PAP. & PROC. ROY. SOC. TASMANIA, 1948 (15TH SEPTEMBER, 1949)

Neonatal Length as a Linear Function of Adult Length in Cetacea

By

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(Read 2nd November, 1948)

FIGS 1-3

In the course of a study of body-form in the False Killer Whale, *Pseudorca crassidens* (Owen, 1846), it appeared expedient to attempt to estimate the length of the neonatus by the indirect method of comparison with the neonatal-adult ratio of length in other Cetacea. A cursory survey of the literature shows the length of the newly born young is said to vary in different species from about twenty to about fifty per cent of that of the adult animal. Among the Mystacoceti, at any rate in the case of the larger, commercially more important species, the mean lengths of calf and adult are known with a fair measure of precision; and it is usually stated (*e.g.*, Pearson, 1936) that in this suborder length at birth is 25-30 per cent of the maximum length. Among a number of the Odontoceti, our knowledge of which in this respect is less extensive and less reliable, these percentages are known at times to be considerably exceeded. There does not appear to be, however, at least in literature available to the writer, any account of a systematic attempt to seek a generalised expression of a possible correlation between the two magnitudes in a group of species. Investigations made in connexion with the special problem noted above soon disclosed the probable existence, among a small series of delphinids, of a significant linear regression of natal length upon adult length; and further consideration has led to the interesting suggestion that the relation may well have a broad (quite possibly an order-wide) applicability.

The purposes of the present paper are, first, to determine, on the basis of what appear to be the best available data for ten species of whales, the regression equation of length of neonatus on length of adult, and, secondly, to examine some of the biological implications of the relationship so formulated. Species dealt with are the Common Porpoise, *Phocaena phocaena* Linné, 1758; Common Dolphin, *Delphinus delphis* (Linné, 1758); White-beaked Dolphin, *Lagenorhynchus albirostris* (Gray, 1846); Bottle-nosed Dolphin, *Tursiops truncatus* (Montagu, 1815); Sperm Whale, *Physeter catodon* Linné, 1758; Humpback Whale, *Megaptera nodosa* (Bonnaterre, 1789); Piked Whale or Lesser Rorqual, *Balaenoptera acutorostrata* Lacépède, 1804; Sei Whale or Rudolphi's Rorqual, *Balaenoptera borealis* (Lesson, 1828); Fin Whale or Common Rorqual, *Balaenoptera physalus* (Linné, 1758); Blue Whale or Sibbald's Rorqual, *Balaenoptera musculus* (Linné, 1758).

1. Equation of Regression of Neonatal Length, ${}_{p}L_{t}$, on Adult Length, ${}_{a}L_{t}$

(a) Sources of Data. An eclectic survey of accessible information on length at birth, ${}_{p}L_{t}$, and adult length, ${}_{a}L_{t}$, in the ten selected species yields the entries in the first two numerical columns of Table I. For the first four species listed the values adopted are those given by conjectural growth curves (unpublished), arrived at by an analysis of the valuable records of British strandings by Harmer (1927): estimates for the remaining six species are based chiefly on dimensions recorded by Matthews (1937, 1938*a*, 1938*b*), Laurie (1937), Pearson (1936), Wheeler (1930, 1934), Mackintosh and Wheeler (1929), Harmer (1927, 1929), Lillie (1915), Beddard (1900), Gray (1866).

(b) Regression Equation. On being graphed the ten variates fall approximately along a straight line (Fig. 1); for which, with dimensions in centimetres, the best fit is

$$ {}_{p}L_{t} = 0{\cdot}2441\ {}_{a}L_{t} + 44{\cdot}3 \qquad (1) $$

Values of natal length computed from this equation are entered in the third numerical column of the table. It will be seen the fit is very close, divergences ranging from 0·3 to 20·0 (mean 8·8) cm., or from 0·2 to 8·9 (mean 3·2) per cent. A test of the significance of the regression coefficient gives $t = 55{\cdot}13$: the correlation coefficient is $r = +\ 0{\cdot}999$, or $z = +\ 3{\cdot}60$.

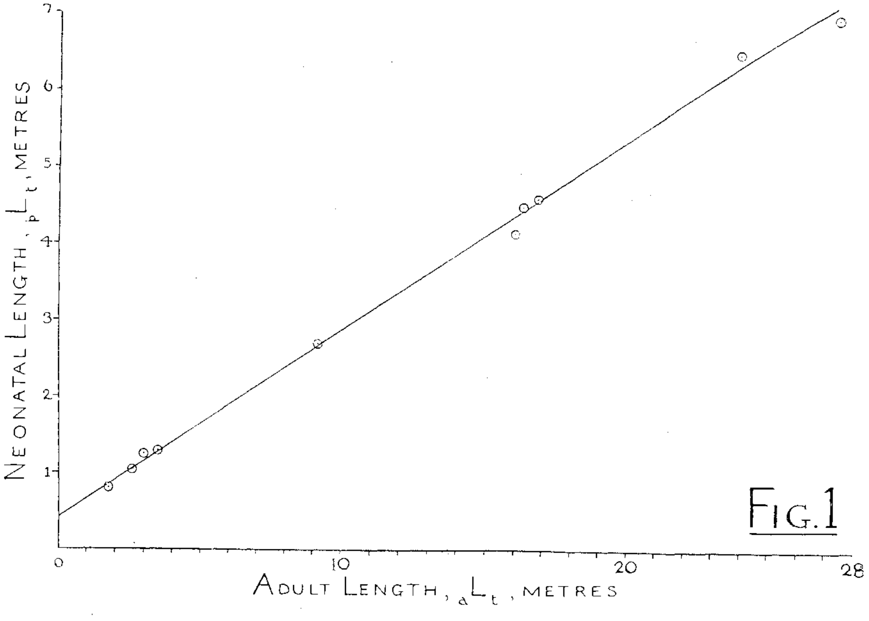

FIG. 1.—Regression of neonatal length on adult length in ten species of whales.

(c) Degree of Reliability, and Statistical Nature, of Equation. In the present imperfect state of our knowledge, the selection of the data for analysis necessarily involves a subjective element; and the high value of t obtained would seem to suggest the danger of bias towards the choice of estimates of a 'favourable' size may perhaps not have been wholly avoided. Even with all necessary allowances

made, however, there can be little doubt there subsists, at least among the species examined, a good measure of correlation: further, it seems highly probable the constants of the function as determined are of the right order of magnitude.

An indication of the extent of the swinging effect exerted by the maximum variate, whose extreme position lends it much weight, is afforded by the fact that, with adult length for the Blue Whale set at 2700 (all other variates remaining unchanged), the equation of the best straight line becomes

$$L_{pt} = 0{\cdot}2467 \, L_{at} + 42{\cdot}3 \qquad (2)$$

With this equation the discrepancies between assigned and calculated values of natal length are 1·3-22·1, mean 7·5, cm., or 0·7-6·9, mean 2·8, per cent; $t = 85{\cdot}36$.

With adult Blue Whale length at 2600 (which seems low), but other variates unchanged, the equation becomes

$$L_{pt} = 0{\cdot}2512 \, L_{at} + 39{\cdot}9 \qquad (3)$$

Discrepancies here are 0·2-26·9, mean 6·0, cm., or 0·1-7·8, mean 2·3, per cent.

For purposes of discussion equation (1) is throughout accepted as definitive.

The relationship as formulated in the regression has, of course, purely a statistical validity. Notable differences in adult size between male and female are familiar in many species: to what extent, if any, sexual size-differences characterise neonatal animals is uncertain (the onset of linear differentiation is set between weaning and sexual maturity in Blue and Fin Whales by Mackintosh and Wheeler (1929), and in the Humpback Whale and the Sei Whale by Matthews (1937, 1938*b*); and at sexual maturity in the Sperm Whale by Matthews (1938*a*): there is, however, some evidence to suggest that some at least of these estimates, which involve a period of from 8 to 15 months after birth, postdate the event). The convention has here been followed of taking as the definitive adult length an estimate of the maximum length generally (not uniquely, or exceptionally) attained, regardless of sex (males are characteristically larger in toothed, females in whalebone, whales). As an indication of the known or estimated extent of individual variation in foetal or young animals, four sets of data may be cited: *(i)* for 3, 2, 2, sets of twin foetuses of Humpback, Sperm, Sei Whales, respectively, included in the British Museum statistics quoted by Matthews, the coefficient of variability, V, is 2·89, 2·81, 39·88; 3·50, 13·29; 0·00, 0·00: *(ii)* records exist for most species of foetal lengths in excess of calf lengths, an extreme case occurring in the Common Porpoise (modal neonatal length *c.* 800 mm.; calves of 711, 500 mm. known): *(iii)* the specimens that appear to constitute the youngest year-class (estimated age 0-4 months) of Harmer's material of the Common Porpoise have $V = 5{\cdot}79$: *(iv)* the extensive *Discovery* data on Blue and Fin Whales, as here interpreted, give for animals of an estimated age of 4-17 months: Blue Whale, male (33 specimens), $V = 5{\cdot}45$, female (38), $V = 6{\cdot}75$, sexes pooled, $V = 6{\cdot}12$; Fin Whale, male (83), $V = 7{\cdot}48$, female (61), $V = 6{\cdot}63$, sexes pooled, $V = 7{\cdot}10$. Examples of estimates of variability in conjectural year-classes in older animals are: Common Porpoise, Common Dolphin, Bottle-nosed Dolphin, oldest (unsexed) year-classes (other than those consisting of a single individual), according to the present interpretation of Harmer's records, $V = 2{\cdot}45$, 3·07, 1·36, respectively; Pilot Whale, assumed age about 5 years, male (6 specimens), $V = 2{\cdot}75$, female (5), $V = 3{\cdot}72$ (Scott, 1942).

It is not improbable that in a given species the length of the calf is, statistically, a function of the length of the individual mother—*i.e.*, the present regression probably possesses (as is known to be the case with certain size-relationships in other forms) an intraspecific, as well as an interspecific, validity.

A point of some interest is the manner in which the regression cuts so decisively across taxonomic boundaries, even that of subordinal rank. Work by Thompson (1942) and by the authors whose researches he reviews has shown, indeed, that, in various groups of animals, quite a number of characters generally considered to represent qualitative and 'inherent' specific or generic differences, and hence, at least by tacit assumption, to be the visible manifestations of phylogenetic diversity, are actually simple functions of absolute magnitude. Morphological specificity is thus seen, in these cases, to reside, less in the individual specificity of the members of a constellation of form-genes, than in a single size-gene or an integrated polygenic magnitude-system. Preliminary investigations suggest that, among whales, such standard taxonomic characters as length of flipper and length to dorsal fin are, to a first approximation at least (due allowance being made for occasional wide divergences apparently interpretable as instances of marked specialisation) simple functions of length of animal.

(d) Minimum Length of Calf and of Adult. It will be observed that the relationship, as formulated, states that, as a limiting case, an adult length of 0 cm. is associated with a calf length of 44·3 cm., or a calf length of 0 cm. is associated with an adult length of −182 cm.; or, again, that for an adult length of 59 cm., or less, the length of the calf exceeds the length of the adult—propositions that are clearly biological fictions. The general paradox that thus arises is pragmatically disposed of by the denial of biological validity to the relation outside those limits of size that are actually encountered in nature: the matter is, however, worthy of being a subject of inquiry, and some aspects of it are discussed in the second section of the paper. At the moment, we need concern ourselves only with the lower limit of actual size. The biological zero on the abscissa is then represented, not by the mathematical zero, but by the minimum adult length that occurs (or, perhaps, could occur) among the Cetacea. Lesson (1826) speaks of a dolphin about 2 feet long, his *Delphinus minimus*, one of the species that 'have been named and figured by the sight caught of them when swimming!'(1) Present-day opinion puts the minimum length in the neighbourhood of 4-5 feet, or, say, 120-150 cm. Such an adult minimum would be associated, according to equation (1), with an initial minimum of 74-81 cm.: that neonatal whales of lesser length than this do, however, occur, even if only as occasional specimens of exceptionally small size, is shown by the record of Van Deinse (*cf.* Harmer, 1919), already cited, of an example of *Phocaena phocaena* Linné only 50 cm. long.

In the right-hand column of Table I the predicted length of the newly born calf is shown as a percentage of the assumed adult length: for the species considered (and the range in size is virtually that of the whole order) it varies from 26·0 to 49·7. Hence natal length ranges from about one-quarter to about one-half of full adult length; and as sexual maturity commonly considerably antedates full physical maturity, it may be expected that, in some of the smaller forms, the neonatal animal may at times be more than half as long as its parent. Among the shorter species the ratio of initial to final length will increase rapidly in value with decreasing size of parent: with adult length, in cm., of 180, 160, 140, 120, for instance, the percentage length of calf, as given by the formula, is 49, 52, 56, 61, respectively.

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(1) The remark of Gray (1866, p. 267) here quoted, together with his exclamation mark, provides, incidentally, an oblique comment on the history of a species, *Lagenorhynchus wilsoni* Lillie, named as recently as 1915: *cf.* Lillie (1915, p. 123), Wilson (1907, p. 9, fig. 7).

2. Some Possible Biological Implications of Equation (1)

(a) General Observations. In the last section it has been noted that the relationship between neonatal length and adult length formulated in equation (1) involves, as a limiting case, an association of a calf length of 44·3 cm. with an adult length of 0 cm., or an association of an adult length of —182 cm. with a calf length of 0 cm., or, again, at an adult length of 59 cm., and below, an excess of natal over adult length. In cases of this kind it is conventional to observe that a formal extrapolation beyond the 'domain of definition', that is to say, beyond, in the present instance, the limiting values of the relevant variables as biologically valid and objective magnitudes, must result, not unnaturally, in quantitative statements that are, by biological criteria, meaningless, anomalous, or erroneous; and to let the matter rest there. It may not prove wholly unprofitable, however, to step for a few moments into, or at least to stand at the frontier of, the realm of free speculation, and to inquire briefly into the possible significance of the constants of the equation. While the relevant mathematical specifications and corollaries are, indeed, evident on inspection, certain biological implications that may tend to be overlooked will repay investigation. Our formal analysis leads us, we find, in the event, first, into the field Haecker (1925) has termed phenogenetics, the study of ontogenesis to determine the stage of development at which the difference between types first becomes manifest; secondly, to aetiology in the Thompsonian sense of a sub-science of the causes operative in both ontogeny and phylogeny; thirdly, at least by implication, to the borders of a region, apparently as yet unnamed, that may be descriptively termed 'extra-somatic morphology'.

(b) Composite Lengths: Mathematical and Conceptual Bracketing. With, as before, L signifying length, the presuffixes a and p denoting adult and prenatal, and the postsuffix t meaning total, we rewrite equation (1) with two significant figures

$$ {}_{p}L_{t} = 0{\cdot}24 \; {}_{a}L_{t} + 44 \qquad (4) $$

Let 0·24 (gradient of the regression line) $= m$; let 44 (intercept on the x-axis) $= c$; let 182 (intercept on the y-axis) $= d$ (Fig. 2A). Then

$$ {}_{p}L_{t} = m \; {}_{a}L_{t} + c \qquad (5) $$

and, rearranging terms,

$$ {}_{p}L_{t} - c = m \; {}_{a}L_{t} \qquad (6) $$

and

$$ {}_{p}L_{t} = m \, ({}_{a}L_{t} + d) \qquad (7) $$

Since the quantities are finite, and the appropriate conventions are observed, this routine algebraic manipulation is, in itself, unobjectionable. Let us now, however, take an additional step, and assume, for the moment, the legitimacy of bracketing, not only the numerical values, but also the biological concepts with which the dimensions may be associated. Thus, the dimension length of calf at birth, ${}_{p}L_{t}$, can be divided into the two components c and $({}_{p}L_{t} - c)$: it is postulated that the concept of length of calf at birth is susceptible of being regarded, for biological purposes, as a composite concept, divisible into two elements, first, a concept of some recognisable kind of calf length (as yet biologically unspecified) legitimately associated with the length-component c, and, secondly, a comparable concept, the correlate of the length-component $({}_{p}L_{t} - c)$. Similarly, the sum of ${}_{a}L_{t}$, the ordinary adult length, and d, the abscissal intercept, is treated, both numerically and conceptually, as a composite length.

It is desirable to have some sematic convention for indicating in which of two senses a reference to a dimension is to be taken. In the notation adopted the symbol of a dimension considered *per se* includes a literal postsubscript written without a dash: to the postsubscript letter of a dimension that is to be thought of in the context primarily as a composite length, or as a component of a composite length, a dash is added. A dashed postsubscript will often point to a concept, an undashed usually to a numerical value. The several lengths, original and composite, with their subdivisions and components are defined ostentively in Fig. 2. In view, however, of the lack of parallelism in structure between adult and neonatal composite lengths, it may perhaps be expedient to set out the specifications formally, as in the next paragraph.

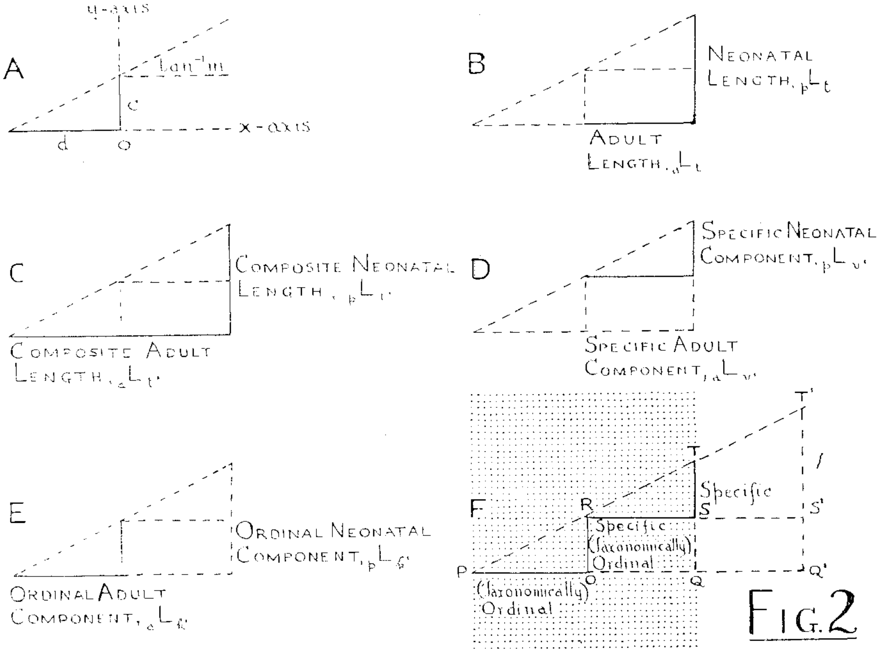

FIG. 2.—A: The constants of the regression equation.
B-E: Ostentive definitions of ordinary lengths, composite lengths, components of composite lengths. The magnitudes defined are shown as continuous lines, set in a reference framework of dashed lines.
F: Relation between specific and (taxonomically) ordinal components of composite calf and adult lengths. The extra-(calf-adult) universe is shaded.
The vertical scale is throughout twice the horizontal scale.

To the existing notation add: postsuffixes v, a variable quantity, and k, a constant quantity, such that $v + k = \text{t}$ (total). Further add that when a dimension-symbol including t is to be read as a composite length, t becomes t^1: when v and k are to be regarded as components of a composite length, they become v^1 and k^1, being then termed (for reasons noticed below) specific and (taxonomically) ordinal components, respectively. Then we have:

(i) Ordinary Lengths (Fig. 2B)

Neonatal length $= {}_{p}L_{t}$. Adult length $= {}_{a}L_{t}$

(ii) Composite Lengths (Fig. 2C)

Composite neonatal length $= L_{p\,t^1} = L_{p\,v^1} + L_{p\,k^1} = L_{p\,t}$

Composite adult length $= L_{a\,t^1} = L_{a\,v^1} + L_{a\,k^1} = L_{a\,t} + d$

(iii) Variable (Specific) Components of Composite Length (Fig. 2D)

Specific neonatal component $= L_{p\,v^1} = L_{p\,t^1} - L_{p\,k^1} = L_{p\,t} - c$

Specific adult component $= L_{a\,v^1} = L_{a\,t^1} - L_{a\,k^1} = L_{a\,t^1} - d = L_{a\,t}$

(iv) Constant (Taxonomically Ordinal) Components of Composite Length (Fig. 2E)

(Taxonomically) Ordinal neonatal component $= L_{p\,k^1} = L_{p\,t^1} - L_{p\,v^1} = c$

(Taxonomically) Ordinal adult component $= L_{a\,k^1} = L_{a\,t^1} - L_{a\,v^1} = d$

Equation (6) can now be rewritten in the form

$$L_{p\,v^1} = m\,L_{a\,v^1} \qquad (8),$$

that is, the specific neonatal component is directly proportional to the adult specific component. Equation (7) can be written

$$L_{p\,t^1} = m\,L_{a\,t^1} \qquad (9),$$

that is, composite neonatal length is directly proportional to composite adult length. These two relationships are evident at sight from Figs 2C, 2D.

Both $L_{p\,t}$ and $L_{a\,t}$ are, of course, theoretically divisible into an indefinite number of systems of components: the justification for the division here of each dimension into two components, and, further, into the particular two components selected, is simply the pragmatic one that the algebraic, or geometrical, situation suggests this as an obvious procedure. The question of whether there is equivalence, or adequate formal correspondence, between the operations and products of algebraic bracketing and those of conceptual bracketing is one of some difficulty: we assume the validity of the procedure provisionally with a view to ascertaining where we are thereby led.

It will be convenient to divide the rest of the inquiry into three sections, the first dealing with the possible biological significance of the concept of composite calf length, the second with possible biological significances of the concept of composite adult length, and the third with a possible interpretation involving a comparison of composite calf and adult lengths below the morphologically valid minima.

A. Biological Interpretation of Composite Calf Length

(a) Ordinal and Specific Components. The problem is to find a more or less evident and 'real' biological meaning for composite calf length, $L_{p\,t^1}$, the sum of the fission products of the measured length at birth of any species, $L_{p\,t}$, in the shape of a component, $L_{p\,k^1}$, of fixed magnitude, and a component, $L_{p\,v^1}$, intraspecifically of (statistically) constant, but interspecifically of variable, magnitude. Now, it is not difficult to conceive of the possible existence of a biologically necessary, or optimal, minimum foetal magnitude of an interspecific validity, a lowest common measure, as it were, of cetaceanesse. The composite concept of composite calf length could thus be the sum of a concept of a constant dimension of specifiable embryonicity and a concept of a variable dimension of specifiable embryonicity.

It would seem natural next to equate the two concepts to the two numerical components of calf length, constant to constant and variable to variable. The ordinary measured length of the neonatus is then seen as the simple arithmetic sum of the linear dimensions of a phase of intra-uterine development, the length of which (44 cm.) is an interspecific constant, and a phase the length of which is directly proportional to (being 0·24 of) the adult length of the relevant species. The constant ${}_{p}L_{k^1}$ it is proposed to call the (taxonomically) ordinal component, the variable ${}_{p}L_{v^1}$ the specific component, of composite calf length, ${}_{a}L_{t^1}$. (Consideration of the context should always resolve any possible confusion between ordinal in the taxonomic sense and—what does, indeed, enter into the present discussion—ordinal in its geometrical sense.) It may here be noted, in passing, that the constant and variable fractions, ${}_{a}L_{k^1}$ and ${}_{a}L_{v^1}$, of composite adult length, ${}_{a}L_{t^1}$, are likewise termed the ordinal component and the specific component, respectively.

Clearly, it is impossible to differentiate observationally in the neonatus itself between the ordinal and specific fractions of its length. And ${}_{p}L_{v^1}$ and ${}_{p}L_{k^1}$ remain biological abstractions unless we can interpret them in terms of morphological development; that is, unless we can regard them, for example, as—to select the simplest possibility—associated with, and representative of, two recognisably distinct embryological phases.

(b) Temporal Relations of Components. If two such phases do exist, a question that immediately presents itself is that of their temporal character, extent, and relation. Are they *(i)* continuous and strictly successive; *(ii)* continuous and partly successive (*i.e.*, with some overlap); *(iii)* continuous, contemporaneous, and of equal duration; *(iv)* continuous, contemporaneous, but of unequal duration; or *(v)* otherwise characterised and related (*e.g.*, exhibiting discontinuity, periodic or aperiodic, manifested wholly contemporaneously, or partly contemporaneously, or successively; and so on)?

(c) Components Continuous and Strictly Successive. If the relation is that of *(i)* above, a moment's consideration of the normal course of ontogeny as one of increasing differentiation leads to the selection of what has been designated the ordinal phase as much more likely to be the prior one. This is so even when the differentiation is regarded solely in its individual ontogenetic context: the likelihood of ordinal phase priority is enhanced when the embryo's history is regarded also as being an approximate correlate of phylogeny, at any rate to the extent of manifesting the same broad temporal sequence of aromorphs or other major landmarks. There is thus tentatively pictured, then, an intra-uterine history whose first epoch, from fertilisation to the achievement of a fixed length of round about 0·4 metre, results in the establishment of a degree of morphological differentiation (associated with an appropriate measure of overall embryonic integration) that is perhaps in some sense constant throughout the order, and whose second, immediately succeeding epoch, culminating at birth, involves an increment in length that varies with the species, but is in all forms equal to about a quarter of adult length. Evidently the constancy of degree of morphological development thus suggested as characterising the first epoch could be a constancy in respect of one or other of various criteria; of which two call for special notice.

Is such a definite morphological status to be interpreted in terms of interspecific or of intraspecific heredity: that is to say, are all cetacean foetuses of length *c* cm., of whatsoever species, indistinguishable from one another; or, alternatively, have all foetuses, no matter of what species, that have attained a length *c* cm. thereby climbed to the same relative rung on their own specific ladders of morphogenesis? That whale foetuses of a length of the order of half a metre should exhibit no sign of specific differentiation would seem to be, on the face of it, a somewhat remote contingency. If a constant measure of bodily organisation is characteristically associated with the ordinal component, it is hence probably definable in terms of the traversing of some fixed fraction of the ontogenetic norm of the species. Since the length-increment $L_{p\,v^1}$ of the second epoch is directly proportional to specific length—equation (8)—a morphological end-point of the period of growth from zero length to a length c that at once suggests itself as probable is that of the acquisition of the characteristic features of the relevant species.

(d) Components Otherwise Related. Considerations such as those just outlined could be valid only if the nature and the position in time of the two presumed developmental epochs were those of *(i)* in par. *(b)*, above, namely, continuous and strictly successive. This will be accepted as the definitive specification of the two phases: accordingly, it will be necessary to do little more than glance at some of the other possibilities. If the situation were that of *(ii)*, the location and extent of the temporal overrun could be determined from a complete time-length graph of foetal growth if the rates of growth were constant, or subject to constant acceleration, but scarcely otherwise. If the situation were that of *(iii)* or *(iv)*, the phases would be unrecognisable by external, visually determinable criteria; but might conceivably be interpretable, more or less directly, in terms of some such element of growth as, for instance, the deposition of a certain amount of non-crescive framework. Situations of the types suggested by *(v)* would almost certainly be of too complex a nature to admit of analysis.

(e) Has the Hypothetical Two-Phase Pattern a Real Existence? It may now be inquired whether the hypothetical two-phase pattern that we have been led from an examination of equation (1) by a process of purely formal reasoning to postulate has any factual existence.(1)

Mackintosh and Wheeler (1929, p. 426) observe regarding the Blue Whale and the Fin Whale. 'It is a characteristic feature of the development of these whales that the form of the body is practically perfected at a stage when the foetus is still very small. A 0·5 m. foetus, for instance, differs very little in appearance and bodily proportions from the adult and so far as the internal structures are concerned the organs are probably all laid down by the time the foetus has reached 0·1 m.'. Matthews (1938*b*, p. 36) notes that pigmentation has begun in Sei foetuses of 0·64, 0·51, 0·4 m., and, again (1938*a*, p. 119), that in the Sperm Whale pigmentation starts before a length of 0·5 m. is reached. Harmer (1927, p. 24) states that Guldberg and Nansen (1894, p. 22), to whose paper I have not at present access, observe of the White-sided Dolphin, *Lagenorhynchus acutus* (Gray, 1828), that the generic characters are acquired when the foetus reaches one-fifth of its full length, which is given as about 950 mm., and the specific characters at about half that length.

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(1) In the paper as originally written there appeared, in place of the paragraph to which this footnote is attached, the following sentence. 'Whether or no' a succession of two phases 'of the nature and magnitude here envisaged actually occurs, is a question that should be readily enough determined by an appropriate investigation: the requisite data may, indeed, already be contained in the literature, but the writer is at present without means of access to likely sources of information'. The striking corroborative evidence in the cases of the Blue Whale and Fin Whale given by Mackintosh and Wheeler, and now quoted, was then not at hand.

It has been thought permissible, in the circumstances, to record here this act of philosophic faith.

(f) Similar General Conclusions Already Reached on Different Grounds. It is of interest to observe that the general conclusions here reached by an inquiry into the formal significance of an extrapolation of the equation of regression of neonatal on adult length beyond the strict calf-adult domain of definition have in large part already been arrived at (with particular reference to two species) by Mackintosh and Wheeler on quite different grounds. At the conclusion of a fairly detailed investigation of the sexual cycle and the growth of the calf in southern Blue and Fin Whales, they remark that the difference in size between the two species is apparent quite early in the development of the foetus. 'This specific difference in size is attained simply by more rapid growth on the part of the larger species and not by growth spread over a longer period. Blue whales are apparently ready for birth at a greater length in, if anything, an actually shorter time than Fin whales. It is probable that in the early stages of the development of the foetus, when the organs are being formed and the limbs completed, the actual increase in length would be approximately the same in both species, and it may be suggested that development up to this point does not differ in any special way from the development of other mammals, and that the foundations for the whale's great subsequent size have not yet been laid down. After this, however, instead of development being quietly finished off and birth taking place, the rest of gestation is devoted to a great burst of growth, the rapidity of which in the different species appears to be proportional to the size of the whale when fully adult. As it is practically certain that the great size of whales is, from the evolutionary point of view, a recently acquired character, it would naturally be expected to make its appearance in the later part of gestation. Thus the great size of a whale does not necessarily imply the need for a long period to attain that size. The capacity for rapid growth is to be regarded rather as one of a number of characters distinguishing certain whales from other mammals.'.

(g) Location in Time of the Ordinal-Specific Ontogenetic Crisis. Conjectural curves of foetal growth have been formulated in the *Discovery* Reports for five species: for the Blue Whale and Fin Whale by Mackintosh and Wheeler (1929)—Laurie (1937) reproduces these authors' curve for the Blue Whale, which he finds closely fits the additional data obtained by the *Southern Princess* and the *Southern Empress* in 1932-3—and for the Humpback, Sperm, and Sei Whales by Matthews (1937; 1938*a*, *b*). Direct readings from the graphs give the approximate age at which a length of 44 cm. is attained as 2·9, 3·0, 4·0, 4·5, 3·4 months, respectively; or about 28, 26, 37, 36, 36 per cent of the estimated period of gestation. (In an unpublished analysis, in which it is shown that three of the five *Discovery* curves are allometric, and, further, that the data for *Balaenoptera borealis* (Linné) and *Physeter catodon* Linné, the published curves for which species are combinations of an earlier curvilinear and a later linear segment, can, by suitable technique, also be fitted by a curve of the form $y = bx^{\alpha}$, the equations found for foetal growth give an estimated mean age, in these five species, at a length of c cm., of 3·5 ± 0·27 months, equivalent to 27·7 ± 1·5 per cent of the gestation period, or, in the four balaenopterids, 3·3 ± 0·27 months, or 27·4 ± 1·9 per cent.)

A period of three-four months would seem, on the face of it, one of sufficient duration to permit of the achievement of the advanced stage of morphological differentiation that the present theory postulates: along another line of approach, there is the evidence of Mackintosh and Wheeler that at a length of the order of that here associated with the presumed ordinal-specific ontogenetic crisis foetuses of the Blue Whale and Fin Whale differ little, except in point of size, from the adult animal.

(h) Mean Ratios of Growth in Ordinal and Specific Phases. On the basis of the allometric curves of foetal growth noted above, and the definitive neonatal and adult lengths of Table I, the estimated mean rates of growth, in cm. per month, of Blue, Fin, Humpback, Sei, Sperm Whales during the ordinal phase are 15·1, 15·3, 10·9, 13·0, 10·6, respectively; while those during the specific phase are 89·5, 73·3, 44·3, 46·7, 30·4.

For the four balaenopterids the regression of mean specific phase growth rate on adult length is linear, with a significance of better than $P = 0{\cdot}01$: the inclusion of the physeterid reduces P to about 0·1. Thus while it is possible the mean rate of growth during the foetal phase given over primarily to increase in bulk is a linear function of adult length in all whales, there may, on the other hand, perhaps exist a series of (probably not greatly dissimilar) family, or other, norms.

In the ten species of whales, representative of three families, here considered it has been established that the actual increment in length of the foetus from a length of 44 cm. to birth, *i.e.*, in the course of the specific phase, is directly proportional to adult length. By the use of the concept of composite lengths this relation assumes the symmetrical and elegant form—equation (8)—of a constancy of ratio of specific components.

B. Biological Interpretation of Composite Adult Length

(a) Contrast between Neonatal and Adult Ordinal Components. Some tentative conclusions having been reached regarding the significance of composite calf length, attention may next be turned to the investigation of composite adult length. In its general sense (with an interspecific application) composite adult length is the sum of an ordinal component, $L_{a\,k^1}$, which is a length, d, of 182 cm., and a specific component, $L_{a\,v^1}$, equivalent to the actual measurable length in cm. of the relevant species. As is shown by equation (9), it is directly proportional to composite, and hence to ordinary, neonatal length.

A marked difference in nature characterises the ordinal fraction of calf length and the ordinal fraction of adult length. The former is a real quantity in the sense that, by hypothesis, it represents the measurable length—if only, in the limit, the instantaneous length—of a foetal organism In the neonatus it continues to make a contribution, numerically specifiable, to the total length of the animal; though, it is true, it no longer constitutes a similarly specifiable morphological fraction—extension, *per se*, is still there, but the matter whose linear distribution was formerly determined by measurement is now (in the form of itself or of metabolic replacement of equivalent mass), by protoplasmic intussusception, redistributed, with loss of its original diagnostic spatial and anatomical quiddity. The latter, on the other hand, is unreal in the sense that it is, so far as can be seen, at all times a purely abstract magnitude, being in no known circumstances directly interpretable as so much 'length of solid whale', and even appearing, in an extrapolation in the neonatal-adult graph, as a negative dimension.

(b) Four Selected Aspects of Problem of Significance of $L_{a\,k^1}$. Of the various aspects of the general problem of the significance of the ordinal adult component that present themselves for inquiry, four only will be noticed here. These centre on the following suggestions: first, that the magnitude of $L_{a\,k^1}$ is determined by the factors of the mathematical situation already examined, and is hence without

recognisable or necessary biological significance; secondly, that $L_{a\,k^1}$ respresents a value more logically associated with a correlation surface than with a regression line; thirdly, that the observed regression of $L_{p\,t}$ on $L_{a\,t}$ involves an intelligible geometrical specification of adult form in terms of extra-somatic magnitudes; fourthly, that $L_{a\,k^1}$ and $L_{p\,k^1}$ represent phylogenetic norms of adult and foetal size. Some of the points raised present some novelty and difficulty; and it will be feasible to state. but scarcely to discuss, them.

(c) Ordinal Component as Mathematically Determined. The existence and magnitude of $L_{a\,k^1}$ are, in a purely mathematical sense, necessary consequences of the magnitude of the numerical coefficient of $L_{a\,t}$ and of the constant term c in equation (1): in graphical terms, d, the abscissal intercept of the extrapolated regression line, is determined jointly by m, the gradient, and c, the intercept on the y-axis. If, then, c and m are accepted as the values of two definitive biological quantities of whose relationship the regression equation is a complete specification d, or $L_{a\,k^1}$, may be a mere logical corollary of them and without any necessary, or recognisable, biological significance.

(d) Biological Situation Better Regarded as a Correlation than as a Regression. With the term correlation used, in a common sense, simply to denote a tendency for two variables to vary in magnitude *pari passu*, and the term regression in a strict sense of a measure of magnitude of mutual change in two quantities standing in a more or less obvious relation of cause and effect, the distinction between correlation and regression is clearly enough marked at the extremes. Borderline cases are, however, not infrequent in practice: and in such instances the regression technique is often adopted as a matter of expediency, with a view to the convenience of having the relationship so formulated as readily to yield estimates of individual variates. Needless to say, there is no difference of formal validity of the results of the two procedures, and the matter at issue is not a mathematical one: the point here to be made is that the mere employment of the regression method of approach may, in itself, be taken to derive from an implicit assumption of a recognisable causal relation between the two sets of variates, and such an assumption may, upon occasion, by estoppel of inquiry, lead to failure to recognise the existence of a less proximate principle. This may be the case here. Of the three quantities c, m, d, the first has, indeed, been provisionally interpreted as length at the close of an earlier, so-called ordinal phase, and the second is the ratio of the increment in length during a second, so-called specific phase to the total adult length; while the third so far remains uninterpreted. We have, however, at the moment, no adequate grounds for selecting m and c, or, indeed, any particular pair of factors, as the unique data of the general problem of significance that arises with extrapolation beyond the confines of the original calf-adult universe; nor, indeed, any logical warrant even for assuming all three to be other than principal and coördinate factors of an esemplastic vital situation in which such an element as, for instance, duration is of comparable significance with extension. It may therefore be suggested it is not unlikely that the two magnitudes for which modal descriptions have been found are, in effect, indices of biological optima themselves as yet unrecognised, though not improbably susceptible of formulation, on further investigation, in terms of measurable quantities (such as—to take instances involving length only, and neither time nor mass—area-volume relations, coelome-foetus size-ratio). In such circumstances the meaning of d is still open to search.

(e) Significance of Extra-Somatic Spatial Frameworks of Reference. Now, a biological length of an extra-somatic or, in one sense, 'imaginary' character, or including an extra-somatic or 'imaginary' segment, may well appear, on the face of it, a somewhat surprising datum. That the concept of a composite length, in the sense of a length made up of a segment, or segments, measured along an axis of the body of an animal and a segment extending freely into space beyond the physical boundaries of the animal can represent a simple and convenient specification of morphological pattern is well exemplified in an admirable study of the body-forms of fishes by Gregory (1928). In the fish figured in illustration of his terminology (Fig. 117A) the opisthion-pygidion interval is—and in most teleosts and elasmobranchs it will be—a composite length, comprising a somatic pygidion-uranion segment and an extra-somatic uranion-opisthion segment. Now, as Gregory points out (p. 337), the distance of the opisthion behind the pygidion is evidently (*cf.* his Fig. 118D) a function of his dorso-posterior angle, which is the upper half of the angle of the run. Here, then, the magnitude of a segment of the produced anteroposterior body-axis that—in those fishes with posturanic opisthion; and they constitute the modal group (Gregory, p. 349)—lies wholly in space outside the body becomes, by a simple geometrical transformation, a direct specification of body-form. Again, the following remarkable relation has been found, on analysis of data collected by the writer, to obtain in the False Killer Whale (there is reason to believe that, with some possible modification, it holds good in various other species also). Let a series of important anatomical landmarks be numbered in sequence of their occurrence, proceeding caudad along the main antero-posterior axis, from 2 to 9 (no landmark has yet been associated with 1). Then the logarithms of the lengths from the tip of the snout (prosthion) to the several points constitute a linear function of the logarithms of the relevant natural numbers. That is, if λ = length from tip of snout to given anatomical landmark; $n = 2, 3 \ldots . 9$, then

$$\lambda_n = A\, n^k \tag{10}$$

The last term, $n = 9$, is the caudal notch, or the morphological end-point of the body. In a world perhaps not wholly devoid of grain of quinary idiosyncrasy it is not unnatural to inquire, what is $n = 10$, and where is it located? As to its location, it clearly lies somewhere on the produced main body-axis in postcaudal extra-somatic space: as to its nature, it has been found to be a point of intersection in a circum-somatic system of axes of reference such that if y is the distance, measured from it as origin, to any point on the anteroposterior axis caudad of the dorsal fin, and if x is the girth at the level of that point, $y = cx^k$.

While in the first of these examples the composite length is, from the point of view of morphological specification, an *à priori* geometrical construction, a subject for prognosis, in the second it is *à posteriori*, a subject for diagnosis, the observed situation (formulated, in this instance, empirically) being interpretable anatomically only by further inquiry (in this instance, the conclusion was reached by *ad hoc* methods). It is possible the position in regard to the present composite length L_{at^1}, of which L_{ak^1}, or d, is the extra-corporeal segment, is analogous to that in the second example cited.

(f) Interpretation of L_{ak^1} and L_{pk^1} as Adult and Foetal Phylogenetic Norms.

It is found—equation (8); Fig. 2D, Fig. 2F triangle RST—that the specific component of calf length $(L_{pt} - c)$ is directly proportional to the specific component

$L_{a\,t}$, the former divided by the latter being tan m. Again, the taxonomically ordinal calf component divided by the taxonomically ordinal adult component d is tan m. Now, in Part A reasons have been advanced for regarding the prenatal specific-ordinal ratio $(L_{p\,t} - c)/c$ as the numerical counterpart of a genuine and significant specific-ordinal concept ratio, $L_{p\,v^1}/L_{p\,k^1}$, in the embryonic history. Does it follow, by symmetry, that the adult specific-ordinal ratio $L_{a\,t}/d$ is the numerical counterpart of a genuine specific-ordinal concept ratio, $L_{a\,v^1}/L_{a\,k^1}$, in adult history?

Expressed geometrically, the argument is as follows. The triangles RTS, PRO, in Fig. 2F, are similar, and TS/RS = RO/PO (= tan m), and TS/RO = RS/PO: but TS/RO is, if our earlier conclusions are valid, the numerical correlate of the biologically interpretable prenatal ratio $L_{p\,v^1}/L_{p\,k^1}$: is it to be expected, by the logic of symmetry, that RS/PO is in similar manner the numerical correlate of a biologically interpretable adult ratio?

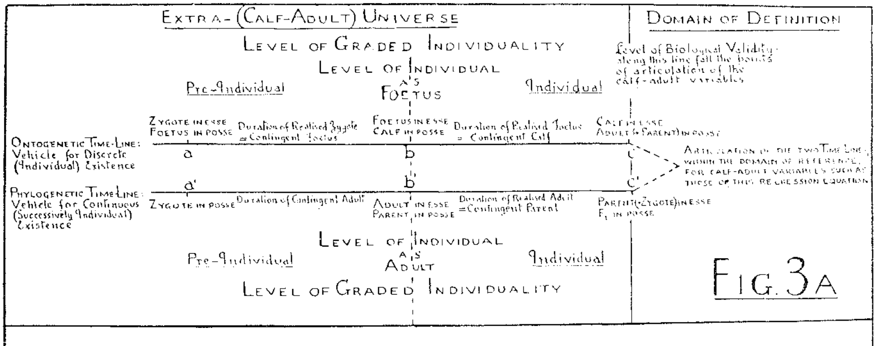
It will be realized, of course, that by interpreting the situation in a purely geometrical sense the original Cartesian formulation has been departed from, and attention is no longer paid to sign. In view of the fact that, taking OQ in Fig. 2E as the measured adult length of the smallest species, everything to the left of the line TQ lies outside the domain of definition of the original variables, it is not altogether surprising, but perhaps rather to be expected, that an anomaly in sign should be encountered. The calf length on adult length regression graph, extrapolated beyond its biologically valid minimal values, is now being asked to bear a heavy weight of extra-limital significance, and is being examined as a potential source of clues to the nature of an evolutionary situation, into which duration, not in itself inherent in the graph, enters as an essential element.

Since $L_{p\,k^1}$, our analysis leads us to conclude, represents a minimum length to which all foetuses, of whatsoever species, must attain before they begin to exist as species-differentiated foetuses, the logical parallel for $L_{a\,k^1}$ would appear to be that of the minimum length to which all adults, of whatsoever species, must attain before they begin to exist as species-differentiated adults. But d is a negative quantity, and does not appear in the ordinary adult length as a measurable quantity. It would seem, accordingly, on this interpretation, to precede the ordinary adult length in time, and apparently to represent the length of a generalised, phylogenetic norm of cetacean adult esse, in short, an archetype. Its non-contemporaneity with the length of the individual specimen of whale would then be symbolically indicated both by its location outside the formal, observable domain of definition and by its negative sign. As specified by equation (1) its value is 182 cm.: the use of equations (2) and (3) give alternative values of 172, 159 cm. In a similar way $L_{p\,k^1}$ could be interpreted as a phylogenetic foetus norm; its length being approximately one-fourth of the length of the phylogenetic adult norm. It should be observed that acceptance of this interpretation of $L_{a\,k'}$ does not of necessity invalidate the suggestions considered above under *(d)* and *(e)* of subsection B, since it represents an apparent justification of *(d)*, and may be an example of, or be exemplified by, *(e)*: again, the present meaning attached to $L_{p\,k^1}$ is not antagonistic to, but is an extension or restatement of, conclusions reached in subsection A.

The formal parallelism that on development of the position here reached is seen to characterise the two original variables of calf length and adult length beyond the original domain of definition is briefly discussed in the next subsection.

C. Formal Correspondence of the Disarticulated Variables beyond the Calf-Adult Domain of Definition

The suggested interpretation of $L_{p\,k^1}$ and $L_{a\,k^1}$ as size-norms of integrated biological units leads, when further developed, to the recognition of a noteworthy correspondence between the original variables of calf length and adult length when these are disarticulated at the level of biologically minimum size, subjected to separate analysis, and then suitably equated. A detailed discussion of the problem lies beyond the scope of the present paper; but the following brief account, taken in conjunction with Figs 3A, 3B, will serve to make clear the more immediately relevant aspects of the general situation.



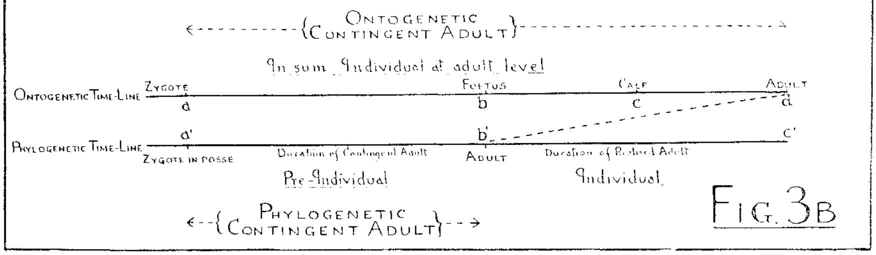


FIG. 3A.—Formal correspondence between the disarticulated variables beyond the calf-adult domain of reference.

FIG. 3B.—Contingent adult in the ontogenetic time-line equated with contingent adult in the phylogenetic time-line. In this diagram a, b, c, a^1, b^1, c^1, have the same connotations as in diagram A.

'Foetus' is here used in a special sense: unqualified, it means a whale foetus of length $L_{p\,k^1}$ (see Fig. 2E); as a 'realised foetus', it means a whale foetus of any length between $L_{p\,k^1}$ and $L_{p\,t^1}$ (see Fig. 2C).

If $L_{p\,k^1}$ and $L_{a\,k^1}$ are, as suggested, phylogenetic norms, they are also, insofar as they persist, ontogenetic norms. Now, the problem of equating the disarticulated variables is found to involve the equating, in some fashion, of ontogenetic history with phylogenetic history. Hence it seems convenient to choose out of $L_{p\,k^1}$ and $L_{a\,k^1}$ one component to be treated (along with its associated variable component for minimum length) from its individual aspect, while the other invariable component, with its associated variable component for minimum length, is treated from its racial aspect. On several obvious grounds, it would seem natural to select the adult disarticulated extra-universe moiety as the phylogenetic time-line, functioning essentially as vehicle for continuous existence, and the calf moiety as the ontogenetic time-line, functioning essentially as vehicle for discrete existence.

The results of the analysis of the time-lines, and the bringing of them into formal correspondence on the basis of the subsistence, recognised earlier, of ordinal equivalence between $L_{p\,k^1}$ and $L_{a\,k^1}$ are shown in Fig. 3A. The disarticulated variables, regarded as time-lines, are marked *abc* and $a^1b^1c^1$, the correspondence between a and a^1 being mathematically one of zeros, biologically one of zygotes *in esse* and *in posse*, the correspondence between b and b^1 being that of the ordinal equivalence between $L_{p\,k^1}$ and $L_{a\,k^1}$ just noted, the correspondence between c and c^1 being that of extra-universe origins: everything to the left of cc^1 lies outside the domain of definition, while to the right of cc^1 the variables, elsewhere disengaged, are articulated as the variates on which the regression equation is based. The figure is otherwise self-explanatory.

In Fig. 3B, in which a, b, c, a^1, b^1, c^1 have the same connotation as in Fig. 3A, attention is called to the fact that the whole ontogenetic time-line ad (that is, the duration of $L_{a\,k^1}$, or $L_{a\,t}$) is that of contingent adulthood, and is hence the formal correlate of a^1b^1 (that is, the duration of $L_{a\,k^1}$, or d) the phylogenetic time-line of contingent adulthood. It is assumed the equivalence may be extended to cover the linear dimensions characteristic of these durations. Hence, if ad is, for a whale of biological minimum, or of otherwise typical, size, say, 150 ± 30 cm., this would be the expected value also for a^1b^1: the difference in sign between a^1b^1 and ad when these are transferred to an algebraic context (the former then becoming $L_{a\,k^1}$, and the latter, in the absence of an available symbol in L_{p}, becoming $L_{a\,t}$) would presumably symbolise the difference between them in respect of individuation, ad being, in sum, individual at adult level (for meaning of individual at adult level, see Fig. 3A), while a^1b^1 is pre-individual, a result that is, in effect, a restatement of that obtained above in subsection B *(f)*.

In this treatment the problem has been subjected to some artificial simplification in two ways: first, by the assumption of the subsistence of identity of meaning between 'adult', which as used in connexion with the original data refers to animals of modal maximum size (*i.e.*, at full physical maturity), and 'sexually mature'; secondly, by the adoption of a convention in accordance with which parenthood is taken to follow adulthood (in the sense of physical maturity), whereas it characteristically precedes it. These are, it will be found, however, merely formal simplifications, the adoption of which does not invalidate the main conclusions, but serves to facilitate their exposition.

Summary

1. Eclectic estimates of length of calf at birth, ${}_{p}L_{t}$, and modal maximum length of adult, ${}_{a}L_{t}$, in ten species of whales (ranging in size from the Common Porpoise to the Blue Whale) yield a highly significant linear regression of neonatal on adult length, the equation of the best fit for the ten pairs of variates being (dimensions in cm.)

$${}_{p}L_{t} = 0{\cdot}2441 \; {}_{a}L_{t} + 44{\cdot}3$$

2. The intercept, c, of the graph on the x-axis (44 cm.) formally denotes the length of the calf of a whale of zero length, and the intercept, d, of the graph on the y-axis (-182 cm.) formally denotes the length of a whale characterised by giving birth to a calf of zero length. These dimensions clearly transgress the limits of the domain of definition of the calf-adult size-ratio problem; and appear to be, on the face of it, merely biological fictions. An attempt is made, however, to find biological meanings for them.

3. The general technique of investigation may be described as 'conceptual bracketing'. Lengths are dissected to give 'composite lengths', each the sum of a constant and a variable. A comparable bracketing of the biological concepts associated with the component dimensions is then carried out. The validity of the procedure is provisionally accepted with a view to ascertaining the results that flow from the assumptions made; and it appears that biologically intelligible meanings can be found for the apparently biologically non-significant extrapolations noted in paragraph 2 above. The introduction of temporal sequence and duration, not formally inherent in the variates, into the region external to the original domain of definition is involved as a necessary feature in the interpretation proposed for c, and it also enters into one or more of the possible interpretations of d.

4. Of the two components of composite calf length, the constant c, or its conceptual correlate ${}_{p}L_{k^1}$, is interpreted as an ordinal character, having a common and invariable manifestation in foetuses of all species, and the variable $({}_{p}L_{t} - c)$, or its conceptual correlate ${}_{p}L_{v^1}$, is interpreted as a specific character, directly proportional to adult length. On ${}_{p}L_{k^1}$ being set earlier in time than ${}_{p}L_{v^1}$, there emerges a picture of cetacean embryonic history as a two-phase pattern, one phase beginning at birth and culminating, at a length of about 44 cm., in the achievement of morphological specificity, the other phase continuing till birth, and being largely given over to increase in mere bulk. In four balaenopterids the approximate age at which the ordinal-specific crisis occurs would appear to be 3-4 months. For the actual existence of such a hypothetical pattern, here formulated by a train of purely formal reasoning from an examination of the neonatal-adult length regression, some direct evidence is available in the case of two or three species.

5. The variable component of composite adult length is ordinary adult length ${}_{a}L_{t}$, with conceptual equivalent ${}_{a}L_{t^1}$. The constant component d, or its conceptual correlate ${}_{a}L_{k^1}$, may be without necessary or recognisable biological significance. If biologically significant, it is perhaps most likely to be interpretable as *(a)* an index, coördinate with the (geometrically) ordinal intercept and the gradient of the regression line, of an esemplastic biological optimum not yet diagnosed (possibly

an area-volume relation); or *(b)* an extra-somatic segment of a body-axis, constituting part of an external framework of reference, and susceptible, on appropriate geometrical transformation, of direct interpretation in terms of ordinary somatic landmarks and dimensions; or *(c)* a dimension, presumably total length, of a cetacean archetype.

6. A development of *(c)* in paragraph 5 above leads to the primary variables being disarticulated at the level of biologically minimum size, treated as ontogenetic and phylogenetic time-lines, and brought into correspondence. It is found the duration of ${}_{a}L_{k^1}$, now indentified as phylogenetic contingent adult length, is equated with the duration of ${}_{a}L_{v^1}$, or ${}_{a}L_{t}$, now identified as ontogenetic adult length. Hence, if ${}_{a}L_{t}$ is associated with a linear dimension of, say, 150 ± 30 cm., this will be the expected value also for ${}_{a}L_{k^1}$; the difference in sign, in an algebraic context, being symbolic of a difference in individuation, the former being, in sum, individual, the latter pre-individual.

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TABLE I

REGRESSION OF NEONATAL LENGTH, L_{pt}, ON ADULT LENGTH, L_{at}:

TEN SPECIES OF WHALES

Data from various sources (see Text)

Species	Assumed Adult Length, L_{at} cm.	Neonatal Length, L_{pt}, cm.		L_{pt} (predicted) as Percentage of L_{at} (assumed)
		Assumed	Predicted	
Phocaena phocaena Linné	175	80	87	49·7
Delphinus delphis (Linné)	260	105	108	41·4
Lagenorhynchus albirostris (Gray)	300	125	118	39·2
Tursiops truncatus (Montagu)	350	130	130	37·1
Balaenoptera acutorostrata Lacépède	910	270	266	29·3
Physeter catodon Linné	1600	415	435	27·2
Balaenoptera borealis (Lesson)	1630	450	442	27·1
Megaptera nodosa (Bonnaterre)	1680	460	454	27·0
Balaenoptera physalus (Linné)	2400	650	630	26·2
Balaenoptera musculus (Linné)	2750	700	715	26·0