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26. A modular strategy for the total synthesis of proteins has been developed based on the convergent chemical ligation of unprotected peptides [L. E. Canne, S. K. Burley, S. B. H. Kent, paper presented at the Annual Meeting of the Protein Society, San Diego, July 1994]. Protein domains (modules) were prepared by chemical ligation of 50 to 70 residue segments; these domains were then stitched together to give the target protein. Mutually compatible ligation chemistries are required: Intradomain ligation should optimally yield a stable, peptide-like bond, whereas interdomain ligation will tolerate a wider variation of properties of the structure formed at the ligation site.
27. Crude synthetic Msc(46-76)αCOSH [Msc, 2(methylsulfonyl)ethyloxycarbonyl] was converted to the 5-thio-2-nitrobenzoic acid ester (-COSNB) by treatment with 5,5′-dithio-bis(2-nitrobenzoic acid) [10 equivalents (eq)] in 8 M urea, pH 4.0 50 mM ammonium acetate buffer. This thioester-containing material was found to be completely stable below pH 6.0, and was readily purified by reversed-phase high-performance liquid chromatography (HPLC).
28. [Ala^{33}]IL-8 was chosen as the synthetic target for convenience; previous work had shown that this mutant IL-8 had full biological activity (*9*), and a supply of the Boc-Ala (Boc, butyloxycarbonyl) thioester resin was on hand for other applications. The folded structure shown is based on the x-ray structure of the IL-8 monomer [E. T. Baldwin *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **88**, 502 (1991)].
29. The IL-8 peptide segments were prepared by optimized stepwise solid-phase synthesis (*23*) and were purified by reversed-phase HPLC and characterized by standard methods. Crude synthetic segment IL-8(1-33)αCOSH was converted to the thiobenzyl ester by reaction with benzyl bromide (15 eq) in 6 M guanidine·HCl, pH 4.6, sodium acetate buffer, prior to purification under standard reversed-phase HPLC conditions.
30. The segments (1-33)αCOSBzl (5.0 mg, 1.3 μmol) and 34-72 (4.8 mg, 1.1 μmol) were reacted in 0.5 ml 6 M guanidine·HCl, pH 7.6, phosphate buffer at 23°C in the presence of benzyl mercaptan (5 μl)]. After suitable reaction time (48 to 72 hours), a ligation yield of ~60% was obtained. The product was purified by reversed-phase HPLC and characterized by electrospray mass spectrometry.
31. We gratefully acknowledge the assistance of T. Walters and M. Baca in the early stages of this work, of L. Canne in providing the thioester resin, of B. Dewald for some of the elastase release assays, and of R. Simon and S. Clark for critical comments on the manuscript. Supported by funding from NIH [GM48897-01 and GM48870-03 (S.B.K.); GM 50969-01 (I.C.L.)].

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A Theropod Dinosaur Embryo and the Affinities of the Flaming Cliffs Dinosaur Eggs

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An embryonic skeleton of a nonavian theropod dinosaur was found preserved in an egg from Upper Cretaceous rocks in the Gobi Desert of Mongolia. Cranial features identify the embryo as a member of Oviraptoridae. Two embryo-sized skulls of dromaeosaurids, similar to that of *Velociraptor*, were also recovered in the nest. The eggshell microstructure is similar to that of ratite birds and is of a type common in the Djadokhta Formation at the Flaming Cliffs (Bayn Dzak). Discovery of a nest of such eggs at the Flaming Cliffs in 1923, beneath the *Oviraptor philoceratops* holotype, suggests that this dinosaur may have been a brooding adult.

Dinosaur eggs are abundant in Upper Cretaceous rocks of the Gobi Desert (*1*, *2*), but embryonic skeletons from these deposits are scarce. Definitive remains include numerous bird embryos (*3*) and a single fragmentary specimen of an ornithischian hind limb (*4*). Because the definitive taxonomic identity of eggs requires the presence of identifiable embryonic remains within them, the identity of most egg types present in Upper Cretaceous beds in Mongolia has been unclear (*1*, *2*).

In 1993, a rich Upper Cretaceous fossil locality in the Gobi Desert was discovered (*5*). The site, Ukhaa Tolgod, is in the northeastern Nemegt Basin, Omnogov Aimak, near the salt extraction settlement of Daus. In addition to over 300 mammal and lizard skulls, 20 theropod skeletons (including several adult and juvenile oviraptorids), and many protoceratopsian and ankylosaurid dinosaurs discovered at this locality, at least five types of eggs were found. Many of these were arranged in nests. One egg, from a heavily weathered nest, contains the nearly complete skeleton of an embryonic oviraptorid dinosaur (Fig. 1). Also among the broken eggshell fragments in this nest were two tiny skulls (~5 cm long) of a dromaeosaurid theropod, one preserved with eggshell adhering to it (Fig. 2).

The red sandstones of Ukhaa Tolgod probably belong to either the Djadokhta Formation or the Barun Goyot Formation and lie 35 km east of the Barun Goyot type section (*6*). Limited studies indicate the presence of taxa typical of either or both the Barun Goyot and the Djadokhta formations (that is, *Velociraptor*, *Mononykus*, and the mammals *Zalambdalestes*, *Bulgaanbaatar*, *Nemegtbaatar*, and *Catopsalis*). These faunas are considered correlative with the Judithian North American land mammal age and the Campanian marine stage (*7*), although this correlation is poorly constrained (*8*).

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Eggs in the nest were arranged in a semicircle. The presence of copious fragments indicates that additional eggs were destroyed by weathering. Adjacent (about 3 cm) to the egg containing the embryo (Fig. 1) was a small nodule with dinosaur eggshell, including a skull (Fig. 2). Also in the nest lay a second skull identical in size and morphology to the first and a few isolated bone fragments.

The skeleton is of an articulated oviraptorid and was preserved with the ventral surface of its mandible and the left side of its postcranial skeleton adjacent to the inner surface of the eggshell (Fig. 1A). The cervical region is in the broader end of the egg; the caudal region was presumably in the missing acute end. The embryo is oriented in a position similar to that of other archosaur embryos with the head tucked near the knees. The skeleton is well ossified; apparently the embryo was close to hatching. The skull has a midline length of $\sim$4 cm. The skull roofing bones are missing; the palate and braincase are thus exposed in dorsal view above the articulated mandible (Fig. 1, B and C). The postcranial skeleton includes humeri, the entire pectoral girdle, most of the left hind limb, portions of ilia, and the precaudal axial skeleton. The distal left forelimb may be present in articulation with the humerus but is not exposed. An eggshell fragment with an articulated tarsus and non-arctometatarsalian metatarsus, found 4 cm from the egg, may be from the same specimen.

The skull displays several apomorphies of the Oviraptoridae (9). The edentulous premaxillae are vertical and tall, and the short, edentulous mandible is strongly arched dorsally and has a large mandibular fenestra. The postcranial skeleton is consistent with that of Oviraptoridae, especially the well-developed furcula. Among Oviraptorosauria, the short, tall dentary allies it with the Oviraptoridae, as would be expected because this family is the only one present in the Djadokhta and Barun Goyot formations. The skull is too incomplete for detailed comparison with the four described oviraptorid species (9), although there is no indication of the excavations in the dorsal process of the premaxilla present in *Oviraptor philoceratops*.

Nearly all the bones are fully ossified, which makes the Ukhaa Tolgod specimen most comparable to the latest stages of avian development. In modern birds, the vertebrae ossify in an anterior to posterior direction. Neural arches are the first vertebral elements to ossify, followed by the centra (*10*). In chickens and skua hatchlings, cervical vertebral zygapophyses are cartilaginous until hatching and the neural arches are separated from the vertebral centra by weak sutures (*10*). In these birds, the posterior vertebral centra are poorly ossified at hatching. In the Ukhaa Tolgod specimen and avian embryos from Khermeen Tsav (*11*), osseous cervical zygapophyses are present. Furthermore, in the Ukhaa Tolgod specimen neural arches are disassociated from ossified centra throughout the cervical and dorsal regions, and the sacral vertebrae are fully ossified. In adult oviraptorids, the mandibular symphyses are fused, whereas in the embryo the bones are unfused on the midline. In some modern birds, the mandibular symphysis fuses before hatching; in others it is unfused until after hatching (*11*).

The egg containing the embryo is incomplete, but the preserved portion is similar to oblong eggs classified as elongatoolithid (*1*), and the entire egg was approximately 12 cm by 6 cm. The shell was deformed during diagenesis, as indicated by the overlap of eggshell fragments, but the skeleton appears to be undisturbed. The outer surface of the shell is ornamented (Fig. 3F) with a series of ridges and nodes rising 0.1 mm above the

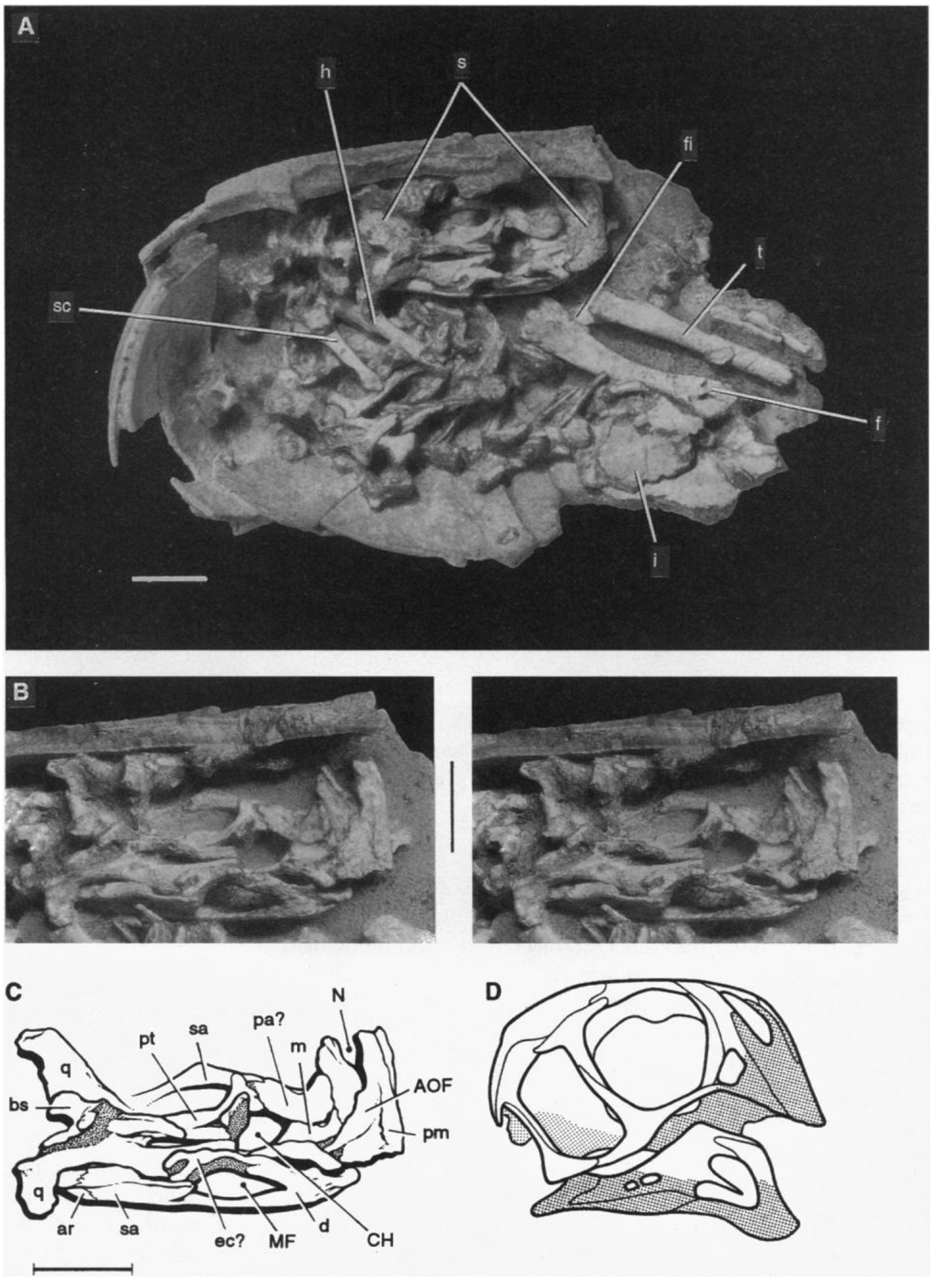

Fig. 1. **(A)** The Ukhaa Tolgod oviraptorid embryo [designated IGM (Institute of Geology, Mongolia) 100/971]. **(B)** Stereopair of the skull. **(C)** Diagrammatic representation of the Ukhaa Tolgod skull. **(D)** The skull of *Ingenia* (*25*). The shaded area represents the portion preserved in IGM 100/971. [Modified from (*25*)]. Scale bars = 1 cm. Abbreviations: AOF, antorbital fossa; ar, articular; bs, basisphenoid; CH, choana; d, dentary; ec?, ectopterygoid; f, femur; fi, fibula; h, humerus; i, ilium; j, jugal; l, lacrimal; m, maxilla; MF, mandibular fenestra; N, nares; pm, premaxilla; pt, pterygoid; q, quadrate; s, skull; sa, surangular; sc, scapula; and t, tibia.

shell. The nodes predominate at the end of the egg, and the longitudinally oriented ridges [of the type termed linearituberculate variant 1 (*2*)] predominate in the midsection.

The microstructure of the shell in radial thin section (Fig. 3, A, C, and E) is angusticaniliculate of the ratite ornithoid type (*2*). Pore canals are uncommon, narrow, straight, and vertical. There are two distinct layers: a thin inner mammillary layer and a thicker outer continuous layer with horizontal layering. The thickness of the eggshell varies substantially; it is thinnest (~0.50 mm) below the hindquarters of the embryo and thickest (~0.95 mm) at the broad end of the egg. In polarizing light (Fig. 3), a sweeping extinction pattern predominates, especially under nodes and ridges, but occasional columnar extinction patterns are also present.

The two skulls of a dromaeosaurid theropod discovered adjacent to the embryo are well preserved. One skull comprises a slightly disarticulated rostrum and orbital region with both mandibles in articulation (Fig. 2); the second preserves an articulated rostrum and a disarticulated braincase and orbital region. They are small, and their bones are less ossified than those of the oviraptorid embryo, which suggests that they are either embryos or hatchlings. Although these skulls are slightly longer than the skull of the oviraptorid embryo, when the relatively short length of oviraptorid skulls is taken into account they are quite similar in length. The outer surface of the eggshell adhering to one of the dromaeosaurid skulls is in contact with the skull, which indicates that the skull was not enclosed by that particular egg.

We assign these two skulls to the Theropoda on the basis of the accessory antorbital fenestra. Their affinities with Coelurosauria and Maniraptora are shown by a lack of separate prefrontal ossification (*12*), a deep pocket in the ectopterygoid, and a subsidiary palatal fenestra (*13*). Among Coelurosauria, the two skulls lack the diagnostic features of Oviraptorosauria, Ornithomimosauria, Metornithes, and *Ornitholestes*. The broad, triangular exposure of the splenial bone on the lateral surface of the mandible is characteristic of troodontids and dromaeosaurids, but the skulls lack the supernumerary teeth of troodontids (*14*). The T-shaped lacrimal bone is typical of those of Dromaeosauridae (*15*) and the elongate premaxilla is a distinctive apomorphy of *Velociraptor* (*16*).

The specimens display apparent interdental plates on the medial surface of the dentary, an intriguing finding in light of disagreement concerning their presence in adult dromaeosaurids (*17*). Also unlike known dromaeosaurids, the teeth are subconical and unserrated rather than being laterally compressed and serrated, a feature previously considered to be diagnostic of Avialae. However, ontogenetic modification of tooth morphology is common in archosaurs; hence, it is possible that laterally compressed, serrated teeth occurred later in the ontogeny of this species. Although far from conclusive, the occurrence of this type of tooth in a neonate dromaeosaurid, together with the close phylogenetic relation of dromaeosaurids to Avialae, raises the possibility that the avian tooth morphology arose through heterochrony. Thus, the early stages of tooth ontogeny in dromaeosaurids may have been expressed as the adult tooth morphology in Avialae.

Most supposed nonavian theropod eggs have been tentatively identified on the basis of associated theropod bones or association with supposed maternally provided food items (*18*). The egg we found is similar to smaller eggs (~100 mm long) reported as those of "?*Troodon*" (*19*) on the basis of undescribed embryonic remains, but the egg we discovered differs from these in surface ornamentation. The similarity of this ratite ornithoid type of microstructure to that of modern birds (*20*), and its association with an unambiguous theropod embryo, allows phylogenetic inferences to be drawn. Assuming the troodontid eggs (*19*) are identified accurately, and because avian monophyly is well corroborated, the ratite type of eggshell is most parsimoniously considered to be primitive for Aves. Ratites therefore retain the primitive condition, and the similarities between the neognath eggshell and that of some ornithischians (*1*, *2*, *19*) are convergent and,

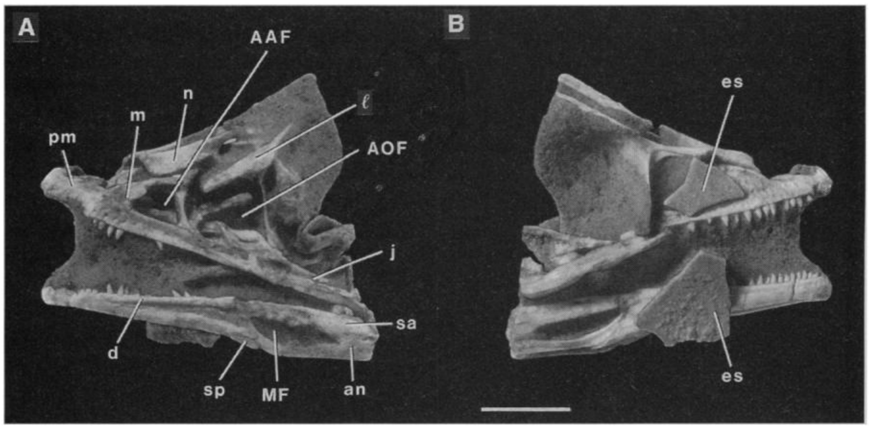

Fig. 2. (**A**) Left side of dromaeosaurid skull IGM 100/972. (**B**) Right side of same skull. Scale bar = 1 cm. Abbreviations are as in Fig. 1; AAF, accessory antorbital fenestrae; an, angular; es, eggshell; n, nasal; sp, splenial.

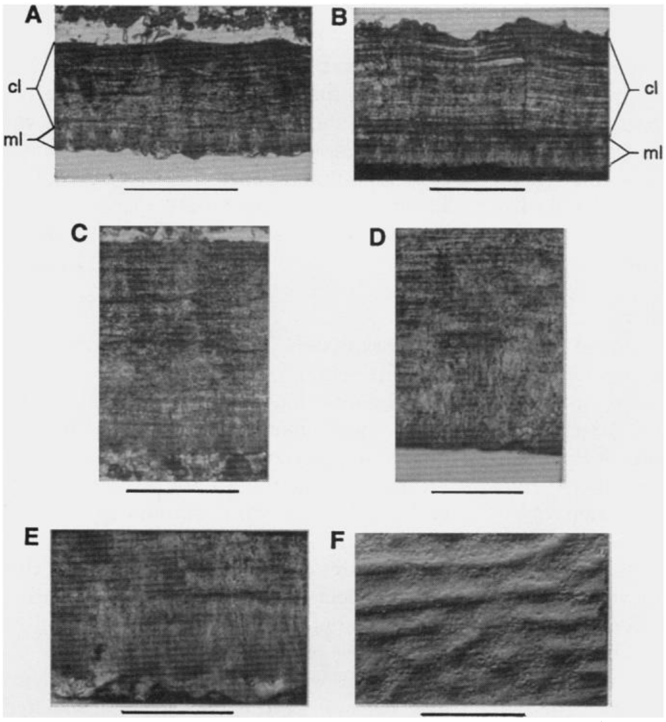

Fig. 3. (**A** through **E**) Histologic sections of oviraptorid eggs in radial cross section; all are shown in polarized light. (A), (B), (E), and (F), IGM 100/972; (C) and (D), specimen AMNH 6508; ml, mamillary layer; cl, continuous layer. (**F**) Scanning electron microscope image showing surface texture of the IGM 100/972 eggshell. Scale bars: (A) and (B), 1 mm; (C) and (D), 0.5 mm; (E), 0.25 mm; and (F), 2.5 mm.

hence, apomorphic for Neognathae.

Definitive fossils of dinosaur eggs and nests were discovered in the early 1920s. The most common type of eggs were initially identified as belonging to the ornithischian dinosaur *Protoceratops* (*21*). This referral was based on the abundance of both *Protoceratops* skeletal remains and this type of egg at Bayn Dzak. No undoubted embryonic remains were found in these eggs. Although embryonic remains were initially reported (*22*), these observations have been shown to be erroneous (*23*).

On the basis of circumstantial evidence, two recent studies of dinosaur eggs (*1*, *2*) suggested that this type of egg is not from *Protoceratops*, but from a theropod dinosaur. The type of egg most common at the Flaming Cliffs is identical in size and shape, surface ornamentation, and microstructure to the egg containing the oviraptorid embryo. Hence, we now provisionally identify these as oviraptorid theropods. However, considering that embryos within eggs are scarce, the possibility that this type of egg has a broad distribution among Dinosauria cannot be discounted, although this possibility is unlikely.

Further evidence for the identification of the Flaming Cliffs eggs comes from remarkable and suggestive associations (*16*, *24*). In 1923, George Olson collected a dinosaur nest (AMNH 6508) of this type of egg (Fig. 3) at the Flaming Cliffs. During excavation, the holotype of *Oviraptor philoceratops* (AMNH 6517) was discovered lying on top of the clutch of eggs, separated by only 10 cm. In his description of this species, Osborn surmised that this animal died while feeding on the eggs—hence the generic name he gave it, meaning "egg seizer" (*16*). Our evidence suggests that the holotype of *Oviraptor philoceratops* perished not while feeding on these eggs, but perhaps while incubating or protecting this clutch of eggs. Since this discovery, another such association of an adult oviraptorid and a nest of this type of egg has been reported from Djadokhta-like beds at Bayan Mandahu (*24*).

The abundance of this type of egg at the Flaming Cliffs, comprising approximately 50% of the eggs (*1*, *2*) encountered, is surprising because skeletal remains of oviraptorids and other theropods are extremely rare. The original collections from the Flaming Cliffs by the Central Asiatic expeditions include 101 specimens of *Protoceratops andrewsi* (*22*), but only one specimen of *Oviraptor philoceratops*, two specimens of *Velociraptor mongoliensis*, and one of *Saurornithoides mongoliensis* (*16*). This is a strong warning against the identification of eggs only on the basis of the relative abundance of eggs and skeletons in the same horizon.

The occurrence of the tiny skulls of dromaeosaurids in association with the oviraptorid egg is an enigma. Skulls of nonavian theropods this small are rare, and the close association of two specimens with the egg of another taxon is unlikely to be due to chance alone. Although they are certainly from animals close to hatchling age, it is unclear whether they are embryos or neonates; the possibility that the dromaeosaurids are from an adjacent nest, were prey items of adult oviraptorids, were predators on the oviraptorid eggs or hatchlings, or even that one of the two taxa was a nest parasite, cannot be discounted. In any case, their intimate association with the oviraptorid eggs provides another reason for caution in identifying eggs on the basis of their associations with embryos not actually enclosed within them.

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Autumn Bloom of Antarctic Pack-Ice Algae

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An autumn bloom of sea-ice algae was observed from February to June of 1992 within the upper 0.4 meter of multiyear ice in the Western Weddell Sea, Antarctica. The bloom was reliant on the freezing of porous areas within the ice that initiated a vertical exchange of nutrient-depleted brine with nutrient-rich seawater. This replenishment of nutrients to the algal community allowed the net production of 1760 milligrams of carbon and 200 milligrams of nitrogen per square meter of ice. The location of this autumn bloom is unlike that of spring blooms previously observed in both polar regions.

Approximately 3 to 4 × 10^6 km^2 of the western sector of the Antarctic Weddell Sea is continuously covered by sea ice (*1*). Low water column biomass and light limitations imposed by the ice and snow restrict primary production in the water column, and dense microbial communities associated with the sea ice are presumed to be the major source of primary production for this region's pelagic ecosystem (*2*). Elucidating the annual production cycle and the factors controlling primary production in this region of the world ocean has been problematic because of the difficulties associated with conducting long-term investigations in drifting pack ice. The deployment in 1992 of the first Antarctic drifting ice station (ISW-1) enabled us, however, to examine in situ microalgal production and nutrient dynamics in relation to changing physicochemical conditions in Antarctic pack ice over a prolonged period.

ISW-1 was deployed on a 2- to 3-km^2 multiyear ice floe (ice surviving a summer melt season) in the southwest Weddell Gyre in a region of 80 to 90% multiyear ice coverage (*3*). Several experimental quadrats were monitored (*4*) as the station drifted