	Number of independent evolutions of complexity in social groups	172
	Complexity, sexual reproduction, and genetic variation	175
6.3	External drivers leading to greater size in social groups	176
	Short-term ecological drivers of greater size in social groups	176
	Long-term evolutionary drivers of greater size in social groups	177
6.4	Effect of increasing size of the social group on group complexity	179
	Reproductive division of labour within multicellular organisms	179
	Non-reproductive division of labour within multicellular organisms	183
	Reproductive division of labour within eusocial societies	184
	Non-reproductive division of labour within eusocial societies	190
6.5	Self-reinforcing social evolution in social group transformation	190
	Positive feedback favouring large group size in multicellular organisms	190
	Positive feedback favouring large group size in eusocial societies	191
6.6	The size-complexity hypothesis: conclusions	193
6.7	Summary	195
7	**Synthesis and conclusions**	**198**
7.1	The principles of social evolution: a summing-up	198
7.2	Open questions in the study of social evolution	201
7.3	The next major transition	201
7.4	Summary	205
References		**206**
Author Index		**245**
Subject Index		**253**
Taxonomic Index		**263**

1

An expanded view of social evolution

You are a scientifically curious protozoan living in a pond in Earth's very distant past, one and a half billion years ago. Having an inventive and adventurous nature, you build yourself a time machine and travel to the future. Your own world is inhabited almost entirely by single-celled creatures (unicells). Some are eukaryotes like yourself, defined by their possessing, among other things, intracellular organelles such as mitochondria or chloroplasts. The rest are prokaryotes (the Bacteria and Archaea), which lack organelles. Only the prokaryotes form multicellular structures, and these are threads, films, or mats that fail to grow very large, cannot move, and lack much in the way of internal complexity.

Arriving at the present day, you don a very small protective suit equipped with sensors and instruments with which to study your surroundings. With a shock, you become aware that the planet is now inhabited by creatures utterly alien to your previous experience. They are huge, many are mobile, and all possess a complex external and internal anatomy. Once your cilia have stopped trembling, you deploy your scientific instruments and begin to study them. With mounting astonishment you realize that each of these organisms is in fact a colony of billions of cells. These cells are like yourself but are physically stuck together by organic glue and diversified into dozens of bizarre forms. Most are sterile, having grown incapable of dividing in order to serve the organism as a whole. In short, you find that your descendants risk seeing their individuality extinguished through becoming tiny, subordinated parts of organisms of a wholly new kind, which have themselves diversified into a multitude of forms. We know these monsters as tigers, trees, toadstools, and their like, or multicellular animals, plants, and fungi.

Thunderstruck by this glimpse of the future, you flee to your own era. Then, perhaps seeking reassurance in an Edenic past, you turn the dial of your time machine in the opposite direction and travel backwards in time for another billion and a half years. Once at your destination, you rediscover your scientific curiosity and again begin to study the fauna of the time. This previous world turns out to be inhabited exclusively by prokaryotes. But your studies deliver another resounding intellectual jolt. Pondering on the lack of eukaryotes, studying the results from your field genome-sequencing kit, and carefully observing bacterial anatomy and behaviour, you realize that you yourself are a colonial organism. You and all other eukaryotic unicells arose from a symbiotic fusion of your ancestors with bacteria. Your formerly distinct bacterial partners live on as your mitochondria or chloroplasts, having propagated themselves inside your forebears in the unbroken line that leads to yourself.

In sum, you are an amalgam of simpler, more ancient cells whose descendants face a future as enslaved subunits of massive, multicellular conglomerates. You think about the processes that brought about such an extraordinary pair of transformations. You wonder what the next one will be.

1.1 The biological hierarchy, the evolution of individuality, and the major evolutionary transitions

Stripped of its elements of obvious fantasy and granted some allowance for uncertainty in the dates, the tale with which this chapter opens reflects science fact. The history of life on Earth has often been portrayed as the succession of different taxonomic groups of organisms, with, for example, the Age of Fishes leading to the Age of Reptiles, and the Age of Reptiles in turn being followed by the Age of Mammals. This is the view of traditional textbooks and lives on in present-day television documentaries, which expertly combine the most astounding twenty-first century photography and computer animation with the stodgiest kind of nineteenth-century zoology. Such a view is discredited by its unfounded assumption that ecological dominance is a one-dimensional quality readily attributable to single taxa. It also fails to see beyond the superficial differences between separate taxa to the more fundamental properties that they have in common. As Knoll (2003) nicely put it, 'Such catalogs of received wisdom can be memorized, but there isn't a lot to think about'. Another view sees the history of life as a succession of technical innovations, such as the origin of photosynthesis, of land-dwelling, of flight, and so on. This view is more defensible because it offers one way of explaining changes in the complexity of life over time. But it again fails to provide any sort of underlying, unifying framework with which to explain the logic of such changes.

An altogether different view of life's history overcomes these deficiencies by focusing on the hierarchical organization of the units of life. Genes occur in cells and cells fuse to form other cells. Cells may occur within multicellular organisms, and multicellular organisms occur, at least in some cases, in societies. Since units at each level also occur independently, and each level requires the presence of the lower ones, it follows that in the history of life there were distinct events in which genes grouped into cells, cells grouped to become a different type of cell, cells further grouped into multicellular organisms, and multicellular organisms grouped into societies. Fundamentally, the history of life has been the history of the grouping of biological units into higher-level units and the subsequent consolidation of the new higher-level units into integrated collectives, with this process, once started, having been repeated several times to generate the biological hierarchy we observe today.

This hierarchical view of life's fundamental evolutionary history arose in the late-nineteenth century and early twentieth century (Mackie 1986; Buss 1987). For example, in a 1924 text, A. Dendy wrote that 'evolution consists to a very large extent, if not mainly, in the progressive merging of individualities of a lower order in others of a higher order' (quoted in Mackie 1986). The construction of analogies between different levels of organization, especially between multicellular organisms and societies, also has a long history (Wheeler 1911; Wilson 1971). However, perhaps because, in their time, these early ideas lacked a clear theoretical underpinning, they failed to achieve widespread influence in the evolutionary synthesis of the mid-twentieth century. Similarly, in the latter half of the century, they suffered in the reaction against the naive group selectionism with which they were frequently linked (Williams 1966).

The modern form of the hierarchical view was foreshadowed by Bonner (1974), who considered 'a number of major steps in evolution where one leaps from one level of complexity to the next' via a 'compounding of units on a previous level'. Along with the origin of cellular life, the steps that Bonner (1974) highlighted were the origin of eukaryotes, the origin of multicellular organisms, and the origin of social organisms. The modern hierarchical view gathered momentum in the late-1980s with the works of Buss (1987) on the evolution of individuality and Maynard Smith (1988) on evolutionary progress and levels of selection. Buss's (1987) book, *The evolution of individuality*, presented the first treatment of the modern hierarchical view in a single, dedicated volume. Evolution of individuality refers to the evolution of individuals, in the sense of stable, integrated collectives, via the grouping together of formerly independent units. (I discuss the use of 'individual' in this sense more fully in Section 1.3.) Buss (1987) focused on the evolution of individuality in multicellular organisms. Conceptually, he placed his exposition in the framework of multilevel selection theory but clouded some issues by unnecessarily setting multilevel selection theory at odds with other theories of selection such as Hamilton's (1963, 1964) inclusive fitness theory. A comprehensive synthesis of the hierarchical view of evolution, spanning many levels and adopting a cogent approach to selection theory, came with the publication of Maynard Smith and Szathmáry's (1995) landmark book on the major transitions in evolution, a concept with which the idea of the evolution of individuality is closely intertwined. The term 'major transition in evolution' was proposed by Maynard Smith and Szathmáry (1995) to describe the evolution of each successive level of life's hierarchy. As we have seen, Bonner (1974) had already written of 'major steps in evolution' in this context. He also used the term 'transition point' to describe each step. Likewise, both Buss (1987) and Maynard Smith (1988) used 'transition' for the same purpose.

The concepts of the evolution of individuality and major transitions are themselves underpinned by a key insight whose roots stretch back to the early 1960s, being based in the gene's-eye (or 'selfish gene') view of natural selection and, by implication, in inclusive fitness theory (Hamilton 1963; Dawkins 1976, 1982). This insight is that the individuality emerging at each major evolutionary transition is a contingent state. Specifically, it is contingent upon the absence or suppression of within-individual conflict (e.g. Leigh 1977, 1991; Alexander and Borgia 1978; Eberhard 1980; Cosmides and Tooby 1981; Dawkins 1982; Buss 1987; Maynard Smith 1988; Bourke and Franks 1995; Maynard Smith and Szathmáry 1995). For, if the level of internal conflict is too great, the higher level of organization either fails to emerge or is unstable and collapses. The challenge has been to understand what kinds of process contribute to the stable evolution of each new level in the hierarchy of major transitions (Buss 1987; Maynard Smith 1988; Leigh 1991; Maynard Smith and Szathmáry 1995).