is characterized by very slow conservative change among species dominated by strong stabilizing selection within species.

Overall, the most interesting suggestion that emerges from this study is that essential features of the cell, such as the structure and function of the spindle, might arise from very simple scaling rules with cell size per se, which makes sense since the spindle itself is stretched during the course of cell division. This relationship also appears to be true within an individual because centrosome and spindle size also scale with cell size as embryogenesis in both *C. elegans* and the amphibian *Xenopus laevis* proceeds to produce smaller and smaller cells [9–11]. Strong relationships between overall size and global organismal features, such as body proportion and metabolic rate, have been a central feature of comparative biology for more than one hundred years [12]. It will be interesting to see whether the scaling relationship observed here is simply an interesting hypothesis that appears to fit data from a particular group of nematodes or whether it is indeed a general rule that explains the structure of the mitotic spindle across all animals. Application of similar methods will also open up other areas of cell biology to similar questions about patterns of organelle variation and evolution, such as the distribution and abundance of mitochondria, Golgi and endoplasmic reticulum. Advances in automated subcellular microscopy pioneered by Farhadifar *et al.* [5], in addition to work from a number of other groups [13], now make it possible to conduct the high-precision, high-throughput analysis needed to examine a large number of specimens from many different species. Their approach of combining an extensive collection of cell structure features with a rigorous evolutionary analytical framework points toward a new unified approach for addressing many long-standing questions in cell biology. In this way, this work is a harbinger of what is sure to be an exciting new era marking the emergence of evolutionary cell biology as a proper field of study [2].

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Life History Evolution: What Does a Menopausal Killer Whale Do?

Menopause evolved in humans and whales, presumably because older females can help their kin. But how do they help? New research shows that post-menopausal female killer whales lead foraging groups. This leadership is most significant when food is scarce.

Hal Whitehead

Menopause, in which human females routinely live a substantial part of their lives after last giving birth, even following their ability to give birth, is an evolutionary puzzle [1]. If the currency of evolution, fitness, is the number of genes passed to subsequent generations, menopause appears to be a “Darwinian abdication” [2]. Even though reproduction may become increasingly problematic with age, as it does for most female mammals, surely they should try? The evolutionary conundrum is avoided if females rarely lived beyond about age 45 during most of human evolution: there would be no selective pressure for reproduction at older ages [3]. However, this “menopause as an epiphenomenon” hypothesis is countered by the presence of numbers of elderly women in societies without the survival benefits of modern societies, such as plumbing, democracy and health care [4]. Even more damning is the presence of menopause in non-human animals, such as killer whales and long-finned pilot whales. Like human women, female killer and sort-finned pilot whales stop reproducing in their early forties, but may live into their eighties [5,6]. So, menopause is a true evolutionary puzzle, and a broader one than had originally been thought. In recent years explanations for menopause have focussed on what have been called the ‘mother hypothesis’ [1] and the ‘grandmother hypothesis’ [7] — that older females help their children and grandchildren, respectively, and that this help outweighs the potential for reproduction when older. But how do they help? In this issue of

Figure 1. Knowledge leads the way.
Post-menopausal female killer whale L2 leads her adult son L78 around salmon foraging grounds. Photo: David Ellifrit, Center for Whale Research.

Current Biology, Brent *et al.* [8] investigate the possibility that postmenopausal female killer whales may possess ecological knowledge that can be used by their kin.

The mother and grandmother hypotheses received important support in the theoretical models of Johnstone and Cant [9]. They showed that in the quite different social systems of humans and matrilineal whales — females staying grouped with their mother while both are alive — and in contrast to most mammal species, females become increasingly surrounded by close kin as they age. In these societies, an older female will typically have plenty of opportunity to help her descendants. The mother and grandmother hypotheses have been tested with empirical data. In pre-modern Finland and Canada, women who had long post-reproductive lives had more grandchildren [10], but their children did not noticeably survive better [11], supporting the grandmother but not the mother hypothesis. In contrast, the death of a female killer whale in her 30s profoundly reduces the survival prospects of her offspring, especially her sons [12], in line with the mother hypothesis. The grandmother hypothesis has not yet been tested in whales.

But how do grannies help? Human grandmothers can and do help their grandchildren by gathering food [7] and in other ways. However, perhaps especially in preliterate societies, human grandmothers also have an informational role: their knowledge can be extremely important to their relatives, for instance in rare but challenging environmental conditions such as the aftermath of devastating storms [13]. It was much less clear how post-reproductive female whales might help [14].

For their new study, Brent *et al.* [8] took advantage of the fact that, compared to almost any other population of wild animals, the ‘southern resident’ population of killer whales (*Orcinus orca*) off southern Vancouver Island is remarkably well known from decades of patient observation and photography [6]. Individuals can be identified visually, and their ages and genealogy are well known. The authors used a simple data source, 751 hours of video of the whales swimming at the surface as they foraged in groups, and noted who was in front (Figure 1). These whales, which live in strict matrilineal societies, principally eat Chinook salmon, and the Chinook may not always be easily found. If the ecological knowledge of the elderly, menopausal females is useful to their kin, the authors predicted that these older females should lead the groups of foraging whales. Indeed, they did. And, in accordance with the demographic data that supported the mother hypothesis [12], they tended to lead their sons more often than their daughters. Male killer whales are impressive animals; at about 6 tonnes they are much larger than the females, and they have dramatic dorsal fins reaching up to 2 m (Figure 1). However, resident killer whale males seem to have challenging lives, with much higher mortality rates than their sisters [12], perhaps because their prey, the salmon, are relatively small. They stay with their mother, effectively doubling the society’s matrilineal nature, and are dependent on her and on what she knows [8].

Because the demography and diet of this population have been so well studied, Brent *et al.* [8] could also look at how these patterns varied with ecological stress. When Chinook salmon become less abundant, mortality in this population rises dramatically [15]. And, as the authors found, the leadership of post-reproductive females became more frequent in these trying conditions.

Apart from the males staying with mother, the highly matrilineal social systems and life histories of killer whales, as well as some other cetacean species, have a lot in common with elephants and a few other large matrilineal mammals. Elephant societies are clearly matriarchal — elderly females lead [16] — but, until this new study [8], there was little evidence for leadership among the matrilineal whales [2]. We can now call the resident killers matriarchal as well as matrilineal. The leadership of elderly females supports hypotheses about the importance of knowledge in whale communities [2]. My colleagues and I have linked such phenomena to the concept of cultural transmission [2,14], but we need to be careful. Using the accumulated knowledge of older relatives — as these killer whales seem to do, and as has been found in elephants [16] — is not by itself culture. Cultural transmission requires the knowledge to be transmitted rather than just used. Although it is a reasonable hypothesis, we do not yet know whether killer whales learn foraging patterns from their elders.

Another note of caution comes with the study species, killer whales. Killer whales, the ocean’s top predators, eat a great diversity of food, from penguins to sharks to the great whales. But each killer whale is a member of an ecotype, and the ecotype's diet may be much more restricted, witness the focus on Chinook salmon of the southern residents [17]. The ecotypes differ in other ways. For instance, members of the North Pacific 'transient' ecotype who can be seen in the same waters as the southern residents, eat marine mammals rather than salmon, have larger ranges and are much less vocal [17]. The differences are so substantial that geneticists have suggested that the different killer whale ecotypes should be considered species or subspecies [18].

The benefits of older mothers for survival and leadership [8,12] only refer to the 'southern' community of the resident, salmon-eating ecotype. Are they also present in other communities of resident ecotype killer whales, which also eat salmon? The residents have a very unusual social system in which neither sex leaves its mother's group: "Momma's boys and girls" [19]. This arrangement leads to the increasing presence of kin as females age, and strong theoretical support for menopause [9]. The mammal-eating transient killer whales are less rigid about spending their whole lives with mother [20], as may be other ecotypes whose social systems are even less studied. Do they have menopause? And who leads? Comparative studies among killer whale ecotypes have much to tell us.

Even more broadly, there are about 87 species of cetaceans — whales and dolphins — with a great variety of diets, habitats and social systems. The short-finned pilot whale, another matrilineal species, seems to have a menopause as pronounced as that in humans and resident killer whales. In other species, such as sperm whales, there are strong indications that reproduction ceases for older females, while many species, including the porpoises and baleen whales, do not have menopause [5]. The social systems of only four of these species of Cetacea have been studied in much detail [2]. There is so much to learn.

We now have a remarkable insight into the lives of the resident killer whales, capped by the study reported in this issue [8], showing how much can be learned by long-term, persistent observation. New technology is adding genomics, as well as fine scale behaviour and physiology from suction-cup tags. The evolution of the southern resident population should before long be traceable at the level of individuals, as they react to their dynamic physical, biotic and social environments.

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Microbial Diversity: A Bonanza of Phyla

Metagenomics and single-cell genomics are now the gold standard for exploring microbial diversity. A new study focusing on enigmatic ultra-small archaea greatly expands known genetic diversity within Archaea, and reports the first complete archaeal genomes reconstructed from metagenomic data only.

Laura Eme and W. Ford Doolittle*

The ribosomal RNA (rRNA)-based universal Tree of Life that appears in biology textbooks, the signal achievement of Carl Woese and his school [1], separates the living world into three domains — Bacteria, Archaea and Eukarya. Characteristically this tree shows long unbranched 'trunks' leading to each of the three domains, these trunks representing the gaps between them (Figure 1A). The gaps were initially interpreted by Woese to indicate a different tempo or mode of evolution early on, before the formation of the domains. But two things are inevitable about trees: first, that if speciation and extinction are in balance, considerable