



## Size and complexity among multicellular organisms

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*Received 19 January 1996; accepted for publication 3 June 1996*

The diversity of specialized cell types ('complexity') is estimated for a wide range of multicellular organisms. Complexity increases with size, independently of phylogeny. This is interpreted in economic terms as the consequence of a greater degree of cooperative division of labour within larger entities. The rate of increase of complexity with size is less in the case of a cooperative division of labour (cell types within bodies) than in the analogous case of a competitive division of labour (species within communities). This is attributed to the inutility of single specialized cells whose goods must be shared among all the many cells of a large organism. Major groups of organisms differ in complexity at given size: animals are more complex than plants, and phaeophytes are simpler than either.

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**ADDITIONAL KEY WORDS:**—development – differentiation – histology – complexity – evolution – economic biology – division of labour – allometry.

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## INTRODUCTION

Diversity and development are two very familiar themes in biology; but the two are seldom apposed. The study of species diversity in communities has a history as long as that of ecology itself; the study of development reaches back still further, to the origins of biology. The intersection of the two is the diversity of the body, the study of which has scarcely begun.

Multicellular organisms are clones of cells that express different phenotypes despite having the same genotype. The number of different phenotypes varies widely among organisms; some, such as *Volvox*, have only two distinct kinds of cell, whereas others, such as chordates, have dozens of specialized cell types. McShea (1996) offers a lucid review of biological complexity. He prefers a narrow definition, that of differentiation: the number of different types of interacting parts or interactions. The number of cell types in an organism is presented as an example of nonhierarchical morphological complexity, one of McShea's four main classes of complexity, and is the measure that we make use of here.

The rules that govern the extent of diversification have aroused little interest, and remain poorly understood. The only generalization that has been widely, if uncritically, accepted is that larger organisms tend to be more complex (Bonner 1965, 1988). This is by no means always the case: among the largest organisms are filamentous fungi and algae that show little somatic differentiation. Nevertheless, among strongly individualized organisms size and complexity seem to be related. Although this may be a conclusion with which few would disagree, it has never been adequately documented, and has not hitherto been investigated quantitatively.

We suggest that a general increase in complexity with size can be anticipated on economic grounds (Ghiselin 1974, 1978). The argument dates from Adam Smith (1776), who distinguished between competitive and cooperative division of labour. In either case, the degree of division of labour is proportional to the extent of the market. In the case of a competitive division of labour, this implies that a greater number of more highly specialized professions should arise when communities are larger, or transport cheaper and more rapid. The biological equivalent of this principle is that larger and more productive areas should support more species. The work of two generations of ecologists who have investigated patterns of species diversity has been reviewed by Rosenzweig (1995). In the case of a cooperative division of labour, the analogous principle implies that larger organizations should possess a more diversified workforce. The biological equivalent of this principle, with which we are concerned in this paper, is that larger organisms should comprise a greater number of specialized cell types. We shall show that this prediction is borne out by observation, but also that the form of the relationship between scale and complexity differs between cooperative and competitive situations.

## MATERIAL AND METHODS

*Raw data*

The data on which this survey is based are listed in Table 1. Organisms were chosen so as to span a wide range of size classes and taxa, but otherwise there was little attempt at selection; our data are by no means exhaustive, were drawn from

the literature which lay most conveniently to hand, and are representative only in that we tried to obtain data from as many major taxa of multicellular organisms as possible. Both the number of different cell types and the total size of organisms raised issues that we were unable fully to resolve. It will be widely accepted that cells are differentiated in distinct ways; but a precise definition of what constitutes a cell type has eluded us. A fundamental definition would no doubt involve discrete patterns of gene expression. However, this information is not available for the great majority of organisms. We have relied mostly on morphological criteria, and have accepted the opinions of the original authors in distinguishing between different types, as shown, for example, in text descriptions or the labelling of diagrams. If this be refuted, our analysis collapses, but we view it as a necessary first step. A similar difficulty attends analyses of species diversity; species may be tolerably distinct in most birds and insects, for example, but in fungi or algae the boundary between species become much more difficult to resolve. Curiously, the estimation of total size is almost as difficult, especially in groups, such as plants or seaweeds, where size is extremely variable. In the case of very small organisms, size can often be expressed as total cell number. In larger organisms, cell number is rarely available, but volume can be estimated from drawings, photographs or measurements. In all cases, we have chosen the maximum size attained. We have chosen to express size in terms of a notional cell number, with each cell having a dimension of 10  $\mu\text{m}$ . This provides a consistent scale, at the expense of a further approximation. We are confident that our estimates are correct to within an order of magnitude, but make no more ambitious claim, and justify our analysis because it spans many orders of magnitude. In short, these procedures are deplorably inexact, but we defend them as being essential in a preliminary treatment of an important problem that has not hitherto been approached quantitatively at all.

Organisms may be asexual or sexual. In sexual organisms the number of cell types is consistently greater, because a range of different tissues is allocated to male function, and, in the female, to functions associated with the receipt and handling of sperm. We have attempted to remove this source of variation by including only asexual reproductive tissues, regarding female tissues as the equivalent of reproductive tissues in obligately asexual organisms. Thus, spores, eggs, and archegonial or megasporangial tissue are included, whereas the corresponding male cells and tissues were not included. Moreover, we excluded female tissues associated with copulation or meiosis, such as the spermatheca or bursa copulatrix.

#### *Standardization*

To provide a standard for our estimates of cell type diversity, we have given our list of cell types in the well-studied nematode, *Caenorhabditis elegans* (Table 2). The list can be questioned; it might be argued, for example, that the diversity of cells in intestinal valves has been overestimated, and that of endothelial tissue underestimated. It seems unlikely that any such objections will greatly modify our final estimate of 27 cell types. At all events, this illustrates the considerations on which all our estimates are based, and provides a yardstick for the other organisms in our survey.

TABLE 1. Estimates of cell type diversity. The first two columns are phylum and species. The third column is the estimated number of cell types. The fourth column is  $\log_{10}$  nominal total cell number, calculated by assuming cell volume to be  $1000 \mu\text{m}^3$ . The fifth column is a code identifying phyla on plots. The authority is given in the final column; if more than one publication was consulted, that giving most information is cited

AMOEBAS, CILIATES AND BROWN SEAWEEDS					
Acrasiomycota	<i>Acrasis rosea</i>	2	2.85	X	Raper, 1984
Acrasiomycota	<i>Dictyostelium minutum</i>	2	3.15	X	Raper, 1984
Acrasiomycota	<i>Dictyostelium discoideum</i>	3	4.1	X	Raper, 1984
Ciliata	<i>Zoothamnion alterans</i>	4	2.15	I	Summers, 1938
Phaeophyta	<i>Ectocarpus siliculosus</i>	4	5.5	P	Knight, 1931
Phaeophyta	<i>Chordaria linearis</i>	6	10	P	Searles, 1980
Phaeophyta	<i>Chordaria flagelliformis</i>	6	9.6	P	Korrmann, 1962
Phaeophyta	<i>Leathesia difformis</i>	6	10.6	P	Bold & Wynne, 1978
Phaeophyta	<i>Elachista fucicola</i>	5	7.2	P	Koeman & Cortel-Breeman, 1976
Phaeophyta	<i>Haplogloia andersonii</i>	7	8.6	P	Peters, 1992
Phaeophyta	<i>Papenfusiella callitricha</i>	7	8.1	P	Wilce, 1969
Phaeophyta	<i>Kurogiella saxatilis</i>	7	10.4	P	Kawai, 1993
Phaeophyta	<i>Colpomenia sinuosa</i>	5	9.3	P	Wynne, 1972
Phaeophyta	<i>Scytosiphon lomentaria</i>	4	8.9	P	Clayton, 1976
Phaeophyta	<i>Haplospora globosa</i>	4	10.4	P	Kuhlenkamp & Muller, 1985
Phaeophyta	<i>Asperococcus fistulosus</i>	5	10.0	P	Bold & Wynne, 1978
Phaeophyta	<i>Dictyosiphon hirsutus</i>	6	10.6	P	Peters, 1992
Phaeophyta	<i>Isthmoploea sphaerophora</i>	3	4.2	P	Rueness, 1974
Phaeophyta	<i>Hummia onusta</i>	5	8.0	P	Fiore, 1977
Phaeophyta	<i>Cutleria</i> sp	7	9.5	P	Bold & Wynne, 1978
Phaeophyta	<i>Ralfsia verrucosa</i>	8	8.8	P	Loiseaux, 1968
Phaeophyta	<i>Heteroralfsia saxicola</i>	9	8.9	P	Kawai, 1989
Phaeophyta	<i>Zecarpha leiomorpha</i>	8	9.9	P	Anderson <i>et al.</i> , 1988
Phaeophyta	<i>Syringoderma phinneyi</i>	6	5.3	P	Henry & Müller, 1983
Phaeophyta	<i>Carpomitra cabrecae</i>	7	9.4	P	Motomura <i>et al.</i> , 1985
Phaeophyta	<i>Sphaecularia bipinnata</i>	9	9.1	P	Clint, 1927
Phaeophyta	<i>Cladostephus verticillatus</i>	8	8.1	P	Sauvageau, 1907
Phaeophyta	<i>Dictyota binghamiae</i>	4	11.4	P	Foster <i>et al.</i> , 1972
Phaeophyta	<i>Fucus vesiculosus</i>	7	12.5	P	McCully, 1966
Phaeophyta	<i>Ascophyllum nodosum</i>	6	11.8	P	Rawlence, 1973
Phaeophyta	<i>Desmarestia antarctica</i>	7	11.8	P	Moe & Silva, 1989
Phaeophyta	<i>Himantothallus grandifolius</i>	14	12.2	P	Wiencke & Clayton, 1990
Phaeophyta	<i>Alaria marginata</i>	14	12.0	P	Kain, 1979.
Phaeophyta	<i>Laminaria dentigera</i>	14	11.1	P	Kain, 1979
Phaeophyta	<i>Durvillea antarctica</i>	6	12.0	P	Naylor, 1949
GREEN ALGAE AND PLANTS					
Chlorophyta	<i>Astrephomene gubernaculum</i>	2	1.65	C	Stein, 1958
Chlorophyta	<i>Eudorina illinoensis</i>	2	2	C	Iyengar & Desikachary, 1981
Chlorophyta	<i>Fritschella tuberosa</i>	5	2.3	C	McBride, 1970
Chlorophyta	<i>Microthamnion kutzingianus</i>	3	1.8	C	Bold & Wynne, 1978
Chlorophyta	<i>Pleodorina sphaerica</i>	2	2.55	C	Iyengar & Desikachary, 1981
Chlorophyta	<i>Ulothrix zonata</i>	3	1.5	C	Floyd <i>et al.</i> , 1972
Chlorophyta	<i>Volvox aureus</i>	2	2.75	C	Iyengar & Desikachary, 1981
Bryophyta	<i>Anthoceros himalayensis</i>	12	4.6	B	Hehra & Handoo, 1953
Bryophyta	<i>Cyathodium barodae</i>	13	7.7	B	Chavran, 1937
Bryophyta	<i>Cyathodium foetidissimus</i>	15	8.8	B	Lang, 1905
Bryophyta	<i>Fegatella conica</i>	15	6.5	B	Maybrook, 1914
Bryophyta	<i>Fumaria hygrometrica</i>	20	8.4	B	Puri, 1981
Bryophyta	<i>Monoclea forsteri</i>	13	6.5	B	Shuster, 1984
Bryophyta	<i>Polytrichum commune</i>	26	9	B	Puri, 1981
Bryophyta	<i>Pogonatum stevensii</i>	21	8.85	B	Chopra & Sharna, 1958
Bryophyta	<i>Sphagnum recurvum</i>	11	8.95	B	Puri, 1981
Bryophyta	<i>Symphogyna brogniarti</i>	13	5.65	B	Puri, 1981
Gymnospermata	<i>Pinus monophylla</i>	30	10	G	Foster & Gifford, 1974
Psilophyta	<i>Psilotum nudum</i>	17	11	B	Sporne, 1975
Pteridophyta	<i>Azolla pinnata</i>	20	9	T	Konar & Kapoor, 1974
Pteridophyta	<i>Helminthostachys zeylandica</i>	5	7.85	T	Lang, 1902
Pteridophyta	<i>Hymenophyllum tunbridgensis</i>	15	9.85	T	Boodle, 1900
Pteridophyta	<i>Ophioglossum palmatum</i>	14	9.8	T	Chrysler, 1941
Pteridophyta	<i>Trichomanes rigidum</i>	5	3	T	Bower, 1928
Spermatophyta	<i>Croonia pauciflora</i>	42	10.2	A	Tomlinson & Ayensu, 1968
Spermatophyta	<i>Fuirena ciliaris</i>	44	10.4	A	Govindarajalu, 1969
Spermatophyta	<i>Lenna minor</i>	18	5.9	A	Daubs, 1965
Spermatophyta	<i>Lomandra hermaphroditicum</i>	36	10.55	A	Fahn, 1954
Spermatophyta	<i>Mamillaria elongata</i>	27	10.8	A	Darbishire, 1904

Spermatophyta	<i>Petermannia cirrhosa</i>	39 10.4	A	Tomlinson & Ayensu, 1969
Spermatophyta	<i>Sagittaria lancifolia</i>	42 11	A	Stant, 1964
Spermatophyta	<i>Selenipedium palmifolium</i>	35 10.1	A	Rosso, 1966
Spermatophyta	<i>Wolffia arnhiza</i>	5 4	A	Luandolt, 1986
Spermatophyta	<i>Wolffia microscopica</i>	7 4.85	A	Maheshwari, 1954
Spermatophyta	<i>Wolffella welwitschii</i>	8 5.6	A	Maheshwari, 1954
Sphenophyta	<i>Equisetum palustre</i>	16 10.75	B	Eames, 1936
RED SEAWEEDS				
Rhodophyta	<i>Beckerella scalaramosa</i>	12 10.5	R	Kraft, 1976
Rhodophyta	<i>Botryocladia wynnei</i>	6 6.6	R	Ballantine, 1985
Rhodophyta	<i>Farlowia mollis</i>	7 9.5	R	Abbott, 1962
Rhodophyta	<i>Gloeophycus koreanum</i>	12 10.8	R	Lee & Yoo, 1979
Rhodophyta	<i>Halymenia asymmetrica</i>	13 10.8	R	Gaetano, 1986
Rhodophyta	<i>Membranoptera subtropica</i>	12 6.8	R	Schneider & Eiseman, 1979
Rhodophyta	<i>Neodilsea natashae</i>	12 10.3	R	Linstrom, 1984
Rhodophyta	<i>Saiconema scinaoides</i>	13 9.4	R	Papenfuss & Edelstein, 1974
Rhodophyta	<i>Schimitzia hiscockiana</i>	14 11.3	R	Maggs & Guiry, 1985
Rhodophyta	<i>Schimmelmannia dawsonii</i>	11 11.4	R	Acleto, 1972
Rhodophyta	<i>Yamadaella cenomyce</i>	7 9.6	R	Abbott, 1970
Rhodophyta	<i>Yamadaphycus carnosus</i>	11 9	R	Mikami, 1973
FUNGI				
Ascomycota	<i>Gymnoascus reessii</i>	5 4.2	F	Gaumann, 1928
Ascomycota	<i>Leptosphaeria</i> sp	9 4.05	F	Gaumann, 1928
Basidiomycota	<i>Sphaerolobus stellatus</i>	9 6.1	B	Buller, 1933
Zygomycota	<i>Rhizopus nigricans</i>	3 2.8	Z	Gaumann, 1928
Zygomycota	<i>Mucor mucedo</i>	3 2.3	Z	Buller, 1931
ANIMALS				
Annelida	<i>Lumbricus terrestris</i>	57 10	W	Stephenson, 1930
Annelida	<i>Apodotrocha progenerans</i>	16 3.8	W	Westheide & Rieger, 1983
Annelida	<i>Hirudo medicinalis</i>	26 10.3	W	Mann, 1962
Annelida	<i>Aelosoma tenebrarum</i>	12 4.7	W	Brace, 1901
Annelida	<i>Nais variabilis</i>	13 5.4	W	Stephenson, 1908
Annelida	<i>Diurodrilus westheidi</i>	14 3.55	W	Kristensen & Nilon, 1982
Annelida	<i>Pomatoceros triquetra larva</i>	12 4.85	W	Segrove, 1941
Annelida	<i>Dasybranchus caducus larva</i>	10 4.5	W	Bookhaut, 1957
Annelida	<i>Pisone remota larva</i>	11 4.65	W	Akesson, 1961
Annelida	<i>Dinophilus conklinii</i>	23 4	W	Nelson, 1907
Arthropoda	<i>Callinectes sapidus</i>	69 11.5	O	Johnson, 1980
Arthropoda	<i>Periplaneta americana</i>	50 9.5	O	Smith, 1968
Chordata	<i>Canis familiaris</i>	99 13.7	V	Adam <i>et al.</i> , 1983
Chordata	<i>Morone saxatilis</i>	122 11.4	V	Groman, 1982
Chordata	<i>Salmo gairdneri</i>	116 11.4	V	Yasutake, 1983
Chordata	<i>Mus musculus</i>	102 11.3	V	Gude <i>et al.</i> , 1982
Cnidaria	<i>Hydra attenuata</i>	15 4.8	J	Campbell & Bode, 1983
Cnidaria	<i>Microhydra rideri</i>	3 2.1	J	Spoon & Blanquet, 1978
Cnidaria	<i>Halicystus halicystus</i>	22 7.5	J	Wietrzykowski, 1910
Cnidaria	<i>Cyanea cyanea</i>	22 13	J	Hyman, 1940
Ctenophora	<i>Pleurobrachia</i> sp	13 4	O	Hyman, 1940
Entoprocta	<i>Loxosoma sultana</i>	16 3.55	E	Harmer, 1885
Entoprocta	<i>Pedicellina echinata larva</i>	10 4.6	E	Hatschek, 1877
Gastrotricha	<i>Turbanella cornuta</i>	18 3.85	H	Teuchert, 1977
Gastrotricha	<i>Chordodasys antennatus</i>	15 3.1	H	Rieger, <i>et al.</i> , 1974
Gnathostomulida	<i>Rastrognaithia macrostoma</i>	13 3.5	G	Kristensen & Norrevang, 1977
Gnathostomulida	<i>Valvognathia pogonostoma</i>	15 3.25	G	Kristensen & Norrevang, 1978
Kinorhyncha	<i>Pycnophyes frequens</i>	16 3.9	K	Hyman, 1951
Mesozoa	<i>Dicyemenea lameerei</i>	3 2.35	M	Dougherty, 1963
Mesozoa	<i>Dicyema typhus</i>	3 3.2	M	Nouvel, 1947
Mesozoa	<i>Conocyema polymorpha</i>	3 1.45	M	Nouvel, 1947
Mesozoa	<i>Dicyemenea abelis</i>	6 1.3	M	Nouvel, 1947
Mesozoa	<i>Rhopalura granosa</i>	3 3.15	M	Atkinson, 1933
Mollusca	<i>Amphibola crenata larva</i>	9 4.3	U	Farnie, 1924
Mollusca	<i>Neomenia carinata larva</i>	7 3	U	Thompson, 1960
Nematoda	<i>Rhabditis monhystera</i>	23 2.65	N	White, 1988
Nematoda	<i>Caenorhabditis elegans</i>	24 2.95	N	White, 1988
Placozoa	<i>Trichoplax adhaerens</i>	4 2.5	L	Grell & Benwitz, 1971
Platyhelminthes	<i>Dugesia mediterranea</i>	14 6.25	Y	Castle, 1928
Platyhelminthes	<i>Anaperus sulcatus</i>	9 8.1	Y	Beklemishev, 1914
Platyhelminthes	<i>Macrostomum gigas</i>	14 5.7	Y	Hyman, 1951
Platyhelminthes	<i>Enterostomula graffi</i>	12 5.55	Y	Ruffin, 1941
Porifera	<i>Spongilla lacustris</i>	16 4	S	Brien, 1932
Rotifera	<i>Apsilus vorax</i>	16 5.15	F	Gast, 1900
Rotifera	<i>Notholca acuminata</i>	13 3.5	F	Pejlar, 1958
Sedes incertis	<i>Salinella salve</i>	3 1.95	?	Frenzel, 1892

TABLE 2. List of cell types for the nematode *Caenorhabditis elegans*. Source: White, 1988. This list is for the hermaphrodite, and excludes the spermatheca and associated sexual structures. In this organism, some ambiguity is introduced by the presence of syncytial tissues; the number of nuclei and the number of cells do not correspond. To make the data comparable with that of most other organisms, it is the number of cells contributing to a given tissue that is listed here

Category	Cell type	Number
Epithelium	Main body syncytium	110
	Seam cells of hypodermis	20
	Head and tail hypodermis	10
	Interfacial cells	9
Nervous tissue	Neurons	302
Mesoderm	Striated muscle cells	113
	Sarcomere muscles of pharynx	20
	Anal depressor	1
	Anal sphincter	1
	Head mesodermal cell	1
	Coelomocytes	6
Intestine	Intestinal tube	20
	Valves: toroidal cell of p/i valve	1
	valve/intestine junction intermediate cells	4 6
Glands	Pharyngeal glands: g1	3
	g2	2
Excretory tissue	Excretory cell	1
	Duct cell	1
	Pore cell	1
	Excretory gland	1
Ovary	Distal tip cell	1
	Sheath cells	2
	Oviduct sheath cells	8
	Anchor cell	1
	Attachment to sheath cells	6
Endothelium	Lining of uterus and rectum	52

Total cells: 703

Total cell types: 27

### *Analytical methods*

Methods for the analysis of comparative data, such as those we have collated here, are currently in flux, so we describe those we have used in some detail.

Preliminary analysis of unmodified character values for species indicated that a power function of the form  $Complexity = cSize^z$  offered a much better fit ( $R^2=0.25$ ) to the data than did linear ( $R^2=0.13$ ) or semi-log ( $R^2=0.16$ ) functions (the latter two having poorly-behaved residuals). Consequently both complexity and total cell number were logarithmically transformed (base ten) in advance of linear regression analyses. The lack of fit to a semi-log function also implies that the relationship between size and complexity is not simply the null expectation due to either smaller organisms being random samples of larger ones (M. A. Steel, pers. comm.) or to a

constraint on the maximum number of different cell types small organisms may contain (May, 1975). As we measured size as notional cell number, any relationship must be constrained to go through the origin (1 cell, 1 cell type). However, the smallest organism in our dataset (The mesozoan *Dicyemmenea abelis*) is composed of 20 cells. Smaller differentiated multicellular organisms are exceedingly rare, and so we do not know the shape of the curve at this extreme end of the scale (in fact, if there are no data, there can be no curve to fit). We therefore do not force our model to go through the origin, but note that the regression model will not be valid for the smallest possible organisms.

The comparative analysis is based on the method of independent contrasts, using Pagel's implementation (Pagel, 1992) of the argument from Felsenstein (1985). The method and its applicability have been discussed by Harvey & Pagel (1991), Pagel (1992, 1993), Purvis (1992), Garland, Harvey & Ives (1992) and Berrigan *et al.* (1993). The argument was implemented through the program CAIC (Comparative Analysis by Independent Contrasts) (Purvis & Rambaut, 1995). Faced with almost complete ignorance of the relative branch lengths on our compound tree, we set all branches to be equal in length. PIC has been found to be remarkably robust to violations of assumptions of branch length (Martins & Garland, 1991).

Model 1 regression of linear contrasts through the origin (Garland *et al.*, 1992) was used to evaluate the functional relationship of cell type diversity to cell number. The linear contrasts slope should provide the best estimate of the underlying evolutionary regression coefficient (Pagel, 1993). However, Model 1 regression will tend to underestimate the true slope if there is appreciable error variance associated with the independent variable. If the amount of error in  $x$  can be estimated, then a structural relations model can be used (Harvey and Pagel, 1991; Berrigan *et al.*, 1993). However, for a PIC analysis, we must assume that the assigned  $\lambda$  (which is the ratio of error variance in  $y$  to that in  $x$ ) remains constant throughout the tree, which will generally not be the case (A. Purvis, pers. comm.). Therefore we repeated the analyses ascribing *all* the error to the independent variable (i.e. simply reversing the  $x$  and  $y$  axes) and performing Model 1 regression. This is equivalent to setting  $\lambda=0$  and will give an upper estimate on the slope. The constant term in the power equation cannot be estimated from contrasts.

The phylogeny used as the basis for the comparative analysis is shown in the Appendix. Because the interpretation of the phylogeny of basic eukaryotic clades is changing rapidly, we adopted a highly conservative procedure. Only nucleic acid sequences (rRNA and rbcL) were used for the basal phylogeny. In Dicotyledonae and Annelida we supplemented this with cladistic diagnoses based on morphology, but treated other major taxa such as mesozoans, 'aschelminthes' (Rotifera, Entoprocta, Gnathostomulida), Chlorophyta, Pteridophyta and seedless vascular plants as undifferentiated 'soft polytomies' (Purvis & Garland, 1993). Each polytomy provided one contrast and one degree of freedom. We did not regard it as practicable or justifiable to calculate all possible contrasts at each polytomy. Our methods are robust to assumptions about branch length (Martins & Garland, 1991), and we chose to assume that all branch lengths are equal. This has the effect of assuming that changes are concentrated in the early history of lineages, rather than accumulating without bound (Harvey & Purvis, 1991). Thus, lineages in which a great deal of diversification has occurred will contribute relatively little to the reconstruction of basal nodes. This will not bias our results, because we are concerned more with trait changes than with ancestral trait values. Each of our procedures can be

justifiably challenged, but we repeat that we have deliberately chosen a conservative approach, rather than basing our analysis on a specific and perhaps evanescent interpretation of eukaryote evolution.

## RESULTS

The scatter-plot of species values of cell type diversity on total cell number is shown in Figure 1a. The independent-contrasts plot is shown in Figure 1b. There are fewer contrasts than raw data both because 14 species could not be placed on the phylogenetic tree (*Salinella salve* plus 13 Brown Algae) and because parts of the tree remain unresolved and so offer fewer than  $n-1$  contrasts. Removing those 14 species does not affect the species slope, nor does simply ignoring the contrasts estimated at multiple nodes (in both cases the slopes are changed less than one standard error). The Model 1 regression slope for the entire set of contrasts is 0.073 (SE 0.008,  $n=80$ ) with an estimated slope of 0.077 under the structural relations model. The estimated parameter values and corresponding statistics are presented in Table 3. The strongest relationship is found in the Plantae/Chlorophyta ( $r^2=0.80$ ,  $n=36$  spp), and the weakest is found in the Phaeophyta ( $r^2=0.19$ ,  $n=31$  spp).

The greatest cell type diversity for given total cell number is found in the Animalia. The contrast slopes for the three taxa with sufficient data (Animalia, Plantae + Chlorophyta and Phaeophyta) are not statistically different (General Linear Model of contrasts for the three groups, forced through the origin: interaction term [clade\*volume]  $F_{2,62}=2.45$ ,  $P=0.09$ ,  $n=67$ ). Therefore we can fit, using the method of least squares, the best estimate of the evolutionary relationship ( $z=0.073$  from Table 3) to the species values for the three groups in turn. This shows that the animal clade has the highest intercept (Animalia,  $c=0.78$  [SE  $\cong 0.040$ ]; Plantae + Chlorophyta,  $c=0.54$  [SE  $\cong 0.038$ ]; Phaeophyta,  $c=0.10$  [SE  $\cong 0.031$ ]). The intercept on the log-log plot affects the shape of the curve describing the relationship between the two variables (Rosenzweig, 1995). While contrasts cannot inform us directly about values for  $c$ , if different rules governing the evolutionary relationship between complexity and volume arose in the lineage leading to animals from that arising in the lineage leading to plants, then the independent contrast between the two clades should be anomalous. Indeed, the contrast between the two clades is the most *negative* of the 80: while the central tendency in size of the Plantae + Chlorophyta clade is marginally larger than that of its sister-group (Animalia + Fungi), measured as the reconstructed size at the basal node of each clade, the reconstructed number of cell types is almost half (3.0 versus 5.5). The assumptions made in the PIC analysis (e.g. that all branches in the tree are the same length) do not allow us to assume that all the contrasts come from the same distribution, and so preclude a formal statistical test. However, this observation is consistent with the comparison of intercepts of the species data. Different rules seem to govern the relationship between size and complexity in plants versus animals. The phaeophytes are the presumed outgroup to the combined clade of plants, chlorophytes, animals and fungi, and the contrast at this slope, though positive, is very shallow. While they are less than twice as complex, the central tendency in size among phaeophytes is some  $10^5$  times as large as that among the combined Plantae + Chlorophyta + Animalia + Fungi clade.



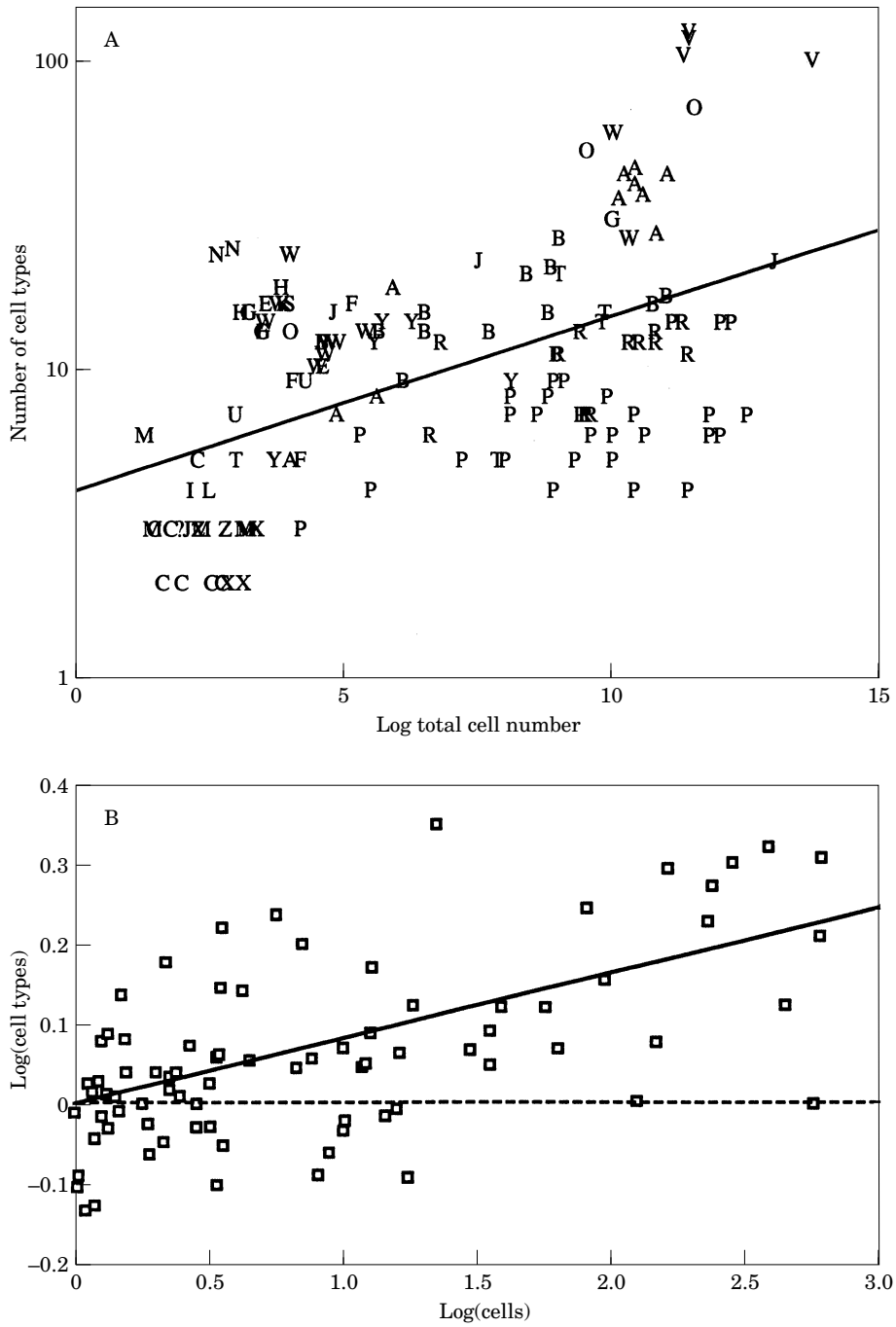


Figure 1. A, plot of total number of cell types on total notional cell number for 134 species of multicellular organisms. The slope of the Model 1 regression is 0.056 (SE 0.0086). The symbols represent phyla (see Table 1). B, plot of contrasts for total number of cell types on total notional cell number for 120 species of multicellular organism. The slope of the Model 1 regression is 0.073 (SE 0.008,  $n=80$ ). The regression is forced through the origin.

TABLE 3. Estimates of parameters describing relationship between complexity (number of cell types) and size (nominal number of cells) for species of multicellular organisms. The equation is of the form  $Complexity = cSize^z$ , with  $c$  and  $z$  estimated from straight line regressions of logarithmically-transformed data. <sup>a</sup>Estimates from Model 1 regression. <sup>b</sup>Estimates from Model 1 regression where all the error is ascribed to size rather than to complexity. \*\*\* $P < 0.001$ ; \*\* $P < 0.01$

	$n$	Across species			Independent Contrasts		
		$c$	$z (\pm SE)$	$R^2$	$n$	$z^a (\pm SE)$	$z^b$
All	134	0.61	0.056*** (0.0086)	0.25	80	0.073** (0.008)	0.15
Animals	45	0.63	0.10*** (0.012)	0.63	34	0.077** (0.014)	0.17
Plantae + Chlorophyta	36	0.26	0.11*** (0.010)	0.80	19	0.10** (0.013)	0.15
Phaeophyta	31	0.50	0.033** (0.013)	0.19	14	0.024** (0.010)	0.10

## DISCUSSION

### *Cell diversity increases with individual size*

Our main result is the quantitative confirmation of a trend that has long been recognised: larger organisms are more complex, in the sense of having a greater number of differently specialized types of cell. The comparative analysis shows that the greater complexity of larger organisms is not attributable to common ancestry alone, but has evolved independently in different groups for functional reasons.

### *Cooperative and competitive division of labour*

We propose that cell diversity can be interpreted as a cooperative physiological division of labour, akin to the specialization of tasks within an economic organization. In small or poor organizations, a specialized task, such as hiring or inventory, may make too small a contribution to the enterprise as a whole for it to be worthwhile to dedicate the work of a single person to this activity exclusively. The members of the organization will then be to a large extent generalists who each participate in a wide variety of tasks. In a large or rich organization, a comparable specialization may constitute the same fraction of overall activity, but because it will make a greater absolute contribution to profitability it may become worthwhile to dedicate the task exclusively to a single person, or group of people. Adam Smith (1776) identified three advantages of a cooperative division of labour: saving the loss of time involved in turning from one task to another; increasing the dexterity with which a repetitive operation can be performed; and encouraging mechanical innovation to replace human labour. The division of labour among cell types within the body, we suggest, has the analogous effect of increasing the rate of reproduction of the individual, although there is in fact little direct experimental evidence for this intuitively attractive idea (see Koufopanou & Bell, 1993). In this case, any advantage is likely to arise from a reduction in the extent to which different tasks performed simultaneously interfere with one another (Ghiselin, 1978).

By contrast, a competitive division of labour—among organizations in a society,

or species in an ecological community—arises because individual productivity, rather than the productivity of any larger unit, is enhanced by specialization. Nevertheless, competitive and cooperative divisions of labour have long been recognized (Adam Smith, 1776) to follow a similar general rule: just as the cooperative division of labour varies with the size of the organism or the organization, the degree of competitive division of labour varies with the extent of the market. Specialization is more profitable in larger markets (i.e. markets that involve more people, are intrinsically wealthier, or possess cheap and rapid means of transport) because as the overall size of the market increases the size of each sector of the market increases, so that a sector that could not engross the whole economic activity of an individual in a small market may do so in a larger market. A biological parallel is the familiar species-area relationship, probably caused by the greater diversity of habitats capable of supporting specialized populations in larger areas (Rosenzweig, 1995).

*The rules for cooperative and competitive division of labour are quantitatively different*

Despite the similarity of the two phenomena, our results suggest that cooperative and competitive division of labour may follow quantitatively different rules. The power law relating the the number of species to the areas of islands within archipelagos usually has an exponent of about 0.3; for non-nested subsamples of continental areas the exponent varies with scale, but remains consistently higher than 0.1, sometimes greatly so (Rosenzweig, 1995). May (1975) presents expected slopes for a series of biologically plausible scenarios of species interactions, including a generalized form of Preston's (1962) canonical relationship. For models that are fit by power laws,  $z$  ranges from 0.13 to 0.5. Sugihara (1980) presents an explicitly competitive model of species interactions which fits  $z=0.26$ . Our estimates show that the exponent of the power law reflecting cell diversity to the size of individuals is consistently less than 0.1. We infer that diversity increases less rapidly with economic scale when labour is divided cooperatively than when it is divided competitively.

*Why cell diversity is low in large organisms*

One possible reason for this tendency can be appreciated by considering the nature of the advantages associated with cooperative and competitive specialization. In a competitive context, a generalist will be only weakly selected for its ability to exploit some rare kind of resource. A specialized type restricted to this resource will be selected more strongly, will thus evolve an enhanced ability to exploit the resource, and will increase in numbers at the expense of the generalist—provided that the resource is sufficiently abundant to support a population at all. This process involves negative frequency-dependent selection that confers an advantage on rarity: so long as a specialized type is rare, its numbers are low relative to the availability of the resource, and its fitness is correspondingly high. In a cooperative context, the reverse is likely to be the case. Any advantage accruing from the specialization of a single cell is, in effect, distributed among all the cells of the body. In a large organism, it is unlikely, as a general rule, that a single cell will have any substantial effect on the performance of the individual as a whole. It is more likely that a tissue consisting of many similar cells will represent the smallest unit that can profitably be assigned

a distinct physiological task. To a point, therefore, the frequency-dependence of cooperative specialization is positive: specialization becomes profitable only when the number of cells dedicated to a particular task exceeds some minimal value. Thus, the number of rare species increases with the size of the community much faster than the number of cell types increases with the size of the body.

*Very small differentiated organisms seldom evolve*

Very small organisms, comprising fewer than about a hundred cells, encounter the contrary constraint. A single cell is the minimal unit of organization; and yet this may be too *large* a fraction of the whole body of a very small organism to commit to a specialized function. In somewhat larger organisms of about a thousand cells it becomes profitable to dedicate single cells to specific functions (see Table 2 for examples from *C. elegans*). In much larger organisms, as we have explained, single cells can seldom make any substantial contribution to the body as a whole, and differentiation is based on tissues. This effect of scale suggests that very small differentiated organisms will seldom evolve. This is, we believe, a little-appreciated general rule. There are multitudes of unicellular taxa, and similar multitudes of taxa whose members are made up of more than  $10^2$  or  $10^3$  cells. There are very few organisms that regularly develop as groups of between 2 and 10 cells. We have been unable to identify any organisms that comprise two differentiated cells: *Gonium* (Chlorophyta; Bold & Wynne, 1978) and the gametophyte of *Syringoderma floridana* (Phaeophyta; Henry, 1984) are two-celled but undifferentiated. Indeed, there seem to be very few examples of differentiated organisms with fewer than a hundred cells: colonial Volvocales such as *Pleodorina*, the endoparasitic dicyemid mesozoans and the enigmatic *Salinella*. The smallest differentiated freeliving animal that can be regularly collected is probably the highly reduced hydrozoan *Microhydra*. This odd gap in organic construction seems to arise from the economics of the cooperative division of labour.

*Cell type abundance is not distributed log-normally*

The constraints associated with cooperative systems of different sizes implies that there may be different processes governing the evolution of complexity at different scales. This means that explanations for patterns of diversity (such as those of May, 1975 and Sugihara, 1980) which assume that large areas or communities are simply larger samples of smaller communities may not pertain to the evolution of organismal complexity. This may be seen by considering the relative abundances of cells of different types in *Caenorhabditis elegans* (Table 2). Cell type abundance is not distributed log-normally, the expected distribution if the abundances were governed by several independent or competitive forces, and which would lead to a  $z$  in excess of 0.13. In fact, the distribution cannot be distinguished from the geometric ( $P=0.22$ , Kolmogorov-Smirnov test), indicating that there are many rare types and few very abundant types (such as striated muscle cells). This distribution is not unexpected given the geometric nature by which cells increase in number. However, this distribution cannot hold for all organisms, as the resulting relationship with size across species would be best fit with a *semi*-log curve, not a power relationship. As

we have pointed out, a very rare cell type may not be functionally effective in a large individual, because of the weakness of its cooperative interaction with the rest of the body.

Adam Smith's vision of the form of larger organizations can be extended. In larger organizations, not only can there be more division of labour (specialization), but opportunities for *new* endeavours should arise (e.g. through inventiveness). In the context of the species-area curve, biological interactions may increase the number of available niches in communities. In the context of individual complexity, as organisms become larger, new roles for communication and transport systems and skeletons may arise (Bonner, 1988).

*Some kinds of organism are more complex than others independently of size*

Our results show that, for given total size, animals are more complex than plants. We suggest very tentatively that this may be attributable to differences in metabolic rate. A higher rate of metabolism implies a greater rate at which resources are processed, analogously to an economy with a greater rate of circulation of wealth, and consequently a greater opportunity for the specialization of rare types.

*Conclusion*

The numbers of cell types increases with the total size of individualized organisms, independent of phylogenetic constraints. The form of the relationship implies that the relationship is not simply the result of larger organisms having more cells, and that there are general rules governing the evolution of organismal complexity. These rules will be governed by cooperative interactions, and may be qualitatively different from the more familiar ecological rules arising from competitive interactions; certainly, they give rise to quantitatively different patterns. We note that cell type number remains a very crude estimate of complexity, and hope that better measures, preferably genome-based, will be developed. We urge that further theoretical effort be directed towards the evolution of organismal complexity, in the light of the relationships that we have uncovered.

ACKNOWLEDGEMENTS

This work was supported by a Research Grant from the Natural Sciences and Engineering Research Council of Canada to GB. AOM was supported by the A.W. Killam Foundation and by an E.B. Eastburn (Hamilton Foundation) Fellowship. We are grateful to the students in advanced courses taught over a period of years by GB for their assistance in the development of this project, and especially to Torsten Bernhardt. We thank Peter Bednekoff, Rueven Dukas, Dolph Schluter and Mike Steel for discussion, and Andy Purvis for many explications of The Comparative Method and statistical expertise.

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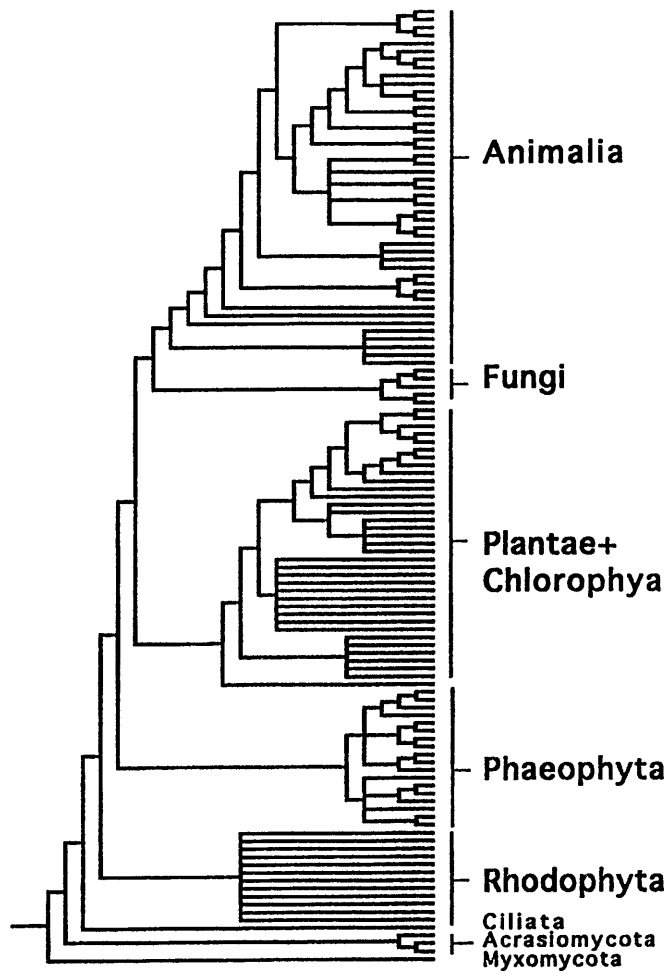


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## APPENDIX

Appendix, Figures 1–4. the composite phylogenetic tree used in the analyses. The following sources were used to construct the composite tree.

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Composite tree

