ABSTRACT
Carbonaceous cherts of the Tarahumara Formation, exposed near Huepac, Sonora, Mexico, contain abundant diatom frustules occurring as benthic filamentous colonies. Stratigraphic and paleontological observations indicate that Tarahumara sediments accumulated in a nonmarine setting; radiometric ages on encompassing volcanic rocks delimit their depositional age to ca. 70 Ma. Tarahumara fossils therefore extend the paleontological record of nonmarine diatoms from middle Eocene to Late Cretaceous. Preserved populations include forms similar to species of the extant genera Amphora and Melosira, as well as filament-forming araphid pennates comparable to species of Fragilaria and Tabellaria. Tarahumara fossils indicate that by 70 Ma, nonmarine diatoms had achieved considerable environmental as well as taxonomic diversity.

Keywords: Cretaceous, cherts, diatoms, frustules, silica.

INTRODUCTION
Diatoms are among Earth’s most widespread primary producers, occurring as diverse and abundant constituents of lakes, the open ocean, and nearly all intermediate ecosystems. Because they form siliceous skeletons, or frustules, diatoms also constitute key elements of the contemporary silica cycle. Marine diatoms began to diversify early in the Cretaceous Period and by the Campanian (74.5–84 Ma) included relatively diverse centric and rare araphid pennate forms (Strelni- kova, 1990; Harwood and Nikolaev, 1995). In contrast, unambiguously nonmarine diatoms have until now been known only from middle Eocene (ca. 39–50 Ma) and younger rocks (Bradbury and Krebs, 1995; Strelni- kova and Lastivka, 1999).

Here we report the discovery of abundant filament-forming centric and pennate diatoms in ca. 70 Ma cherts of the Tarahumara Formation, Mexico. The encompassing sediments were deposited under lacustrine to coastal brackish-water conditions, demonstrating that by the time diatoms became widespread as fossils, they had already undergone substantial environmental as well as taxonomic diversification.

GEOLOGIC SETTING
The ~400-m-thick Tarahumara Formation, in the Sonora Province of northern Mexico (Fig. 1), consists predominantly of andesitic to rhyolitic volcanic flows, breccias, tuffs, and sandstones that unconformably overlie Upper Triassic and underlie Oligocene successions (Amaya-Martinez and Gonzalez, 1993; Jacques-Ayala et al., 1993). Locally, stromatolitic limestones and intercalated cherts occur in the (informally designated) middle member of the formation. Rhyolitic tuffs immediately subjacent to the sedimentary member yield U-Pb zircon dates of 72.5 ± 0.5 and 70.2 ± 0.6 Ma; tuffs just above the sediments are 69.7 ± 0.6 Ma (McDowell et al., 2001). Thus, the fossiliferous cherts are ca. 70 Ma.

On the basis of sedimentological features and mapped distribution, the limestone-ternite clastic units have been interpreted as lacustrine (González de León, 1994). Plant fossils, including abundant palms, a taxodiaceous conifer, isoe- talean lycopods, and an aquatic angiosperm, further support a freshwater to brackish-water interpretation (Cevallos-Ferriz and Ricalde-Moreno, 1995; Hernández-Castillo and Ceval- los-Ferriz, 1999), as does a newly described Tetraedron-like green alga (Beraldi-Campesi, 2000). The beds also contain ostracods, but no diagnostically marine invertebrates or protists. As described in the following paragraphs, several of the preserved diatom taxa appear to be related to extant diatoms found in nonmarine environments.

DIATOM FOSSILS
Diatom fossils were found in several cherty horizons at Huepac, in east-central Sonora, where they occur in abundance along with organically preserved cyanobacteria (Chacón-Baca and Cevallos-Ferriz, 1995; Beraldi-Campesi et al., 1997) and broadly spheroidal cells of likely protistan origin. For the most part, only the gross morphology of frustules is evident; fine structures, such as areolae, pores or vela, are rarely preserved, although collapsed cytoplasm occurs in many specimens. This circumstance limits systematic interpretation. Nonetheless, preserved morphologies closely approximate frustules found in extant diatom clades. Preservation is clearly linked to early diagenetic silification that entomed...
Figure 2. Girdle views of frustules of pair- and triplet-forming centric diatoms similar to species of modern Melosira and Skeletonema. Note that spheroid sometimes separated frustules, well-developed cingulum, and corona-like spines (arrows). Scale bar in A = 20 μm; B = 15 μm, and in C and D = 10 μm.

Figure 3. Solitary and ribbon-forming frustules similar to extant species of Fragilaria and related araphid taxa. Note organic debris within each frustule. A: Abundance of solitary frustules in valvar view and frustules in ribbon-like colonies in apical view. B: Scattered frustules in valvar view. C: Frustules in ribbon-like colony in girdle view. Scale bar in A = 15 μm and in B and C = 12 μm.


Fragile diatom frustules before they could dissolve. Weathering of ambient volcanic rocks provided a ready source of silica.

Most diatoms in the Huepac assemblage are colonial forms that built short chains or longer ribbons. Spheroidal frustules with hemispherical valves 10–25 μm in maximum dimension occur principally as pairs or triplets connected by epivalvar spines and a well-developed cingulum (Fig. 2). The short colonies of adherent frustules approximate those of living Melosira species. Some of the fossils, however, are distinct in preserving evidence of non-interactive division; i.e., in leaving a space between sibling frustules that is bridged by long spines (as in modern Skeletonema; Round et al., 1990). A more general similarity can also be noted with the modern freshwater genus Aulacoseira (Round et al., 1990) and its proposed Cretaceous ancestor, Archeopyrgus (Gersonde and Harwood, 1990), known from marine strata (Harwood and Nikolaev, 1995).

Closely associated with the chains of centric diatoms are twisted ribbon-like colonies of elongate (~30 μm long) lanceolate frustules (Fig. 3) comparable to species of Fragilaria and related taxa. Fragilaria is a genus of araphid pennates known predominantly from non-marine environments (Hustedt, 1985; Round et al., 1990). Three genera of Fragilariaceae have been identified in Upper Cretaceous marine rocks (Moshkovitz et al., 1983; Harwood, 1988; Harwood and Nikolaev, 1995); this, however, is the first report of a nonmarine species from pre-Tertiary strata.

Other common fossils include distinctive ribbons of cruciform frustules at least broadly comparable to species of the extant genus Tabellaria (Fig. 4, A–D). Today, Tabellaria species live in nonmarine environments (Round and Sims, 1981); unambiguously identified fos-
solitary diatom assemblage in the Huepac Chert, particularly distinctive epithea and axial features, 30–35 μm long, that are longitudinally folded and remnant in cross-sectional view, with both wall surfaces facing the concave side (Fig. 4, E–G). Among living diatoms, only a handful of genera exhibit comparable gross morphology; all are within the raphid families Catene- laceae and Cymbellaceae. The freshwater genus *Cymbella* is characterized by straight parvalvar and transapical axes and a curved apical axis; valve faces are nonparallel, and raphes are slightly displaced toward the ventral margin of valves. In contrast, the unique frustule symmetry of the genus *Amphora* consists of curved parvalvar and apical axes, and a straight transapical axis; raphes are strongly displaced along the curved edges of the frustule. Raphle slits are not easily seen in individual sections of these diatoms, but become apparent as one scrolls downward through a single specimen, creating a series of optical sections that combine to reveal aspects of three-dimensional structure. The slits (arrows in Fig. 4, F–G) extend along the curved edges of frustules, as in living *Amphora*. *Amphora* species occur today in freshwater, brackish, and marine environments (Round et al., 1990).

**DISCUSSION**

Until now, nonmarine diatoms were known unambiguously only from the middle Eocene (ca. 50–39 Ma) onward (Bradbury and Krebs, 1995; Strelnikova and Lastivka, 1999). Thus, the Huepac Chert extends the known stratigraphic range of nonmarine diatoms by 20 m.y. or more. Moreover, preserved morphologies suggest that at least some of these brackish-water to freshwater taxa belonged to derived lineages. In a phylogeny based on sequence comparisons of nuclear-encoded small subunit RNA genes, Medlin et al. (1996) recognized two principal clades of diatoms, both known to have been present in Late Cretaceous oceans: a group of radial centrics and a more heteromorphic clade that includes additional centrics and a monophyletic pennate subclade. If preserved morphologies provide accurate guides to taxonomy, the Huepac diatom assemblage includes relatively derived taxa within the radial centric clade, as well as araphid pennates and at least one member of the raphid clade that is nested phylogenetically within the pararaphylic araphids. Huepac fossils thus provide evidence for considerable divergence of diatom lineages before 70 Ma. Filament-forming colonies are conspicuous in the Huepac diatom flora. Filament formation has been linked to both predation resistance and biological control of sinking and ascent through the water column (Round et al., 1990). This does not necessarily mean, however, that early nonmarine diatoms inhabited turbid water or had high levels of grazing. Filament formation is a conspicuous feature of early marine diatoms (Harwood and Nikolaev, 1995), so the abundance of filaments in the Huepac assemblage may reflect ancestral characters of nonmarine colonists as much as any specific adaptation to brackish or lacustrine conditions. Likewise, the abundance of non-colonial species in younger nonmarine floras may principally reflect an evolutionary radiation of motile diatoms and need not relate to any secular decline in grazing intensity.

**CONCLUSIONS**

The exceptional window provided by the fossiliferous cherts at Huepac enlarges our view of early diatom evolution, furnishing evidence for substantial environmental as well as taxonomic diversification by the Late Cretaceous Period. Like other Cretaceous assemblages, Huepac fossils focus the continuing search for early diatoms on diagenetic nodules that prevented dissolution of delicate frustules in near-surface sediments. The Huepac fossils also provide new encouragement for micropaleontological exploration of continental sedimentary rocks that may further narrow the stratigraphic gap between the earliest marine and nonmarine diatom records.

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Elizabeth Chacón-Baca, H. Beraldi-Campesi, S.R.S. Cevallos-Ferriz, A.H. Knoll and S. Golubic

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