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## *Paleopleurocapsa wopfnerii* gen. et sp. nov.: A Late Precambrian alga and its modern counterpart

(paleontology/phycozoology)

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**ABSTRACT** Silicified dolomite of the approximately one billion year old Skillogalee Dolomite of the Adelaide Geosyncline, South Australia, contains organically preserved microfossils of a structurally complex, crustose pleurocapsalean cyanophyte, herein described as *Paleopleurocapsa wopfnerii*. Although actual cell contents have been degraded, lamellar sheath material faithfully preserves the morphology of the alga. Comparison with specimens of the modern genus *Pleurocapsa* Thuret demonstrates affinities at the family level and quite possibly even generic identity.

The common crustose and stromatolitic cyanophytes (blue-green algae) of the modern ocean comprise the orders Chroococcales, Nostocales, Oscillatoriales, and Pleurocapsales (1). During the past two decades, paleontological study of Precambrian rocks has established the great antiquity of three of these groups. Chroococcalean cyanophytes morphologically indistinguishable from the modern genus *Entophysalis* have been found in approximately two billion year old cherts from the Belcher Islands in Canada (2, 3), and the ancestors of such coccoid algae were in existence at least one billion years earlier (4). Nostocalean-type filaments are reported from the 2.2 billion year old Transvaal Dolomite in South Africa (5), and it may be inferred that the less highly advanced filamentous order, the Oscillatoriales, evolved prior to this time, although the oldest presently known filamentous forms of the oscillatorian type are preserved in the 1.9 billion year old Gunflint formation of Ontario, Canada (6). No pleurocapsalean algae are known from any deposits of this age.

During the billion years that lapsed between the deposition of the Gunflint cherts and those of the 900 million year old Bitter Springs formation of central Australia (7-9), an essentially modern blue-green algal flora evolved. Yet, although the Bitter Springs flora has been extensively studied, it has not been found to contain any pleurocapsalean algae. The question might reasonably be asked, when did the Pleurocapsales evolve?

Fortunately, we can now provide at least a partial answer to this question. Examination of silicified dolomites from the Skillogalee formation of South Australia demonstrates that algae strikingly similar to the modern genus *Pleurocapsa* were well developed more than one billion years ago.

### Geologic setting

The Precambrian history of the Adelaide Geosyncline of South Australia is recorded in over 15,000 m of sedimentary strata exposed in a longitudinally oriented belt extending from the Peake-Denison range in the north to the city of Adelaide on the south coast of the continent (10). This predominantly shallow water marine sequence can be divided into four distinct stratigraphic units: (in order of decreasing age) the Callanna Beds, the Burra Group, the Umberatana

Group, and the Wilpena Group (10, 11). The Skillogalee Dolomite occurs in the lower portion of the second oldest division and consists of dark, fine-grained carbonate with minor interbedded clastic units. The dolomite is silicified in places, this being most common in the upper part of the formation (12, 13). In a recent detailed analysis of the depositional environment, Preiss (12) concluded that the Skillogalee sediments were deposited on a lagoonal platform of considerable lateral extent. Stromatolites are abundant in certain horizons; numerous minor transgressive and regressive sequences are recorded; and the frequent occurrence of mudcracks and intraformational conglomerate suggests that subaerial exposure was not uncommon.

The samples containing the new taxon are from a chert unit near the top of the "magnesite zone"—a laterally persistent horizon in the upper part of the formation containing abundant sedimentary magnesite (11). The silica cuts across bedding planes, indicating its diagenetic formation. This interpretation is borne out by petrographic analysis which demonstrates that the original sediment consisted of small (up to several millimeters in diameter) intraformational clasts set in a fine carbonate matrix. The clast containing the alga is cut by a small quartz vein which does not extend beyond the boundaries of the grain into the surrounding matrix. "Ghosts" of algal sheaths are preserved near the periphery of the vein, but are obscured in the center.

The presence of the quartz vein indicates that the clast was silicified prior to its final deposition and demonstrates that this silicification must have been primary or very early diagenetic. The history of this fossil, then, can be characterized as follows: the alga grew in shallow water, probably forming a mat surface. After silicification, a minor erosional period detached small clasts that were redeposited in a fine carbonate matrix. A second episode of silicification completed the depositional history.

How old is the Skillogalee Dolomite? Unfortunately, an early Paleozoic metamorphic event has altered the isotopic composition of many of the rocks of the Adelaide Geosyncline, and consequently, radiometric isochron plots exhibit much internal scatter and must be used with great caution (14). The only isotopic date that brackets the age of the Skillogalee in any more than the broadest terms ( $<1350 \pm 45$  Myr) is a single Sr-Rb date of  $867 \pm 32$  million years determined by Cooper and Compston (15) for a metamorphic event that apparently affected Calanna rocks but preceded Burra deposition. The authors clearly indicate the problems associated with this determination, and as Walter (16) points out, the date is not supported by lithologic or biostratigraphic data.

Regional biostratigraphic analysis using stromatolites indicates that the Skillogalee Dolomite is approximately correlative with the Bangemall Group of northwestern Australia,

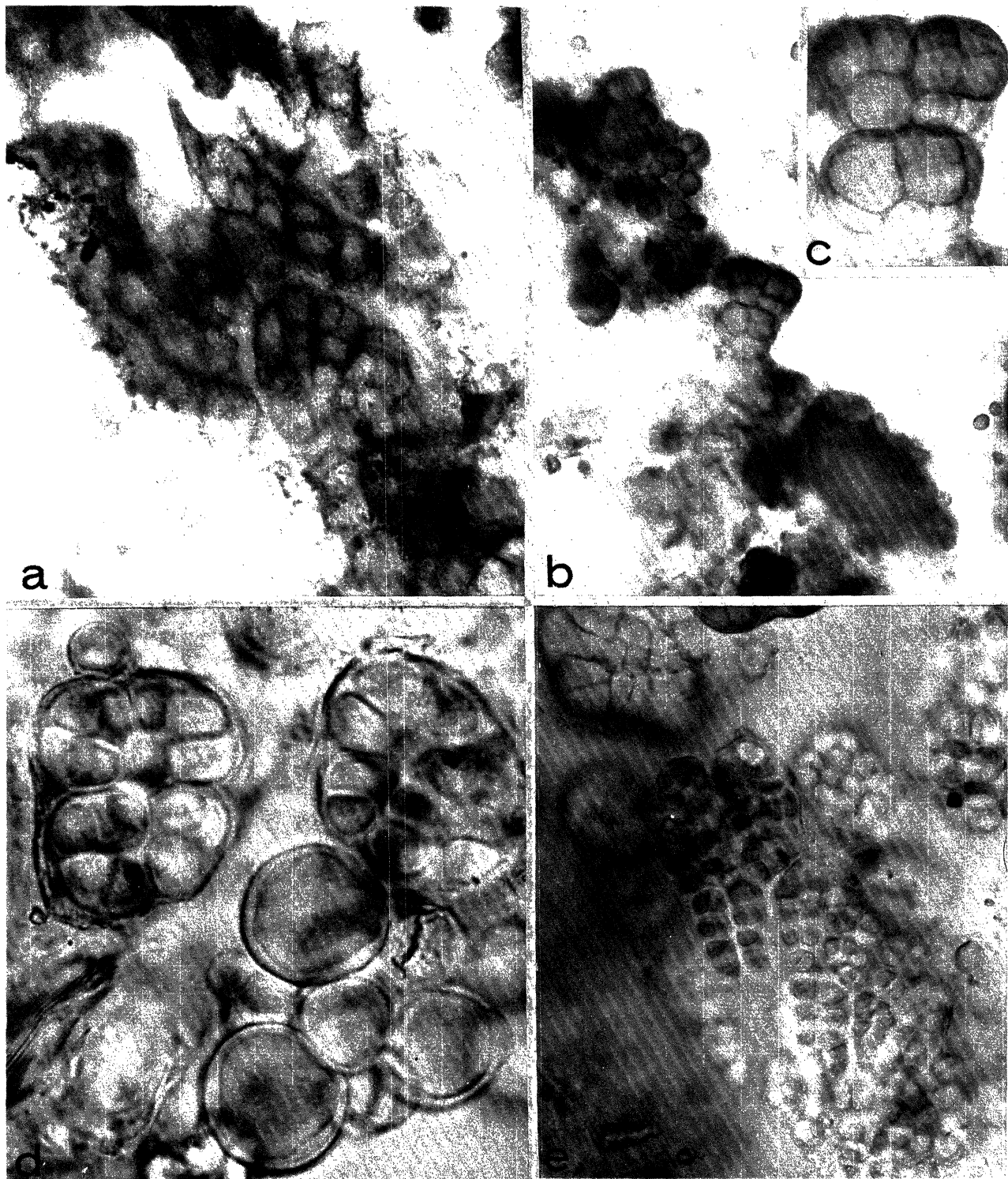


FIG. 1. (a, b, and e  $\times 450$ ; c and d  $\times 1200$ ). (a) *Paleopleurocapsa wopfnerii* gen. et sp. nov.; Harvard Paleobotanical Collections Slide no. 58305C-2, coordinates  $36.4 \times 100.7$ . Intact portion of preserved thallus. (b) *Pleurocapsa moralis* Lagerh., a freshwater species. (c) Enlarged detail of b. (d and e) *Pleurocapsa fuliginosa* Hauck, type species of the genus *Pleurocapsa*, marine.

which is well-dated by Sr-Rb whole rock analysis of unmetamorphosed shale at  $1085 \pm 80$  million years (14). The date is in accord with the presence of the stromatolite form genus *Baicalia* which occurs in both Burra and Bangemall rocks (16); *Baicalia* is restricted to strata of Middle Riphean ( $1350 \pm 50$ – $950 \pm 50$  Myr) age (16; 17). Thus, we can infer a minimum age for the Skillogalee Dolomite of  $950 \pm 50$  million years and agree with other workers (16, 18) that an age of 1200–1000 million years is likely.

#### Systematic description

Division (Phylum): CYANOPHYTA

Class: Coccogoneae

Order: Pleurocapsales

Family: Pleurocapsaceae

Genus: *Palaeopleurocapsa* Knoll, Barghoorn & Golubic n. gen.

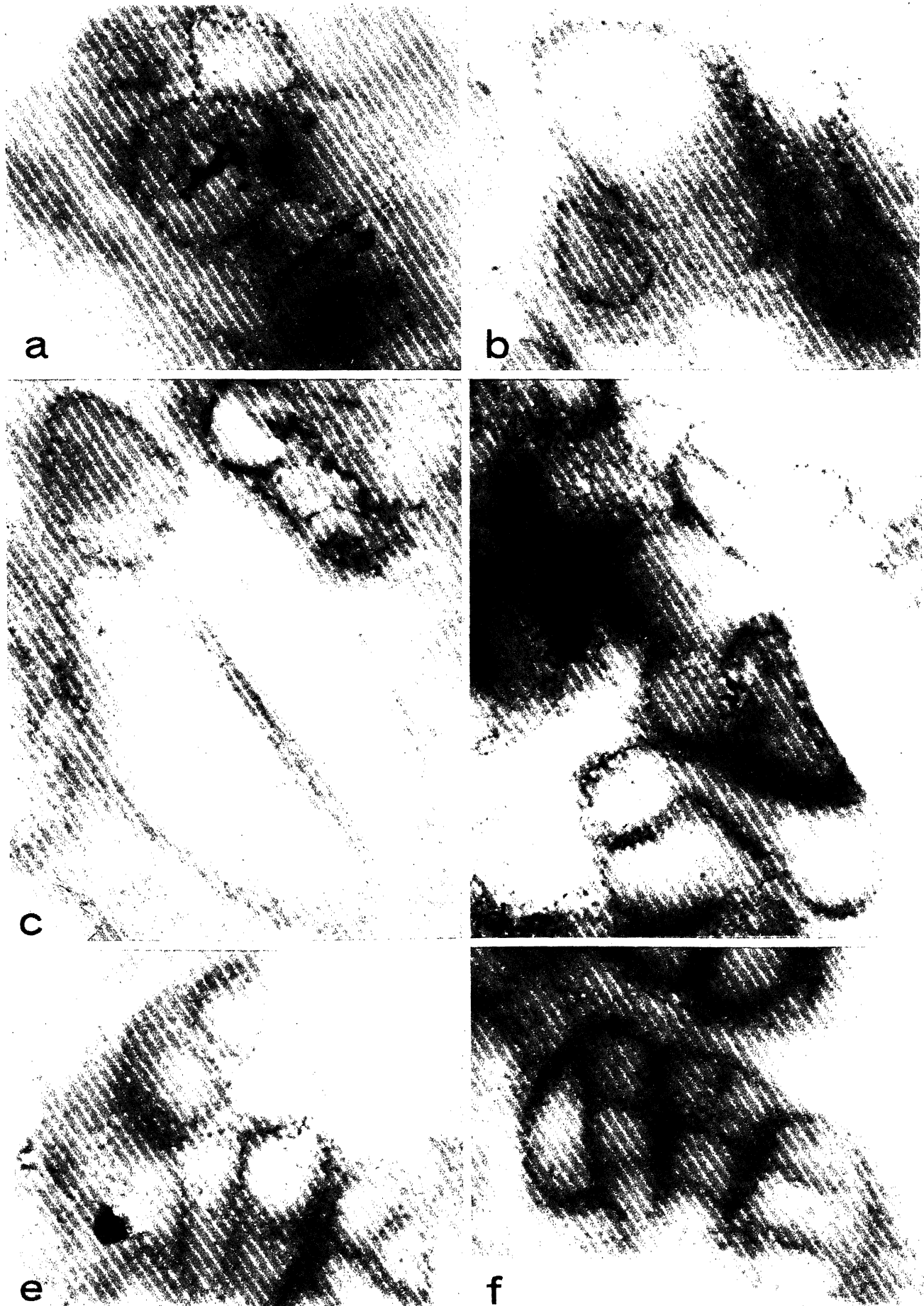


FIG. 2. (Legend appears at bottom of the next page.)

**Diagnosis.** Thallus crustose, variable: ensheathed cell packets generally aggregated into a pseudoparenchymatous system, but with elongated, more or less parallel, dichotomously branched filaments arising from points within the thallus. Multiple, concentrically enclosed sheaths of uniform consistency are present within filaments. Collapsed and shrunken cell remnants are present locally within sheaths. Actual cell sizes are impossible to ascertain because protoplasts have been degraded, but sheaths are well preserved, the innermost of which indicate the maximum possible size for the enclosed cells. Sheath dimensions are highly variable, but uniform within local portions of the thallus:  $4 \times 4 \mu\text{m}$ ;  $15 \times 20 \mu\text{m}$ ;  $11 \times 12 \mu\text{m}$ . For the entire thallus the diameters range from 4 to  $26 \mu\text{m}$ , with an average of approximately  $15 \mu\text{m}$ . Filamentous sheaths are up to  $72 \mu\text{m}$  long and  $26 \mu\text{m}$  wide, subdivided into smaller enveloped sections and cell envelopes. The largest single packet measures  $52 \times 36 \mu\text{m}$ . Individual envelopes are elongated in the direction of the filament axis, the narrower end indicating the direction of growth. Ramifications of filaments are dichotomous, apparently originating from occasional longitudinal cell divisions. The branches remain parallel, and the "points" of the terminal envelopes are turned inward toward the common filament axis. Close packing within the thallus causes polygonal outlines of the envelopes and sheaths. The preserved thallus fragment covers an area of  $2.0 \times 1.5 \text{ mm}$ ; smaller fragments with remnants of cells and/or sheaths are sparsely scattered throughout observed material.

**Etymology.** With reference to the morphological similarity to modern blue-green algae of the genus *Pleurocapsa* Thuret.

**Type species.** *Palaeopleurocapsa wopfnerii* Knoll, Barhoorn & Golubic n. sp.

**Diagnosis.** As for genus.

**Etymology.** In honor of the Australian geologist H. Wopfner.

**Type locality.** Cherty units in upper portion of Skilloleale Dolomite, exposed in meridionally trending ridges about 16 km east-northeast of Port Augusta, South Australia.

**Type specimen.** The portion of the algal thallus shown in Fig. 1a and Fig. 2b-f has been designated as the type for the new taxon. Slide no. SKIL 58305C-2, Paleobotanical Collections Harvard University no. 60218; stage coordinates of "X" inscribed on slide  $63.9 \times 88.2$ ; stage coordinates of type specimen  $41.7 \times 88.9$ .

### Interpretation

Comparison of *Palaeopleurocapsa wopfnerii* with members of the modern cyanophyte family Pleurocapsaceae demonstrates a great similarity between ancient and recent forms. Pleurocapsacean blue-green algae are characterized by a filament-like arrangement of coccoid cells, resulting from cell division primarily in a single plane. Apparent ramifications are common and are the result of "slippage" of individual cells out of the linear arrangement, or occasional division in a different plane. Pseudoparenchymatous packing often obscures the filamentous arrangement (1). Multiple sheaths occur as a rule, frequently pigmented by a yellow-brown extracellular pigment in response to high light intensity.

The genus *Pleurocapsa* Thuret, recently re-examined by Bourrelly (19) and Komarek (20), represents well the main features of the family. It reproduces by production of numerous small endospores that are liberated when the endosporangial wall bursts. Often, the spores settle before dispersal so that new algae develop among the parent population. It is not uncommon to discern several generations of cells with distinct size ranges growing within the same tuft or crust. This mode of reproduction is common within the family Pleurocapsaceae and has also been observed in the hyellacean genera *Xenococcus* (21, 22) and *Hyella* (23). Species of *Pleurocapsa* occur commonly in marine (e.g., *P. fuliginosa* Hauck) and freshwater (e.g., *P. minor* Hansgirg) environments, where they form compact 1- to 2-mm thick crusts over the rocks. Related genera include *Xenococcus* Thuret and *Hyella* Bornet & Flahault, which are epiphytic and endolithic forms, respectively.

A comparison of the fossil *Palaeopleurocapsa wopfnerii* (Fig. 1a) with specimens of the modern genus *Pleurocapsa*, including *P. fuliginosa*, the type species of the genus (Fig. 1b-e), shows that many of the described characteristics are shared by the two forms although they are separated in time by over one billion years. The interpretation of the similarities and differences, however, needs to take into account probable alterations that may have occurred after the death of the organisms, as well as subsequent diagenetic changes, because the preserved morphology is very much the product of these processes. Dead cells of cyanophytes in extant intertidal algal mats tend to collapse and shrink, losing their turgid, convex appearance, while their gelatinous envelopes and sheaths retain their original shape (24). The cells degrade rapidly into polyhedral, star-shaped and, finally, irregular granules, or disappear completely. The gelatinous envelopes, however, when stained with extracellular pigments, remain recognizable in the sediment for thousands of years (25), shrinking evenly without noticeable distortion of shape.

Structures indicating shrinkage deformation are observed occasionally in *Palaeopleurocapsa* (Fig. 2a), and are interpreted here as remnants of collapsed cells. Circular, convex-polygonal or elongated, often multiple, outlines arranged in pseudoparenchymatous packets or in dichotomizing series are interpreted here as remnants of pigmented gelatinous sheaths and envelopes. Fading of some of these envelopes and possible size reduction due to dehydration and silicification render accurate size determination of the original organism impossible; however, the arrangement of sheaths and envelopes does reveal mode of growth and patterns of cell division. Co-existence of subpopulations with distinct but uniform size ranges identifies a pleurocapsacean mode of reproduction.

One other point bears mention. *Palaeopleurocapsa wopfnerii* is large (a single tuft is visible to the unaided eye and individual filaments exceed  $70 \mu\text{m}$  in length) and complex (apparent dichotomous branching and variability in the shape and size of sheaths and envelopes); however, despite these attributes it is clearly prokaryotic. A number of modern cyanophytes and bacteria have attained such a size and level of morphological organization, and some, for example, members of the order Stigonematales of the blue-green algae, have reached a still higher level of differentiation.

FIG. 2 (on preceding page). ( $\times 1200$ ) *Palaeopleurocapsa wopfnerii*. (a) Note dark patches of organic matter in the center of some cells. We interpret this material to be degraded protoplasm. Morphological fidelity is preserved by sheath material. (b) Note trilamellar sheath. (c) Note smaller sheath completely encompassed by large elongate sheath. (d and e) Various sheath configurations within thallus. (f) Parallel dichotomizing ramifications preserved in growth position.

Thus, morphological complexity of a microfossil does not necessarily indicate eukaryotic affinity. Recognition of the full range of cyanophytic size and organization is essential in evaluating the Precambrian fossil record.

In summary, comparison of *Palaeopleurocapsa wopfnerii* with the modern algal genus *Pleurocapsa* demonstrates affinities at the family level and quite possibly even generic identity. This remarkable similarity between two microorganisms separated temporally by approximately 1.0–1.2 billion years provides further evidence for the evolutionary conservatism of the blue-green algae.

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