologists rather than by observers of living forms. Any such belief in the potency of an internal tendency is, I think, open to the criticism made by Thisleton Dyer in his address to Section D at Bath in 1888: 'This appears to me much as if we explained the movement of a train from London to Bath by attributing to it a tendency to locomotion. Mr. Darwin lifted the whole matter out of the field of mere transcendental speculation by the theory of natural selection, a perfectly intelligible mechanism by which the result might be brought about. Science will always prefer a material *modus operandi* to anything so vague as the action of tendency.'.[38]

Julian Huxley also firmly rejected orthogenesis as a viable evolutionary mode in his classic text *Evolution. The Modern Synthesis*:[39]

> To sum up, the only important agency restricting the direction of evolutionary change is the historical one, leading to a purely apparent orthogenesis.

Criticism of orthogenesis was not confined to neontologists: the vertebrate palaeontologist Simpson[40] even went as far as to claim that:

> A dispassionate survey of many of the phenomena of orthogenesis, so called, strongly suggests that much of the rectilinearity of evolution is a product rather of the tendency of the minds of scientists to move in straight lines than of a tendency for nature to do so.

A late defence of orthogenesis appeared in 1940, written by the invertebrate palaeontologist Arthur E. Trueman.[41] Trueman upheld orthogenesis on the following grounds:

> the term orthogenesis has been so frequently misinterpreted also because at the present time it seems that a somewhat closer comparison between the results achieved by geneticists and the conclusions reached by palaeontologists can be made.
>
> The chief objections which have been made against it resulted from a belief that the term covers

> something mystical and akin to teleology, or that it involves predetermination; but I know of no palaeontologist who has put forward any such views. If they have spoken of an internal factor, an inherent tendency, or of "compulsion from within" (Lang, 1921, p. xviii) they have usually made it clear that some physiological or chemical factor may be involved.

Trueman drew a distinction between three terms that had become intertwined: 'trend', a tendency for parallel evolution to occur; 'orthogenesis', a trend driven by the action of some factor internal to the organism; and 'programme-evolution', a trend which was predetermined.

Despite the pleas of Trueman, orthogenesis had become inextricably linked with notions of predetermination and internal organismic control of evolution ("vitalism") which were totally out of tune with the emerging evolutionary consensus of Neodarwinism. Today, orthogenesis has effectively disappeared from the vocabulary of evolution, save for the occasional historical aside.

4. Orthogenesis and bryozoan evolution: Lang's thesis

As mentioned above, Lang began his research on bryozoans by studying the taxonomy of Mesozoic cyclostomes. His interest in evolution is first evident in 1905 with the publication of a scheme showing the proposed phylogeny of *Stomatopora* during the Early Jurassic.[42] However, Lang's orthogenetic ideas on bryozoan evolution did not emerge in print until 1916 by which time his systematic research had switched from cyclostomes to cribrimorph cheilostomes (Figure 2). The thesis he developed of Cretaceous cribrimorph evolution was complex and entailed the following principal propositions: (1) cribrimorphs evolved from membranimorph ancestors by fusion of marginal mural spines over the frontal membrane to produce a costate frontal shield (or secondary frontal wall); (2) cribrimorphs originated on at least 11 separate occasions from different membranimorph ancestors during the Cretaceous; (3) each distinct cribrimorph 'lineage' followed a trend through time of increasing elaboration and calcification of the zooid, such changes occurring in parallel in the different lineages; (4) these trends led to increasingly maladapted species and culminated in the extinction of the lineage; (5) from their initial appearance, each lineage was programmed to follow this evolutionary trajectory, with environmental change and natural selection playing no more than subsidiary roles; (6) calcium carbonate was secreted by the zooid primarily as a waste product but, through the action of natural selection, it was laid down in sites where it was of most use, or of least harm, to the bryozoan; (7) trends towards ever greater calcification resulted from the progressive removal over geological time of a physiological factor inhibiting calcium carbonate secretion until, finally, calcification occurred without inhibition, the bryozoan zooid was buried beneath its own waste products, and the lineage became extinct.

Lang's 1916 paper *Calcium carbonate and evolution in Polyzoa*[43] first expounded his

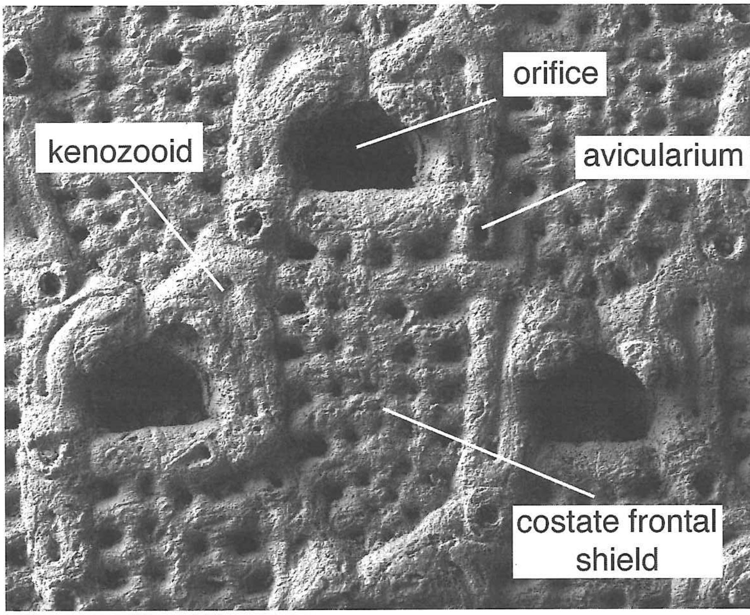

Figure 2. Scanning electron micrograph of a few zooids of the Cretaceous cribrimorph bryozoan Pelmatopora marsupitum *Lang, 1916 from the Campanian Chalk (*pilula *Zone), near Rottingdean Gap, Sussex, England; NHM D41056. The elongate autozooids have a semicircular distal orifice and a frontal shield consisting of costae with lateral fusions and pelmata (pores). Between the autozooids are smaller polymorphs - avicularia and kenozooids ('interoecial secondary tissue' of Lang). Magnification about x60.*

orthogenetic theories. Its starting point was a paper on trepostome bryozoans published the previous year by Cumings and Galloway.[44] This landmark paper on the skeleton of Palaeozoic trepostomes includes the following passage:[45]

> The thickening of the interzooecial walls, due to the development of the cingulum, is often very great … . There is an actual reduction in the size of the zooecial chamber. … We believe that this extreme development of secondary deposits is a senile feature, analogous to the great thickening of brachiopod shells and the shells of Mollusca in old age.

While Cumings and Galloway were concerned with the ontogeny of individual zooids, Lang[46] extended the idea of calcification and senility onto phylogeny and evolutionary time:

> Cumings and Davenport [sic for Galloway] attribute the secondary thickness of the walls to senility of the individual, at least they say it accompanies senility. We claim, further, that it marks the senility of the lineage to which the individual belongs

Lang's willingness to make such an exact analogy between ontogeny and phylogeny must be seen in the light of the widespread acceptance of Haeckel's Biogenic Law by palaeontologists at this time – if the ontogeny of modern organisms accurately recapitulates their phylogeny, is it not reasonable to infer the reciprocal, that phylogeny passes through equivalent stages to ontogeny leading to senility and ultimately to the death (extinction) of the lineage?[47] The notion that the precipitation of calcium carbonate in invertebrates in general evolved as an excretory function that had the unfortunate consequence of dooming the lineage to extinction is explicit in the following quotation:[48]

> Say that some metabolic process, such as one involved in nitrogenous excretion, resulted in the precipitation of calcium carbonate in the tissues or upon the surface of a marine organism - Mollusc, Brachiopod, or Polyzoan, and was turned to useful account as affording a supporting or protecting skeleton or shell; that this production of calcium carbonate became increasingly constitutional so that the mere need for a skeleton or shell was more than met; that the process could not be arrested or countered in all the organisms that had acquired it, and in these the disposal of superfluous calcium carbonate became a pressing problem; that, finally, those organisms that found no way out of the difficulty were doomed to extinction under a mass of calcium carbonate of their own making.

Referring specifically to cheilostome bryozoans, Lang[49] stated:

> The most hopeful of the Cheilostomes are those which have a skeleton of chitin only. When once calcium carbonate has begun to be deposited the whole lineage is doomed to a more or less stereotyped sequence of calcification until, in the end, it becomes extinguished under its superfluity of skeleton. .... The general phylogenetic future of ... 'Cribrimorphs' - can be predicted with certainty, though the details vary in every lineage. Further calcium carbonate is laid down in connection with (1) the spines that form the intraterminal frontal wall - the costae; (2) those that surround the aperture - the 'apertural spines' (considered with the first pair of costae, those which bound the aperture proximally, and, fused, form the 'apertural bar'); and (3) the extraterminal frontal wall, finally filling up the interzooecial spaces; and the process may take place in one or more of these directions simultaneously in any lineage. ... It is inconceivable that Steginomorphs [an advanced, heavily calcified group of cribrimorphs] can have any evolutionary future. In extreme cases they present externally a thick crust of calcium carbonate pierced here and there by holes representing apertures and avicularia, that tend to become smaller and more choked as more calcium carbonate is laid down. So the cingulum of Trepostomes marks the senility of the race, and the Palaeozoic Polyzoa fell victim to the same disease as those Cretaceous forms which, owing to their calcareous skeletons, have been preserved to us to study.

The evolutionary themes explicit here are parallel evolution and the predictable, predetermined evolutionary trajectories followed by the lineages that drove them to extinction.

Lang's first paper on cribrimorph systematics was also published during 1916.[50] Here he remarked that:[51]

> The evolutionary aim in the development of all families appears to be the disposal to the best advantage or least detriment to the organism of superfluous Calcium Carbonate.

Three years later he published a larger work dealing with the systematics and evolution of one particular subfamily, the Pelmatoporinae.[52] Once again, Lang expounded the notion of increasingly uncontrolled formation of a calcium carbonate skeleton in cribrimorph zooids, propelling the lineage towards a self-imposed extinction. At most, natural selection served only to determine the locations where the calcium carbonate was deposited by the zooid, not the fact of its secretion or the quantity produced:[53]

> The evolutionary aim, then, behind the elaboration of the skeleton in the Cretaceous Cribrimorphs is the disposal of an increasing secretion of Calcium Carbonate where it will be least in the way; and it is mainly deposited, independently, in three positions, namely, on the intraterminal frontal wall [=costate frontal shield], so as further to solidify it; around the aperture, so as to build up a secondary aperture; and in the interoecial depressions. To explain the increasing complexity of aperture and intraterminal front-wall thus, is not, however, to deny to the organism any power of elaborating its skeleton to a useful end. It only claims that this secretion is unavoidably there to be disposed of, and, if the organism can employ it usefully, it is by so much the gainer; but sooner or later it will fail to cope with the abundance of its secretion, and the race will perish.

Two further threads in Lang's thesis are mentioned in this paper. The first is his conviction that all of the Cretaceous (including Danian) cribrimorph families became extinct before the end of that period and are in consequence not closely related to extant cribrimorph genera (e.g., *Cribrilina*) which must have evolved independently. The second is that the mural spines present in certain membranimorphs, including the ancestors of cribrimorphs, evolved as a response to the need to secrete calcium carbonate. More primitive, non-spinose membranimorphs fared less well according to Lang:[54]

> The Cribrimorph, then, only puts off the evil day. That it does put it off with some success seems likely when the more primitive Membranimorphs are considered. In a colony of these it is common to find individuals completely sealed up [i.e. with closure plates], with the scar of the aperture showing on the calcareous covering of the oecium. It is probable that this is the only answer that the Membranimorph individual can give to the demands of its deranged metabolism - it simply deposits Calcium Carbonate over its whole surface, building its own tomb, and thus experiencing the final doom of the race. The race, however, saved itself from such a crudely immediate ending by the capacity it acquired for limiting the areas of super-secretion to definite spots along the termen; and thus terminal spines arose, which, by further increase of size and by inter-fusion, form the Cribrimorph intraterminal front-wall.

A second paper published in the same year (1919) dealt with the morphology and evolution of a single subfamily, the Kelestominae.[55] The theme of excessive calcification during cribrimorph evolution is again discussed:

it became a pressing problem in the organism's bionomy where to dispose of its increasing superfluity of calcium carbonate so as least to interfere with its normal functions. There is no evidence that the Polyzoa ever gained control over this derangement of metabolism, or that they ever learned to counter it by resorption; but a good deal to show that these calcareous lineages are doomed to ultimate extinction under their masses of superabundant skeletal tissue.

The first part of the cribrimorph *Catalogue of Cretaceous Bryozoa*[56] afforded Lang the opportunity to explain his thesis of cribrimorph orthogenesis more fully. In order to avoid any misinterpretation, it is worthwhile quoting some of the key passages from Lang's lengthy exposition:

when a Cretaceous [cribrimorph] lineage can be followed to any considerable length, the amount of calcium carbonate in the skeleton becomes so pronounced that, not only does the skeletal structure become secondarily simple by the piling up of calcareous matter, so that further evolution is inconceivable, but the very life-processes of the organism appear to be in danger of obstruction, so constricted and tunnel-like become all the apertures in the skeleton, by which the organism communicates with its environment.[57]

It is usual to consider a calcareous shell as an adaptation for protection. But to regard it (and its chitinous predecessor) as primarily a fortuitous metabolic product, is not to deny the shell a protective function. Rather, it is to emphasise the inevitability of the shell; its subsequent adaptation to protective purposes, though in keeping with organic behaviour, and to be expected from our knowledge of organisms, is yet a secondary production.

Extravagances of growth ... have been referred to as being caused by a loss of equilibrium ... . In Vertebrates, it has been suggested that the original condition of equilibrium is controlled by those substances called hormones, contained in the secretions of the ductless glands, and that hormones act as inhibiting agents limiting the growth that otherwise would continue indefinitely.

environment may provide the first stimulus whereby inhibitions are ultimately removed, and an expression-point reached in the evolution of a lineage.

calcareous matter ... is always piled up according to the same architectural plan - a plan repeated in each lineage

given a Membranimorph with well-developed terminal spines, it may be said with certainty that, either the lineage will go no further than a specialised Membranimorph, or, if it has a further history, the spines will arch over and form a Cribrimorph front-wall ... that this will ... become more and more solidified; that, if further evolution takes place, secondary calcium carbonate will be laid down either in the interoecial valleys, or in connection with the aperture, or in both places simultaneously; finally, if the lineage persists still longer, the areas of the secondary tissue will grow above the level of the intraterminal front-wall, and, spreading laterally, will fuse one with another to form a secondary (really tertiary) front-wall.

Now, while it is conceivable that the environment might so affect an organism as to throw out of gear its normal metabolism, it seems improbable that it should be directly responsible for causing independent groups of lineages of Cheilostome Polyzoa to run through a similar evolutionary history..' Such a phenomenon points rather to a compulsion from within - to a tendency in the ancestral form which becomes actual as its evolution is worked out in the offspring. ... Such predetermined evolution is very like what has been termed Orthogenesis by Eimer, and my friend Dr. F. L. Kitchin has spoken of it as Programme-Evolution.

potentiality .... is the quality inherent in a radical organism whereby all its descendant modifications develop according to a common general plan; its expression is controlled by inhibiting agents, which may ultimately be removed by environmental means; this release is apt to occur periodically, and to result in the realisation or actualising of potentiality pent up and hitherto repressed

Lang's summary states:

An organism, then, is regarded as a synthesis of structure and function, and as possessing tendencies* for structural development
* The question of the origin of these tendencies is not touched upon. But my friend Dr. Kitchin, who agrees with me in recognizing their importance, considers that they are not present *ab initio*, but that they arise as evolution proceeds, and that the environment has a share in their origin.

As for the role of natural selection, Lang made his position clear:

in so far as Natural Selection is present, its action is rather a negative one - insuring that the superfluous calcareous matter shall be laid down where it is least in the organism's way, than that the structure it builds should be directly useful.

By now Lang's detailed and comprehensive research on cribrimorph systematics was complete and he was able to classify Cretaceous species into 11 families: Myagroporidae, Otoporidae, Ctenoporidae, Thoracoporidae, Taractoporidae, Lagynoporidae, Andrioporidae, Calpidoporidae, Disheloporidae, Rhacheoporidae and Pelmatoporidae.[58] These families were largely founded on 'the nature of the secondary intraterminal front-wall, and of the costae which compose it'.[59] According to Lang:

it may be supposed that they have independently evolved from as many Membranimorph stocks. It is also possible that some of the sub-families comprised in a single family really had an independent evolution from Membranimorph ancestors, and, consequently, should be regarded as independent families.

Lang repeated his doubt that post-Cretaceous cribrimorphs were descended from Cretaceous cribrimorphs, all or most of which belong to lineages that became extinct during the Cretaceous:

if the majority of Cretaceous lineages are found to end in forms not only incapable of further evolution, but apparently becoming extinct under the products of their secretory activity, it

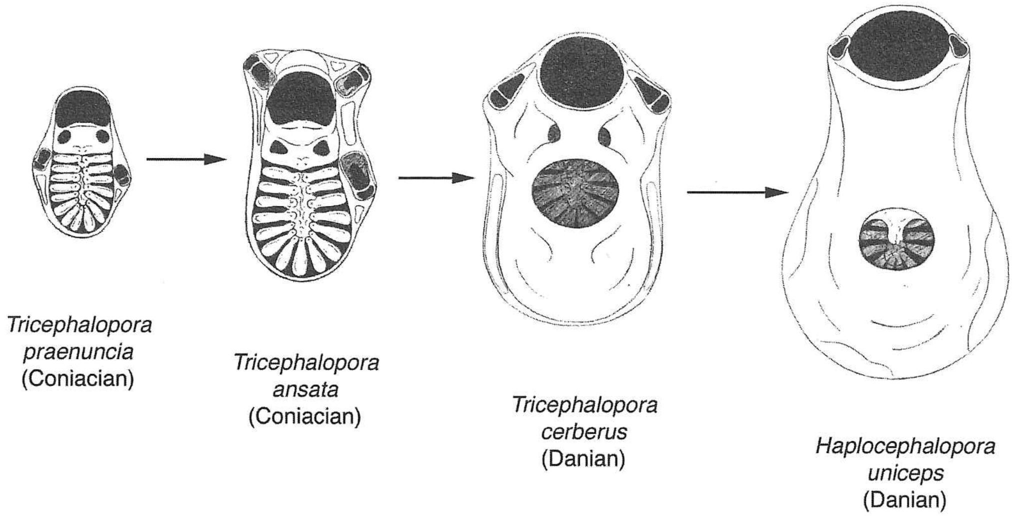

Figure 3. Zooids from four species constituting the central lineage in Lang's evolutionary tree of the Tricephaloporinae.[60] *The two Coniacian species have exposed costate frontal shields. The costate shield is largely overgrown by a tertiary frontal wall in the two Danian species, remaining visible through a small window. Further skeletal elaboration in* Haplocephalopora uniceps *takes the form of a long peristome.*

> follows that few, if any Cretaceous genera persisted into Tertiary times; and that the ancestors of Tertiary and Recent forms must be sought in the chitinous Cretaceous species which have left no remains

The two volumes of Lang's *Catalogue* contain numerous evolutionary trees expressing inferred phylogenetic relationships between species placed in stratigraphical order. Both anagenetic and cladogenetic evolutionary patterns are depicted in these trees, i.e. Cretaceous cribrimorph evolution according to Lang consisted of a mixture of ancestor-descendant transitions without branching of the lineage (chronospeciation), and splitting of the lineage into two (speciation *sensu stricto*). As an example of the evolutionary changes considered to occur in cribrimorphs by Lang, Figure 3 uses Lang's own drawings of four of the six species forming one of his inferred lineages.

Whereas Lang's thesis was devised at a time when orthogenetic theories were very much in vogue, during the next few decades the climate changed from one of widespread acceptance to almost universal refutation of orthogenesis. An early critic was Lang's colleague F.A. Bather who wrote of Lang in 1920:[61]

> He speaks of living matter as if it were the over-pumped inner-tube of a bicycle tyre, 'tense with potentiality, curbed by inhibitions' [of the cover] and 'periodically breaking out as inhibitions are removed' [by broken glass]. A race acquires the lime habit or the drink habit, and, casting

off all restraint, rushes with accelerated velocity down the easy slope to perdition.

A melancholy picture! But is it true? The facts in the case of the Cretaceous Polyzoa are not disputed, but they can be interpreted as a reaction of the organism to the continued abundance of lime-salts in the sea-water. If a race became choked with lime, this perhaps was because it could not keep pace with its environment. Instead of 'irresistible momentum' from within, we may speak of irresistible pressure from without.

Lang ceased publishing on evolution during the 1930s. His later publications and documents demonstrate, however, a continuing scepticism of Neodarwinism.[62] While still maintaining that the fossil record revealed constrained, parallel evolutionary trends, his correspondence shows that he came to regard seeking explanations for these trends as lying outside the realm of science:

To my mind, a Natural Science at most can demonstrate a chain of proximate causes and effects, which is rather a matter of description than explanation. Explanations belong (as I think) to the realm of Metaphysics, and depend upon one's philosophical background and outlook on matters such as the nature of time, and ultimately upon ones religious views. ... I hold that Darwin's theory of Natural Selection is logically bound to be true up to a point; but in any one instance the range of deviation possible to a character may vary from a little to a great deal before the axe of Nat. Selc. Cuts off the straggler; and it needs much much more than his theory to account for the origin of species.[63]

5. Scientific influences on Lang

It seems likely that Lang's orthogenetic theory of cribrimorph evolution originated sometime around 1910 and was quite probably complete by the outbreak of the First World War. There is some evidence in his correspondence and publications of the major influences on his work during this critical time. Among a small number of letters from the American palaeontologist E.R. Cumings of Indiana University is one dated 13th February 1911 which reveals the tide of feeling against Darwinian evolution, especially the Weismann Dogma, as well as the support for the Biogenic Law, and hints at the existence of a schism between biologists and palaeontologists interested in evolution:

I feel now that Hyatt is soon to come into his own, The experimentalists are about to prove the inheritance of acquired characteristics; and, as for the law of acceleration, it is based on such an array of paleontologic facts that it will very easily take care of itself. Beecher used to say that he "hoped Weismann would live to see the error of his ways" — and I guess he has. Zoologists are altogether too prone to neglect the geologic history of organisms. Your results from the Bryozoa are worth tons of Weismannian speculation.

Two letters in 1914 from the Geological Survey palaeontologist F.L. Kitchin (1870-1934), who was working on Jurassic *Gryphaea*, are also significant in that they discuss parallel evolution and orthogenesis in terms of internal predisposition and racial senility:

> The "*Gryphaea*" style of shell must of course represent only a particular evolutionary phase repeated again and again in different ostrean stocks. ... It is clear that this morphic trend - reduction of attached stage *plus* increasing arcuation, prepared for rapid genetic decline; the end result was so often the inordinate thickening and foliaceous growth of degeneracy ... I have some views (good or bad) on limited potentialities and predispositions, on the bringing of these to particular expression by causes apart from adaptive selection or response, and on genetic old-age being reached more as a result of internal than external conditions.[64]

> It is clear that the expression of a predisposition (inherited in common by separate genetic series) to evolve along certain definite lines has often been deferred for a very long time ("latent or potential homology" of Osborn). In other cases there has been some sudden evolutionary efflorescence, as in many ammonite genera, resulting in several or many little separate genetic lines which at once go through the same programme, evolving the successive transformation-stages in certain characters in just the same manner and order (though not necessarily at the same rate), thus, surely, showing the immediate results of the same predisposition bequeathed by the common ancestors.[65]

Lang's supposition that there existed physiological (hormonal) controls on skeletal growth which if removed would lead to excessive and potentially maladaptive growth of the skeleton may have originated from, or was at least reinforced by, a short and speculative paper published by Arthur Dendy in 1912.[66]

Another strong influence on Lang was Sidney S. Buckman, well-known for his meticulously detailed work on Jurassic biostratigraphy, who visited the British Museum (Natural History) during the early part of Lang's career there to work on the brachiopod collections. Lang himself wrote:[67]

> Contact with Buckman was most stimulating. ... Buckman's enthusiastic, though often blind, acceptance of "biogenetic law" as applied to ammonites by Alpheus Hyatt, according as it did, with the work of many palaeontologists at that time, attracted me strongly for its direct appeal to serial change of form. At that time I was very much alive to the implications of "recapitulation", as we palaeontologists generally termed the biogenetic law, and I already saw that the principle could not be applied blindly, as Buckman apparently applied it, but that its expression was continually modified and masked by environmental conditions.

6. A current perspective on Lang's thesis

In a rare critique of Lang's work published during the past 25 years, the evolutionary palaeobiologist Thomas J. M. Schopf concluded:[68]

> In the modern view, Lang's general observation of increasing complexity in calcification, with subsequent extinction of these lineages, is confirmed (Larwood, 1962, 1969). But we would neither interpret this, nor the trends noted by Voigt (1939), as being due to a vital force gone berserk, for which no other evidence has been uncovered in this or any other group of

organisms.

Schopf's dismissal of a vitalistic force driving orthogenetic trends would be supported by all but the most heterodox of modern evolutionary biologists. However, as noted above (p. 281), Lang's thesis was complex and it is worth examining individually each of its seven main propositions:

(1) *Cribrimorphs evolved from membranimorph ancestors by fusion of marginal mural spines over the frontal membrane to produce a calcareous frontal shield (or secondary frontal wall).* Larwood[69] affirmed the origin of cribrimorphs from such an ancestral group, his model showing how initially erect costae in a membranimorph could become prostrate, lie over the frontal membrane as in myagromorphs,[70] and then fuse at their inner, distal ends in cribrimorphs proper (Figure 4). The membranimorph ancestors of cribrimorphs envisaged by both Larwood and Lang[71] would nowadays be regarded as pseudomalacostegans belonging to the 'grade' Family Calloporidae. There is as yet no published rigorous (i.e. quantitative cladistic) analysis of cribrimorph relationships that might support (or refute) a nesting of cribrimorphs within the Calloporidae. Nevertheless, this certainly seems likely to be true on the basis of both morphological and stratigraphical evidence.[72]

(2) *Cribrimorphs originated on at least 11 separate occasions from different membranimorph ancestors during the Cretaceous.* Lang's claim that Cretaceous cribrimorphs evolved polyphyletically has not been evaluated cladistically. However, the fact that these supposedly independent lineages have a considerable number of advanced characters in common suggests that the outcome of a cladistic analysis would be unlikely to support polyphyly. It is revealing that Lang was able to construct a hierarchical key[73] for the identification of his families and subfamilies of Cretaceous cribrimorphs: the fact that the families in this key are nested within as many as four levels gives an indication of how much homoplasy would need to have occurred in order for the families to have been derived independently from non-cribrimorph ancestors.

(3) *Cribrimorph lineages followed parallel trends through time of increasing elaboration and calcification of the zooids.* Once again, the lack of a cladistic analysis hampers adequate testing of this proposition. Larwood's comments[74] on the evolution of individual genera belonging to one subfamily (Pelmatoporinae) suggest that some genera (e.g. *Pelmatopora*) increased in complexity through time, whereas others did the just the opposite (e.g. *Aeolopora*). Nevertheless, heavily calcified cribrimorphs with tertiary frontal walls did not appear until relatively late in the Cretaceous; indeed, they are particularly characteristic of the terminal Maastrichtian stage.[75]

(4) *Evolutionary trends led to increasingly maladapted species and culminated in the extinction of the lineage.* Some of the more advanced cribrimorphs from the Upper

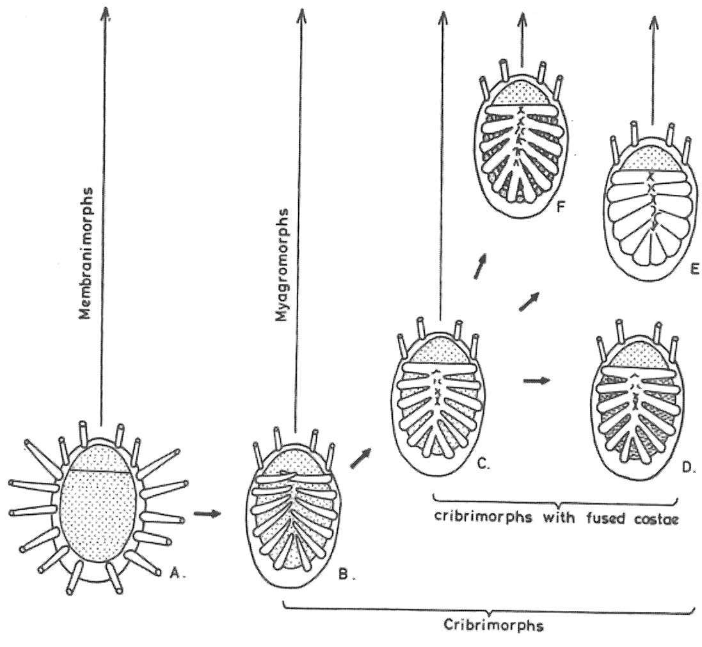

Figure 4. The origin of cribrimorphs from a membranimorph (calloporid) ancestor as envisaged by Larwood.[76]

Cretaceous exhibit 'bizarre' and complex skeletal morphologies which to Lang were of no or doubtful adaptive value. In some cases, particular skeletal structures appeared to impede the normal functioning of the zooid, as in the oral avicularia that almost occlude the orifice in *Ichnopora denticulata*,[77] leaving little space for the protrusion of the tentacle crown. At the time of Lang's research almost nothing was known about predation on bryozoans, but it is now clear that a wide range of small predators attack individual bryozoan zooids,[78] and that structures such as avicularia, spines and thickened frontal shields can be reasonably interpreted as adaptations against such predators.[79] Schopf[80] proposed that the overarching spines forming the frontal shield in cribrimorphs functioned in defence, and it has been suggested that progressive trends towards increased calcification in late Mesozoic bryozoans may have been driven by escalating predation pressure.[81] However, it remains to be demonstrated whether any trends in Cretaceous cribrimorphs are driven and require an explanation, or are simply passive and reflect increasing variance and the inevitable drift of morphology from the left-wall of simplicity.[82]

As Schopf noted, specializations of the type found in the most derived Cretaceous cribrimorphs may have made them particularly vulnerable to environmental changes, likely accounting for some of the many extinctions of Lang's 'senile' lineages. Recent research on the origins of ascophoran cheilostomes by Dennis P. Gordon[83] raises another possibility. Ascophoran cheilostomes, the dominant marine bryozoans at the present day, are a polyphyletic grade grouping that first appeared in the Late Cretaceous. The ancestry of at least some ascophorans undoubtedly lies within the cribrimorphs, with one or more cribrimorph-ascophoran transitions entailing lateral expansion of kenozooids over the costate frontal shield, to form an umbonuloid ascophoran frontal shield, coupled with reduction and eventual loss of the overgrown costate frontal shield. Gordon and Voigt[84] wrote:

> It is ironic that W.D. Lang perceived the so-called interzooecial secondary tissue (i.e., adventitious kenozooecia) as an orthogenetic liability – "Lineages which secrete calcium carbonate are ... doomed lineages" (Lang 1921, p. xxv). Far from heralding 'doomed lineages', the skeletal modifications of late Cretaceous pelmatoporine cribrilinids appear to have been a major innovation ... contributing to one of the greatest flourishings of bryozoan diversity in geological history.

If correct, this view means that one or more of the apparent extinctions of cribrimorph 'lineages' identified by Lang was in reality a taxonomic pseudoextinction, the result of transition from a cribrimorph grade to an ascophoran grade of organization.

(5) *From their initial appearance, each lineage was programmed to follow a particular evolutionary trajectory, with environmental change and natural selection playing no more subsidiary roles.* As noted already, these views are totally out of keeping with current evolutionary orthodoxy.

(6) *Calcium carbonate was secreted by the zooid primarily as a waste product but, through the action of natural selection, it was deposited in sites where it was of most use, or of least harm, to the bryozoan.* Although little is known about the physiology of skeleton formation (biomineralization) in bryozoans, the idea that the skeleton is primarily a waste product is unconvincing. Excretion in living bryozoans is accomplished by cyclical degeneration of the polypide (tentacles and gut) producing a brown body of waste material which is typically disposed of in the faeces of the newly regenerated polypide. There is no reason to suppose that this mechanism could not have been employed in Cretaceous cribrimorphs for the disposal of any excess calcium carbonate as an inert residue together with nitrogenous material and the products of cellular breakdown. Furthermore, bryozoans as a group include a spectrum of species, from those with entirely unmineralized organic skeletons to others with minor amounts of biomineralization to yet others with massively calcified skeletons, all seemingly representing successful survival for at least 450 million years of geological time. Highly calcified skeletons are not a necessary consequence of excretory processes in bryozoans.

(7) *Trends towards ever greater calcification resulted from the progressive removal*

over geological time of a physiological factor inhibiting calcium carbonate secretion until, finally, calcification occurred without inhibition, the bryozoan zooid was buried beneath its own waste products, and the lineage became extinct. Even in the paucity of information about processes of biomineralization in bryozoans, it is evident that bryozoans exert a high degree of control over the formation of their skeletons. This is apparent from the complexity and precision of the skeletons they are capable of building, an observation particularly true of cribrimorphs. At the finest scales, bryozoan skeletons are characterised by ultrastructural fabrics with specific orientations and shapes of calcite or aragonite crystallites.[85] Biomineralization in all studied bryozoans falls within the 'biologically controlled' category of Lowenstam and Weiner,[86] and it is difficult to imagine progressive, initially non-fatal loss of this control as envisaged by Lang.

7. Conclusions

W.D. Lang was an earnest, knowledgeable and philosophical naturalist. His orthogenetic thesis of cribrimorph evolution was a bold attempt to explain the evolutionary patterns he perceived in this group of bryozoans which radiated to a high diversity during the Late Cretaceous. It was devised at a time when natural selection was under attack, especially from palaeontologists, many of whom favoured orthogenesis as an alternative. In Lang's case it is unclear to what extent his strong religious beliefs led him to reject natural selection, with its large component of chance, and to opt for orthogenesis, which may have been more palatable to him, especially in its more extreme variant with factors internal to the organism powering predetermined evolutionary trends. Later in his life, however, Lang came to believe that seeking explanations for evolution fell within the remit of metaphysics rather than science.

A comprehensive evaluation of Lang's orthogenetic theories of Cretaceous cribrimorph evolution cannot be undertaken until a phylogenetic framework has been established through restudy of cribrimorph morphology[87] coupled with cladistic analysis. For the most part, the processes proposed by Lang have no place in modern evolutionary theory but would be difficult to falsify conclusively. However, the evolutionary patterns he inferred are both testable and worthy of future study. Such research would be of specific importance in clarifying the origin of ascophoran cheilostomes, and of more general interest in understanding evolutionary trends and the evolution of complexity.

8. Acknowledgements

I am grateful to Dennis Gordon, Andrew Smith, Phil Palmer, David Lewis and Mark Wilson for their critical readings of the manuscript.

Notes

1 P.J. Bowler, *The Eclipse of Darwinism* (Baltimore and London, 1983).
2 Arthur Trueman provided a rare exception, describing Lang's work as stimulating and brilliant. A.E. Trueman, 'The meaning of orthogenesis', *Transactions of the Geological Society of Glasgow*, 20 (1940), 77-95.
3 H.H. Swinnerton, *Outlines of Palaeontology* (Edward Arnold, 1947).
4 For example, K.J. McNamara (editor), *Evolutionary Trends* (Tucson, 1990); S.J. Gould, *Life's Grandeur* (London, 1996); D.W. McShea, 'Metazoan complexity and evolution: is there a trend?' *Evolution*, 50 (1996), 477-492; J. Alroy, 'Understanding the dynamics of trends within evolving lineages', *Paleobiology*, 26 (2000), 319-329.
5 Lang's correspondence files are archived in the Earth Sciences Library at the NHM, London.
6 E.I. White, 'William Dickson Lang', *Biographical Memoirs of Fellows of the Royal Society*, 12 (1966), 366-386. Two other biographies, both untitled, of Lang are known: H.D.T. [Henry Dighton Thomas], *Proceedings of the Geological Society of London*, 1636 (1967), 202-203; M.A.A., *Proceedings of the Geologists' Association*, 78 (1967): 387-389.
7 Lang himself was a staunch Christian, see W.D. Lang, 'Human Origin and Christian Doctrine', Nature, 136 (1935), 168-170.
8 M.K. Howarth, personal communication, May 2001.
9 A copy of a letter written by Lang to fellow Harrovian Sir Reginald Spence in September 1960 in the Lang correspondence archive at the NHM notes that 'In 1897 a visiting Master arrived to teach Biology as a "special subject" for 2 hours a week. Being a born Naturalist, I took to biology as to no normal school subject, ..".
10 C.P. Palmer, 'William Dickson Lang: his Liassic work appraised', *Proceedings of the Dorset Natural History and Archaeological Society*, in press.
11 Lang's retirement house in Charmouth was appropriately called 'Lias Lea'.
12 White, note 6, p. 374.
13 H. Woods, *Palaeontology Invertebrate* (Cambridge, 1893).
14 Lang, for example, criticized Bather's philosophy of how fossils should be exhibited to the public. W.D. Lang, 'Palaeontology and the public: a curator's aspirations.', *Proceedings of the Geologists' Association* 41 (1930), 175-179.
15 F.A. Bather, 'Fossils and life', *Report of the British Association for the Advancement of Science*, 88th Meeting (1920), 61-86.
16 W. T. Stearn, *The Natural History Museum at South Kensington*, p. 240 (London, 1981)
17 Lang was unfit to serve in the armed forces during the First World War and instead undertook war work which led to an entomological publication, *A handbook of British mosquitoes* (London, 1920).
18 G.F. Elliott, personal communication, *c.* 1980.
19 W.D. Lang, 'The Jurassic forms of the 'genera' *Stomatopora* and *Proboscina*', *Geological Magazine*, Decade 5, 2 (1904), 315-322.
20 Lang followed the practice then prevailing and included the Danian within the Cretaceous whereas it is now recognized as the first stage of the succeeding Paleocene. Some of the families which Lang regarded as becoming extinct during the Cretaceous can therefore now be seen to have survived into the Tertiary.
21 W.D. Lang, *Catalogue of the fossil Bryozoa (Polyzoa) in the Department of Geology, British Museum (Natural History). The Cretaceous Bryozoa (Polyzoa). Volume III. The cribrimorphs.*

– *Part I.* (London, 1921); *Catalogue of the fossil Bryozoa (Polyzoa) in the Department of Geology, British Museum (Natural History). The Cretaceous Bryozoa (Polyzoa). Volume IV. The cribrimorphs. – Part II.* (London, 1922).

22 W.D. Lang, 'Polyzoa' in L.R. Cox, 'The fauna of the basal shell-bed of the Portland Stone, Isle of Portland', *Proceedings of the Dorset Field Club*, 46 (1925), 52-55.

23 Lang summarised his approach to palaeontology in a short *Nature* 'birthday' article from which the following passage is taken: 'Palaeontological investigation, therefore, should I think, be carried out along the lines of bed-by-bed collecting; of tracing lineages; of noting growth-stages; and of observing trends and the evolutionary history of individual characters; and, whether investigating Palaeozoic corals, Cretaceous Polyzoa, or the faunal succession of the Dorset Lias, I have followed, and continue to be guided by, these methods of research.' W.D. Lang, *Nature*, 128 (1931), 1085.

24 For example, a congratulatory letter from W.B.R. King dated 23 February 1929 remarks 'Better late than never.'

25 See C. Tickell, *Mary Anning of Lyme Regis* (Lyme Regis, 1996).

26 Bowler, note 1.

27 W. Haacke, *Gestaltung und Vererbung: Ein Entwickelungsmechanik der Organismisen* (Leipzig, 1893)

28 G.H.T. Eimer, *On Orthogenesis and the impotence of Natural Selection in Species-Formation* (Chicago, 1898).

29 Lang discussed Eimer's butterfly work as an example of orthogenesis but, perhaps surprisingly, sought to explain the evolutionary trends postulated in these butterflies by Eimer as resulting from Natural Selection. W.D. Lang, 'Evolution: a resultant.', *Proceedings of the Geologists' Association*, 34 (1923), 7-20.

30 G.H.T. Eimer, *On Orthogenesis and the impotence of Natural Selection in Species-Formation* (Chicago, 1898), 21.

31 S.J. Gould, *Ever since Darwin* (New York, 1977), 84.

32 This idea bears an obvious relationship to the 'Biogenic Law' which states that ontogeny recapitulates phylogeny, and results from the tendency for evolutionary novelties to be added to the terminal developmental stages of individuals; here, however, phylogeny is considered to progress through stages paralleling those seen in ontogeny (e.g., youth, senility and death/ extinction).

33 According to Lang himself (1919, 61): 'A large part of the evolution of Jurassic and Cretaceous Ammonites is concerned with their catagenesis or decline.' This decline is manifested by the appearance of such features as uncoiling, sutural simplification, and a reversion to unornamented shells. W.D. Lang, 'The evolution of ammonites. A demonstration given at the British Museum (Natural History)', *Proceedings of the Geologists' Association* 30 (1919), 49-65.

34 G.G. Simpson, *Tempo and Mode in Evolution* (New York, 1944).

35 Plate (1913) coined the term 'orthevolution' to describe the evolutionary pattern of linear (or rectilinear) trends, and used the terms 'orthoselection' and 'orthogenesis' respectively for what might now be seen as Darwinian and non-Darwinian evolutionary processes. Confusion between pattern and process is also evident in two other terms - rectilinear evolution and programme-evolution – which were used as alternatives to orthogenesis, the former applying to a pattern and the latter to a process. L. Plate, *Selektionsprinzip und Probleme der Artbildung* (Leipzig, 1913).

36 R.S. Lull, *Organic Evolution* (Revised edition, New York, 1929).

37 E.B. Poulton, 'The history of evolutionary thought as recorded in meetings of the British Association', *British Association for the Advancement of Science, Nottingham*, 1937, 17-18.

38 Lang's response to Poulton was published the following year: '..the doctrine of trends (and this is where it has been misunderstood) does not explain; it describes: it is not a matter of speculation, but of observation. I suppose that, whatever Eimer exactly meant by Orthogenesis, he would have included the phenomenon of Trends under that term; yet Sir Edward Poulton, in his Presidential Address to the British Association last September, opposed Orthogenesis both to Darwinism and, by inference, to Lamarckism. .... [a trend] is only relevant to Darwinism in what it takes as given, namely, limited variation in definite directions, instead of unlimited variation in all directions.' W.D. Lang, 'Some further considerations on trends in corals', *Proceedings of the Geologists' Association*, 49 (1938), 149.

39 J. Huxley, *Evolution. The Modern Synthesis* (London, 1942).

40 Simpson, note 34, p. 164.

41 Trueman, note 2.

42 W.D. Lang, '*Stomatopora antiqua*, Haime, and its related Liassic forms', *Geological Magazine*, New Series, Decade 5, 2 (1905), 258-268.

43 W.D. Lang, 'Calcium carbonate and evolution in Polyzoa', *Geological Magazine*, Decade 6, 3 (1916), 73-77.

44 E.R. Cumings and J.J. Galloway, 'Studies of the morphology and histology of the Trepostomata or monticuliporoids', *Bulletin of the Geological Society of America*, 26 (1915), 349-374.

45 Cumings and Galloway, note 44, p. 362.

46 Lang, note 43, p. 75.

47 This idea can be traced back to Alpheus Hyatt. According to Gould "Hyatt believed that the sequence of new stages added to a lineage during the course of phylogeny runs parallel to the stages of an individual's ontogeny." S.J. Gould, *Ontogeny and Phylogeny* (Cambridge, Massachusetts, 1977), 93.

48 Lang, note 43, p. 75.

49 Lang, note 43, pp. 76-77.

50 W.D. Lang, 'A revision of the "cribrimorph" Cretaceous Polyzoa', *Annals and Magazine of Natural History*, Series 8, 18 (1916), 81-112.

51 Lang, note 50, p. 82.

52 W.D. Lang, 'The Pelmatoporinae, an essay on the evolution of a group of Cretaceous Polyzoa.' *Philosophical Transactions of the Royal Society of London*, Series B, 209 (1919), 191-228.

53 Lang, note 52, pp. 195-196.

54 Lang, note 52, p. 196.

55 W.D. Lang, 'The Kelostominae', *Quaterly Journal of the Geological Society of London*, 74 (1919), 204-220.

56 W.D. Lang, *Catalogue of the fossil Bryozoa (Polyzoa) in the Department of Geology, British Museum (Natural History). The Cretaceous Bryozoa (Polyzoa). Volume III. The cribrimorphs. – Part I.* (London, 1921);

57 Lang here added a cautionary footnote : 'It is true that not many lineages can be followed to such an extreme development. But it could hardly be otherwise with the fragmentary phylogenies at our disposal. What is significant is that when term links with term into a lineage, progress is *in that direction.*'

58 In the Discussion at the end of Lang's paper on the Kelestominae, Sidney F. Harmer, the leading British authority on Recent bryozoans at the time and a former teacher and now colleague of

Lang at the BM(NH), questioned the large number of families and subfamilies erected by Lang, believing that most could be accommodated within the extant family Cribrilindae. W.D. Lang (note 55), 219.

59 Harmer, note 58, p. xxxviii.

60 W.D. Lang, *Catalogue of the fossil Bryozoa (Polyzoa) in the Department of Geology, British Museum (Natural History). The Cretaceous Bryozoa (Polyzoa). Volume IV. The cribrimorphs. – Part II.* (London, 1922).

61 F.A. Bather (note 14), 78-79. Also highly critical of Lang's theories was R.M. Brydone who had first hand experience of Cretaceous cribrimorphs; R.M. Brydone, *Further notes on new or imperfectly known Chalk Polyzoa* (London, 1929).

62 'I sometimes wonder whether the gene is made to carry more burdens than it can reasonably bear'. Brydone, note 61, p. 377.

63 W.D. Lang, draft of a letter written to A. Arber, 23rd August 1945.

64 F.L. Kitchin, letter to W.D. Lang dated 3rd March 1914.

65 F.L. Kitchin, letter to W.D. Lang dated 6th March 1914.

66 A. Dendy, 'Momentum in evolution', *Report of the 80th Meeting of the British Association, Portsmouth 1911* (1912), 277-280.

67 W.D. Lang unpublished autobiography quoted at length by E.I. White (note 6).

68 T.J.M. Schopf, 'Patterns and themes of evolution among the Bryozoa', in *Patterns of Evolution*, edited by A. Hallam (Amsterdam, 1977), 159-207.

69 G.P. Larwood, 'Frontal calcification and its function in some Cretaceous and Recent cribrimorph and other cheilostome Bryozoa', *Bulletin of the British Museum (Natural History)*, (Zoology Series), 18 (1969), 171-182.

70 Further discussion of myagromorphs can be found in G.P. Larwood, 'Form and evolution of Cretaceous myagromorph Bryozoa', in *Bryozoa: Ordovician to Recent*, edited by C. Nielsen and G.P. Larwood (Fredensborg, 1985), 169-174. A further stage in the origin of cribrimorphs, not discussed by Lang or Larwood, is the loss of articulation at the spine bases.

71 e.g., Lang, note 56, pp. xxxvi-xxxviii.

72 D.P. Gordon, 'Towards a phylogeny of cheilostomes – morphological models of frontal wall/shield evolution', in *Proceedings of the 11th International Bryozoology Association Conference*, edited by A. Herrera Cubilla and J.B.C. Jackson (Balboa, Republic of Panama, 2000), 17-37.

73 Lang, note 56, pp. 4-6.

74 G.P. Larwood, 'The morphology and systematics of some Cretaceous cribrimorph Polyzoa (Pelmatoporinae)', *Bulletin of the British Museum (Natural History)*, (Geology Series), 6 (1962), 1-285.

75 G.P. Larwood, 'Colonial integration in Cretaceous cribrimorph Bryozoa', in *Advances in Bryozoology,* edited by G.P. Larwood and M.B. Abbott (London, 1979), 503-520. E. Voigt, 'The Bryozoa of the Cretaceous-Tertiary boundary', in *Bryozoa: Ordovician to Recent*, edited by C. Nielsen and G.P. Larwood (Fredensborg, 1985), 329-342.

76 Larwood, note 69, figure 1.

77 Larwood, note 76, text-figure 7c.

78 J.S.Ryland, 'Physiology and ecology of marine bryozoans', *Advances in Marine Biology*, 14 (1976), 285-443.

79 See discussion and references in P.D.Taylor, 'Bryozoans', in *Functional morphology of the invertebrate skeleton*, edited by E. Savazzi (Chichester, 1999), 623-646.

80 Schopf, note 68, pp. 188-189.

81 G.P. Larwood and P.D. Taylor, 'Mesozoic bryozoan evolution: response to increasing predation pressure?, in *Recent and Fossil Bryozoa*, edited by G.P. Larwood and C. Nielsen (Fredensborg, 1981), 312-313. F.K. McKinney and J.B.C. Jackson, *Bryozoan Evolution.* (Boston, 1989).

82 D.W. McShea, 'Mechanisms of large-scale evolutionary trends', *Evolution*, 48 (1994), 1747-1763.

83 D.P. Gordon and E. Voigt, 'The kenozooidal origin of the ascophorine hypostegal coelom and associated frontal shield', in *Bryozoans in Space and Time*, edited by D.P. Gordon, A.M. Smith and J. Grant-Mackie (Wellington, 1996), 89-107. D.P. Gordon, 'Towards a phylogeny of cheilostomes – morphological models of frontal wall/shield evolution', in *Proceedings of the 11th International Bryozoology Association Conference*, edited by A. Herrera Cubilla and J.B.C. Jackson (Balboa, Republic of Panama, 2000), 17-37. Note that defining an ascophoran cheilostome is not straightforward; at least some Cretaceous 'cribrimorphs' probably had proximal outpocketings of the frontal membrane forming a functional ascus, conventionally treated as the defining character of an ascophoran (D.P. Gordon, personal communication, June 2001).

84 Gordon and Voigt, note 83, p. 105.

85 e.g. M.J. Weedon and P.D. Taylor, 'Skeletal ultrastructure in primitive cheilostome bryozoans', in *Proceedings of the 11th International Bryozoology Association Conference*, edited by A. Herrera Cubilla and J.B.C. Jackson (Balboa Republic of Panama, 2000), 400-411.

86 H.A. Lowenstam and S. Weiner, *On Biomineralization* (Oxford, 1989).

87 This was begun but not completed by G.P. Larwood (note 75).