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Modular Construction of Early Ediacaran Complex Life Forms

Guy M. Narbonne

Newly discovered, exceptionally preserved, soft-bodied fossils near Spaniard's Bay in eastern Newfoundland exhibit features not previously described from Ediacaran (terminal Neoproterozoic) fossils. All of the Spaniard's Bay taxa were composed of similar architectural elements—centimeter-scale frondlets exhibiting three orders of fracticality in branching. Frondlets were combined as modules atop semi-rigid organic skeletons to form a wide array of larger constructions, including frondose and plumose structures. This architecture and construction define the "rangeomorphs," a biological clade that dominated the Mistaken Point assemblage (575 to 560 million years ago) but does not appear to be ancestral to any Phanerozoic or modern organisms.

The Ediacara biota is a distinctive fossil assemblage of impressions of centimeter- to meter-scale, soft-bodied organisms that represent the oldest large and complex organisms and ecosystems in Earth history (*1*–*3*). The long-standing morphological view that the Ediacara biota contains the oldest animal megafossils is supported by the presence of probable animal embryos (*4*), burrows attributable to coelomic animals (*5*, *6*), and a community organization that resembles that of modern suspension-feeding animals (*7*, *8*). However, some Ediacaran taxa are more difficult to relate to living animal groups and have elicited interpretations that span virtually all extant kingdoms of macroscopic eukaryotes (*9*–*11*) as well as a hypothesized extinct kingdom (*12*).

Fossils of the Mistaken Point assemblage (575 to 560 million years ago) in eastern Newfoundland, Canada (Fig. 1) represent the oldest reliably dated examples of the Ediacara biota (*13*–*15*). In contrast to younger Ediacaran assemblages from Australia and Russia, which contain segmented forms that are at least broadly comparable with modern animal phyla (*16*–*18*), the Mistaken Point assemblage is dominated by fossils exhibiting fractal-like quilting and whose relationships with modern taxa are not obvious at even the phylum level (*12*). Previous research on the Mistaken Point assemblage has focused on southeastern Avalon Peninsula, particularly outcrops in the vicinity of Portugal Cove South and Mistaken Point (*7*, *8*, *11*–*12*, *15*, *19*–*23*). Preservation of these fossils as census populations beneath beds of volcanic ash provides a superb database for stratigraphic and ecological studies, but because of the grain size of the ash and subsequent penetrative tectonic deformation, fossil preservation is limited to two-dimensional impressions, with little resolution of features <1 to 2 mm in diameter (*8*, *19*, *20*).

A newly discovered and exquisitely preserved fossil assemblage in the Trepassey Formation of the Spaniard's Bay area of northern Avalon Peninsula (Fig. 1) provides more than an order of magnitude finer resolution of the fossils of the Mistaken Point assemblage. The fossils occur in a deep-water, turbiditic slope succession that contains decameter-scale slump beds and lacks any evidence that storm waves or light reached the sea floor. More than 100 frondose and plumose fossils are present on this surface. Their consistent unimodal current alignment, similar to that of other assemblages of the Mistaken Point biota (*19*, *20*), implies that they were tethered to the sea floor and were then buried in place. The fossils show no evidence of tectonic cleavage and are preserved as uncompressed external molds (or rarely as natural casts) within a muddy, distal $T_{D\text{-}E}$ turbidite, permitting resolution of features less than 30 μm in diameter on the best preserved specimens (Fig. 2). Their preservation within the fine sediment differs from the rapid preservation associated with microbial mats described from other Ediacaran localities (*24*); moreover, some Spaniard's Bay specimens partially decomposed before lithification, revealing internal structures previously unknown from the Ediacara biota (Fig. 3, B and D). Information provided from this unique taphonomic window helps to elucidate previously unknown attributes of the architecture and construction of the earliest Ediacaran organisms.

All taxa at the new Spaniard's Bay locality, and most of the 20 to 30 other taxa of the Mistaken Point assemblage elsewhere (*8*, *21*, *23*), are composed of varying constructions of the same architectural building block—a centimeter-scale module herein termed a "rangeomorph frondlet" (Fig. 2A). Each frondlet consists of inflated, self-similar branches that are indistinguishable from the "fractal pneus" defined by Seilacher (*12*). Pneus pass from the midline at an acute angle in an alternate pattern, but variable orientations of rangeomorph frondlets can give the appearance of asymmetric branch lengths or even branching on only one side of the frondlet (Fig. 2). The pattern of branching is remarkably self-similar over three orders of fracticality: Major branches with diameters ranging from 1 to 5 mm are composed of minor branches 0.3 to 0.6 mm in diameter, which, in the best preserved specimens, appear to be composed of tertiary branches <150 μm in diameter (Fig. 2, A to D). Partially overturned specimens reveal that both sides of a rangeomorph frondlet are identical and that each pneu has a circular cross section (Fig. 2, C and D).

Isolated rangeomorph frondlets at Spaniard's Bay exhibit a proximal stem (Fig. 2A) and are aligned parallel with the other fronds on the surface, and thus were probably miniature, free-living fronds attached to the sea floor.

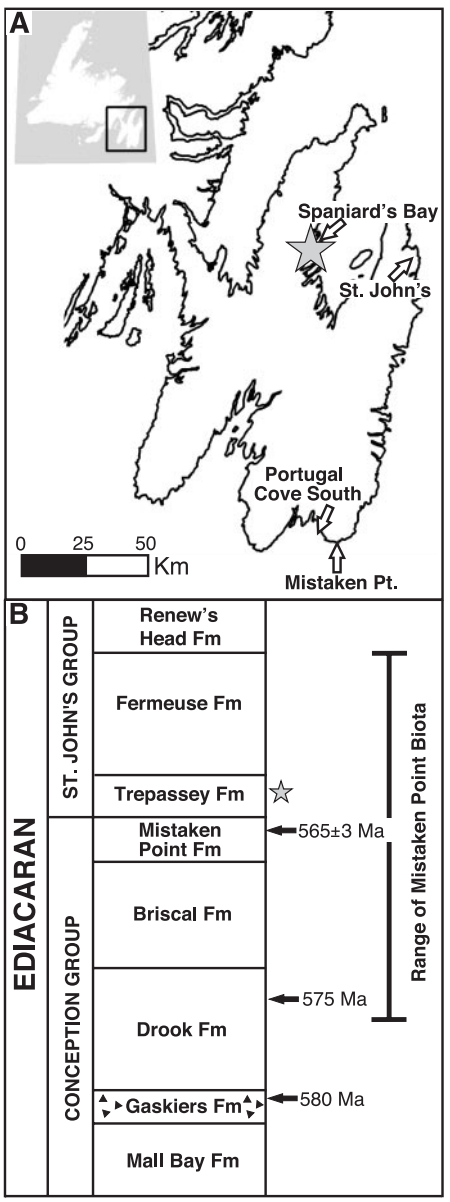


Fig. 1. Location (**A**) and stratigraphic setting (**B**) of the newly discovered bed of fossil rangeomorphs in the Trepassey Formation of the Spaniard's Bay area, eastern Newfoundland, Canada. The star (★) shows the geographic and stratigraphic position of the new fossil occurrence. U-Pb dates are from (*13*, *14*) and references therein.

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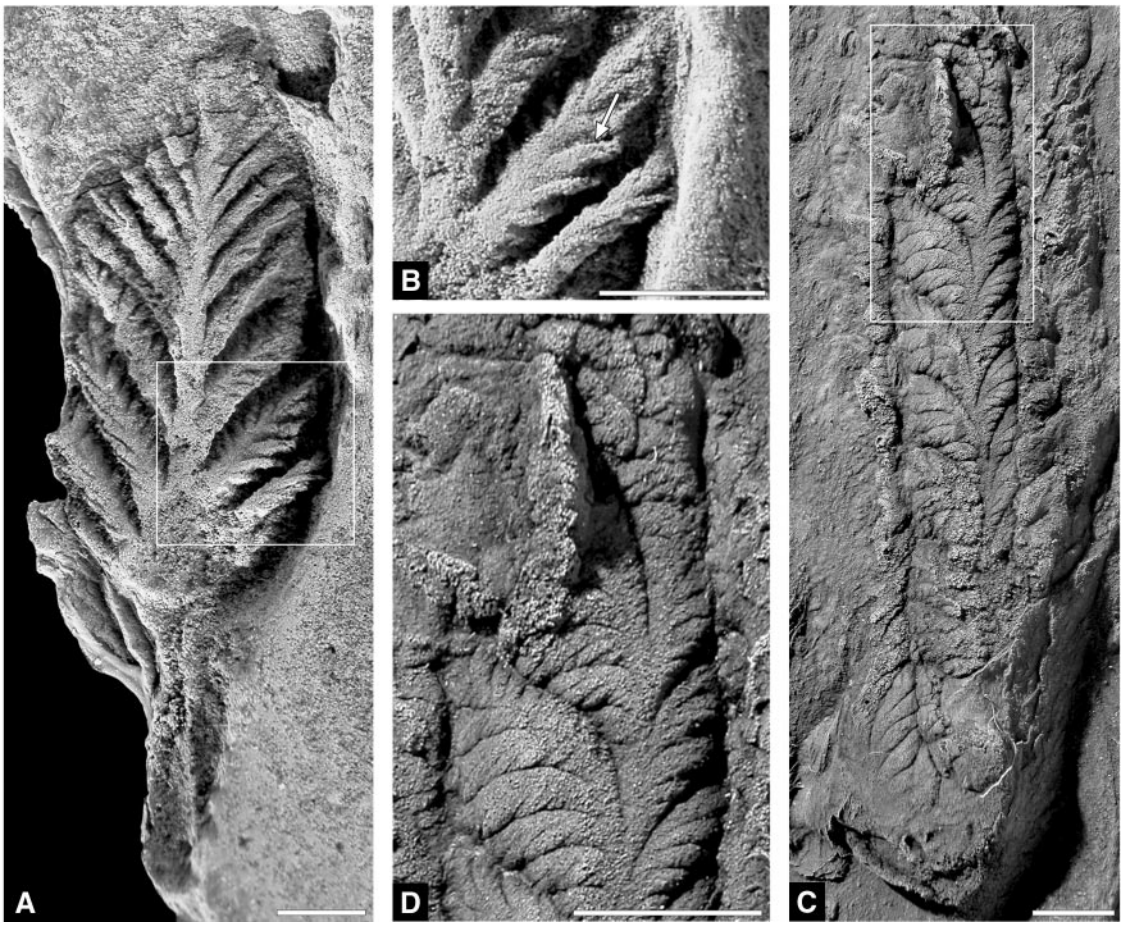


Fig. 2. Rangeomorph architecture from the Trepassey Formation at Spaniard's Bay. (**A**) Isolated rangeomorph frondlet. Specimen whitened with ammonium chloride. (**B**) Enlarged view of the area indicated in (A), showing details of the fractal-like branching pattern. The smallest branches are indicated by the arrow. (**C**) Plumose rangeomorph. Latex mold whitened with ammonium chloride. (**D**) Enlarged view of the area indicated in (C), showing details of the fractal-like branching pattern and the cylindrical cross section of the branches in the ripped and partially overturned frondlet in the upper left. Scale bars, 0.25 cm [(A) and (B)], 0.5 cm [(C) and (D)].

More commonly, rangeomorph frondlets were combined as modules to construct larger and more complicated structures (Fig. 2, C and D; Fig. 3, A to F).

The most familiar rangeomorph constructions are fronds, in which the rangeomorph frondlets were elevated above the sea floor by a stalk attached to a holdfast (Fig. 3, A to C). Previously described rangeomorph fronds are generally referred to *Rangea*, in which the rangeomorph frondlets are arranged in parallel arrays attached to multifoliate sheets surrounding the stalk (*25*–*27*). At least six different constructions of rangeomorph fronds are evident at different stratigraphic levels in the Mistaken Point assemblage (*28*). A new form at Spaniard's Bay differs from typical specimens of *Rangea* in exhibiting rangeomorph frondlets that are arranged as isolated, overlapping petal-shaped elements, each of which is attached at its proximal end to a central stalk (Fig. 3A). A second undescribed taxon at Spaniard's Bay exhibits rangeomorph frondlets that hang downward in a pendant array from a thin, presumably semi-rigid, zigzag central stalk with lateral struts (Fig. 3, B and C). The very close similarity in size and morphology between each "petal" of these fronds and the free-living rangeomorph frondlet (Fig. 2A) raises the distinct possibility that these fronds, and probably other rangeomorphs, were capable of vegetative reproduction.

Jenkins (*25*) regarded the cosmopolitan Ediacaran frond *Charnia* as a rangeomorph, a view supported by our reports of a rangeomorph pattern within individual segments of *C. masoni* (*21*) and *C. wardi* (*15*) lower in the Mistaken Point succession. One specimen at Spaniard's Bay (Fig. 3D) shows a *Charnia*-like quilted pattern of curved major branches arranged in an alternate pattern about the midline that are divided at right angles into secondary branches, but this has been removed in places to reveal struts of an internal organic skeleton beneath the inflated branches. All rangeomorph taxa at the Spaniard's Bay locality show evidence of an internal, semi-rigid, organic skeleton on which the rangeomorph frondlets were suspended above the sea floor, an internal feature not previously reported from rangeomorphs or any other Ediacaran taxa.

Five specimens of a "plumose rangeomorph" also occur at Spaniard's Bay (Fig. 2, C and D). Their construction superficially resembles that of a garden leek, with a basal holdfast surrounded by layered sheets that extended upward in a plumose pattern. Each sheet consists of a vane-like pattern of rangeomorph frondlets, connected at their proximal ends, that pass off the midline at an acute angle. The rangeomorph frondlets in each sheet are oriented with their distal tips pointing out and toward the base of the fossil. Plumose rangeomorphs are oriented parallel to the fronds on the surface, implying that they were also tethered to the sea floor.

Three other rangeomorph constructions are present in the Mistaken Point assemblage at other localities and stratigraphic levels, and these serve to emphasize the importance and diversity of rangeomorphs in early Ediacaran ecosystems. Bush-shaped rangeomorphs (Fig. 3E) are broadly similar in structure to the plumose forms but are more complex three-dimensional constructions with larger frondlet sheets, a more rounded shape, and lack of an obvious attachment disc. Specimens are similar to *Bradgatia* from Avalonian strata in central England (*29*) but are smaller, with frondlets that are more crowded and less distinct. Well-preserved specimens of the previously enigmatic "comb-shaped fossils" (*22*) from Mistaken Point suggest that these consist of a row of identical rangeomorph frondlets connected by a basal stolon. Spindle-shaped rangeomorphs (Fig. 3F) exhibit a vane-like pattern of rangeomorph frondlets that pass off the midline at right angles in an opposite or alternate pattern to end at the outer margin of the specimen. Par-

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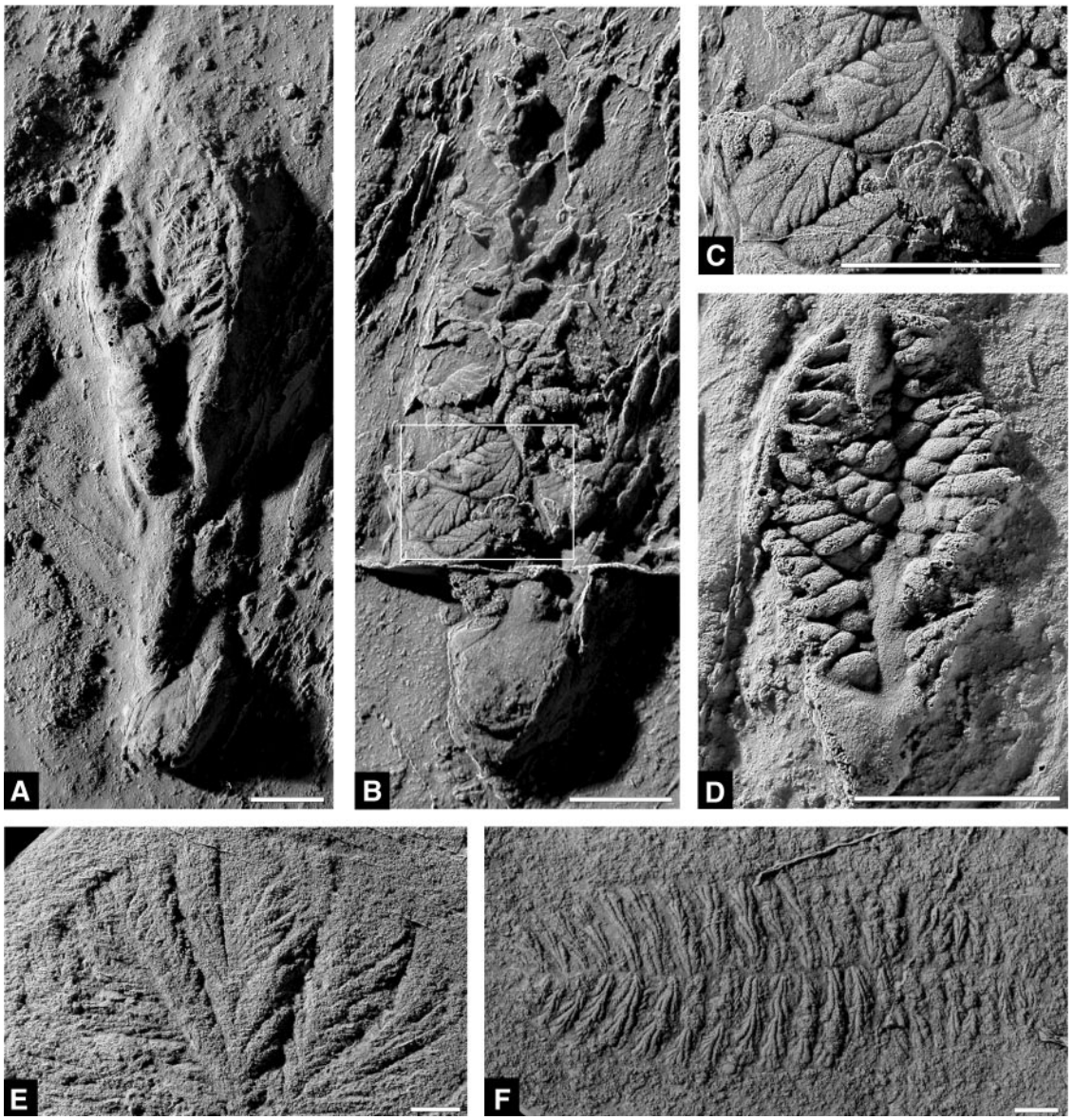


Fig. 3. Rangeomorph constructions from the Trepassey Formation at Spaniard's Bay (upper panels) and from the Mistaken Point Formation at Mistaken Point (lower panels). All specimens are latex molds whitened with ammonium chloride. (**A**) Long-stemmed rangeomorph frond with leaf composed of overlapping rangeomorph frondlets attached at their bases to the central stalk. Elements are partially deflated. (**B**) Short-stemmed rangeomorph frond with leaf composed of pendant rangeomorph frondlets hanging from a thin central stalk with side struts. (**C**) Enlarged view of the area indicated in (B). (**D**) *Charnia*-like frond with quilted array of major and minor branches overlying an internal organic skeleton. (**E**) Bush-shaped rangeomorph construction. (**F**) Spindle-shaped rangeomorph construction. Scale bars, 1 cm.

tially overturned specimens reveal that the other side of the specimen is identical (*12*). Crowding and fusion of adjacent rangeomorph frondlets in the spindles have caused them to become considerably elongated relative to the free-living rangeomorph frondlet, but their structure is otherwise indistinguishable. Spindle-shaped rangeomorphs were not aligned by currents (*19*, *20*) and probably functioned as recliners attached to the sea floor.

The morphologic features described above provide strong support for the view that rangeomorphs represent a single clade, a high-level taxon that went extinct in the terminal Proterozoic (*12*, *25*). It is probable that the Ediacara biota included stem groups for the Cambrian explosion of animals (*16*–*18*), but there are no obvious analogs for rangeomorph architecture and construction among modern taxa. Recent comparison of rangeomorph structure with the radial canals of fossil and recent ctenophores (*26*) seems remote from a morphological standpoint and is also inconsistent with the internal organic skeletons documented above. It would be tempting to regard the two-dimensional view of a rangeomorph frondlet as representing the bases of an array of open tubes that housed polyps or other filter-feeding organisms, but this is not consistent with partially overturned specimens that show that both sides are identical (Fig. 2D); the very small diameter of the secondary (300 to 600 μm) and tertiary (<150 μm) pneus would also specifically rule out cnidarian polyps as the originators of the tubes.

These modular constructions effectively partitioned food resources: Spindle-shaped rangeomorph recliners lay on the sea floor, whereas bush-, plume-, comb-, and frond-shaped rangeomorphs were elevated above the sea floor and fed from different levels within the water column (*7*). Rangeomorphs dominated the earliest Ediacaran ecosystems, with no evidence for burrowing, mobile, or metameric megascopic organisms among the taxa of the Mistaken Point assemblage. Rangeomorphs occur only sporadically in younger Ediacaran assemblages (*16*, *25*–*27*), perhaps as a result of competition with early animals, and have not been reported from any Phanerozoic assemblage including fossil Lagerstätten such as the Burgess Shale. It is difficult to relate rangeomorphs to any modern group of macroscopic organisms, and they appear to represent a "forgotten" architecture and construction that characterized early stages in the terminal Neoproterozoic evolution of complex multicellular life.

References and Notes

1. D. H. Erwin, J. Valentine, D. Jablonski, *Am. Sci.* **85**, 126 (1997).
2. G. M. Narbonne, *GSA Today* **8**, 1 (1998).
3. A. H. Knoll, *Life on a Young Planet: The First Three*

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Billion Years of Evolution on Earth (Princeton Univ. Press, Princeton, NJ, 2003).
4. S. Xiao, Y. Zhang, A. H. Knoll, *Nature* **391**, 553 (1998).
5. M. A. Fedonkin, in *The Vendian System*, B. S. Sokolov, A. B. Iwanowski, Eds. (Springer-Verlag, Heidelberg, 1990), vol. 1, pp. 132–137.
6. R. J. F. Jenkins, *Precambrian Res.* **73**, 51 (1995).
7. M. E. Clapham, G. M. Narbonne, *Geology* **30**, 627 (2002).
8. M. E. Clapham, G. M. Narbonne, J. G. Gehling, *Paleobiology* **29**, 527 (2003).
9. T. D. Ford, *Proc. Yorks. Geol. Soc.* **31**, 211 (1958).
10. A. Yu. Zhuravlev, *Neues Jahrb. Geol. Palaeontol. Abh.* **190**, 299 (1993).
11. K. J. Peterson, B. M. Waggoner, J. W. Hagadorn, *Integr. Comp. Biol.* **43**, 127 (2003).
12. A. Seilacher, *J. Geol. Soc. (London)* **149**, 607 (1992).
13. M. W. Martin *et al.*, *Science* **288**, 841 (2000).
14. S. A. Bowring, P. M. Myrow, E. Landing, J. Ramenzani, *NASA Astrobiology Unit, General Meeting 2003*, Abstract 13045 (http://nai.arc.nasa.gov/institute/general_meeting_2003/AbstractBook.pdf).
15. G. M. Narbonne, J. G. Gehling, *Geology* **31**, 27 (2003).
16. J. G. Gehling, *Mem. Geol. Soc. India* **20**, 181 (1991).
17. J. G. Gehling, J. K. Rigby, *J. Paleontol.* **70**, 185 (1996).
18. M. A. Fedonkin, B. M. Waggoner, *Nature* **388**, 868 (1997).
19. A. Seilacher, *Palaios* **14**, 86 (1999).
20. D. A. Wood, R. W. Dalrymple, G. M. Narbonne, J. G. Gehling, M. E. Clapham, *Can. J. Earth Sci.* **40**, 1375 (2003).
21. G. M. Narbonne, R. W. Dalrymple, J. G. Gehling, *Geol. Assoc. Can. Field Guide B5* (2001).
22. S. B. Misra, *Geol. Soc. Am. Bull.* **80**, 2133 (1969).
23. M. M. Anderson, S. Conway Morris, *Proceedings of the Third North American Paleontological Convention* (Montreal, August 1982), vol. 1, part 1, pp. 1–8.
24. J. G. Gehling, *Palaios* **14**, 40 (1999).
25. R. J. F. Jenkins, *Paleobiology* **11**, 336 (1985).
26. J. Dzik, *J. Morphol.* **252**, 315 (2002).
27. D. Grazhdankin, *Paleobiology* **30**, 203 (2004).
28. Systematic paleontology will be presented elsewhere.
29. H. Boynton, T. D. Ford, *Mercian Geol.* **13**, 165 (1995).
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Intracellular Acidosis Enhances the Excitability of Working Muscle

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Intracellular acidification of skeletal muscles is commonly thought to contribute to muscle fatigue. However, intracellular acidosis also acts to preserve muscle excitability when muscles become depolarized, which occurs with working muscles. Here, we show that this process may be mediated by decreased chloride permeability, which enables action potentials to still be propagated along the internal network of tubules in a muscle fiber (the T system) despite muscle depolarization. These results implicate chloride ion channels in muscle function and emphasize that intracellular acidosis of muscle has protective effects during muscle fatigue.

Contraction in a twitch skeletal muscle fiber in response to a nerve impulse is the result of a complex series of events known as excitation-contraction-coupling (*1*) (ECC). ECC consists of (Fig. 1) (i) initiation and propagation of an action potential (AP) along the surface membrane and into the T system, (ii) activation of the voltage sensors (VSs) in the tubular wall, (iii) signal transmission to the sarcoplasmic reticulum (SR) from which the activator ion Ca^{2+} is released, and (iv) activation by Ca^{2+} of the Ca^{2+}-regulatory system associated with the contractile apparatus. Intense muscle activity leads to a decline in mechanical performance (power output, force, and velocity of shortening), which is generally known as muscle fatigue (*1–4*). Intracellular acidification of the working muscle associated with the production of lactic acid has been said to contribute to muscle fatigue (*2*). This is because intracellular acidification reduces the sensitivity of the contractile apparatus to Ca^{2+} and, under some circumstances, the maximum Ca^{2+}-activated force that is generated (*2*). However, the adverse actions of intracellular pH are not as great as originally thought (*5*, *6*). Another factor in muscle fatigue is reduced ability of the T system to conduct APs as a result of excitation-induced accumulation of K^+ in the T system (*3*, *4*). The accumulation of K^+ causes depolarization, which inactivates the

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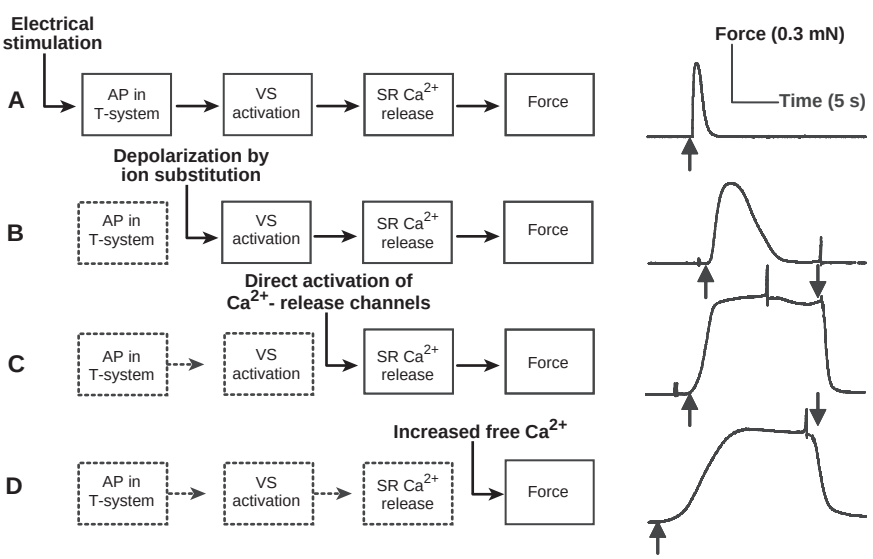


Fig. 1. Modes of activation of mechanically skinned muscle fibers. The force responses (right) were all obtained with the same preparation. Calibration bars for all force responses: vertical, 0.3 mN, and horizontal, 5 s. Upward-pointing arrows indicate time of activation and downward-pointing arrows indicate subsequent relaxation in a heavily buffered EGTA solution ($[Ca^{2+}] < 1$ nM). (**A**) Electrical stimulation initiates APs in the sealed T system. Shown is a tetanic contraction at 25 Hz stimulation with square pulses of 2-ms duration for 1s and field strength of 70 V/cm in a standard K-hexamethylene-diamine-tetraacetate (K-HDTA) solution with Cl^- (*10*, *11*, *21*). (**B**) Depolarization of the T system (by replacing all K^+ in the solution with Na^+) activates VSs independently of APs in the T system. The force response resulted from transfer of the preparation from a standard K-HDTA solution to depolarizing Na-HDTA solution (*5*). (**C**) Direct activation of SR Ca^{2+}-release channels, causing Ca^{2+} release from the SR, and force production when free $[Mg^{2+}]$ in the solutions was lowered from 1 mM to 0.015 mM (*5*). (**D**) Direct activation of the contractile apparatus in Ca^{2+}-buffered solutions (*5*, *10*, *11*, *21*). The preparation was transferred from the standard K-HDTA solution ($[Ca^{2+}] = 100$ nM) to heavily buffered Ca-EGTA solution ($[Ca^{2+}] = 30$ μM).

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