

REPRODUCTIVE AND VEGETATIVE ORGANS WITH AFFINITIES TO HALORAGACEAE FROM THE UPPER CRETACEOUS HUEPAC CHERT LOCALITY OF SONORA, MEXICO¹

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From the Upper Cretaceous (Maastrichtian-Campanian) Huepac Chert Locality of the Tarahumara Formation, a new extinct aquatic plant of the Haloragaceae (Subclass: Rosidae), *Tarahumara sophiae* Hernández-Castillo and Cevallos-Ferriz, is presented. It is reconstructed on the basis of both reproductive and vegetative organs preserved in chert. Its description and comparison with extant plants are based on the analysis of 350 permanent slides made with thin section and peel techniques. A mosaic of anatomical and morphological characters found in the extant *Myriophyllum*, *Meziella*, and *Haloragodendron* is used to characterize the new taxon. The development from flower to fruit in the fossil plant follows similar stages found in some extant species of *Myriophyllum*. However, a floral cup is reported for the first time in the family, and it is compared to the persistent fused sepals (terminal corona) of *Meziella*. This plant reconstruction increases the morphological diversity of the Haloragaceae, demonstrates the presence of a new dispersal mechanism compared with those known for the family, suggests that this lineage had originated by at least the Upper Cretaceous, and refutes the interpretation of several haloragacean Tertiary reports as representing genera of extant plants.

Key words: anatomy; Haloragaceae; floral cup; Mexico; Myriophylleae; Upper Cretaceous.

The study of Cretaceous plant material from Mexico has been scarce and mostly based on compression-impression fossils (e.g., Weber, 1972, 1980 [1982]; Silva-Pineda, 1984; Weber and Cevallos, 1994). In recent years permineralized fruits with in situ seeds have been reported from Campanian sediments near Saltillo, Coahuila (Rodríguez de la Rosa and Cevallos-Ferriz, 1994), and vegetative stems and roots of *Palmae* from northern Mexico were described by Cevallos-Ferriz and Ricalde-Moreno (1995). One of these northern fossiliferous outcrops, the Huepac chert from Sonora, has been known since the

late 1970s. However, it was not until almost two decades later that Ricalde-Moreno and Cevallos-Ferriz (1992) mentioned the presence of permineralized plants. Among these fossil plants are reproductive (flowers and fruits) and vegetative (stems and leaves) organs.

In the last two decades much has been clarified about Cretaceous flowering plants. However, despite this, little information on the internal anatomy of these fossils has been provided. Nevertheless, preliminary results that call for more detailed and comprehensive studies would yield valuable results. For example, seeds of Cretaceous zingiberalean plants have an integumentary anatomy clearly distinct from their extant counterparts, but their gross seed anatomical structure clearly aligns them with the Zingiberales and allows recognition of families within the order (Manchester and Kress, 1993; Rodríguez de la Rosa and Cevallos-Ferriz, 1994). In this context, the permineralized material from the Deccan Intertrappean Series, India, is important not only in documenting plant diversity, but in understanding the anatomical evolution of plants (e.g., Trivedi and Chandra, 1933; Rao, 1936; Sahni, 1941, 1943a, b, 1947; Shukla, 1944; Chitaley, 1955, 1964). Similarly, although not in Cretaceous sediments, fruit and seed anatomy of reproductive organs with nymphaealean affinity suggest greater diversity of this group of plants during the early Tertiary (Collinson, 1980; Cevallos-Ferriz and Stockey, 1989). Anatomical studies of seeds of Vitaceae also support the presence of Tertiary extinct plants (Cevallos-Ferriz and Stockey, 1990), and comparative anatomy of Eocene and extant vegetative axes of this family documents a larger diversity in the group (Wheeler and LaPasha, 1994). Much more information is

¹ Manuscript received 16 November 1998; revision accepted 27 April 1999.

The authors thank Antony Orchard, Environment Australia Biodiversity Group, Alejandro Novelo (Instituto de Biología, UNAM), Enrique Martínez (Instituto de Geología, UNAM), and Sonia Vázquez (Facultad de Ciencias, UNAM) for their comments on different aspects of this work; Judith Márquez and Gullermina Murguía for their guidance in histological techniques (Laboratorio de Citología, Facultad de Ciencias, UNAM); Mario Souza (MEXU) for permission of herbarium comparisons; Carlos M. González, Jaime Roldán, Cesar Jacques, José Luis Rodríguez, and Juan C. García (ERNO-UNAM) for help during field work; Jaime R. Bonilla (UAEM) for help with the collection of extant plant material; Antonio Altamira (Instituto de Geología, UNAM) for help with photography; and Juan T. Vázquez (Instituto de Geología, UNAM) for facilitating the processing of thin sections; and Steven R. Manchester (Florida Museum of Natural History) and Alan Graham (Kent State University) for helpful comments on the original manuscript. This work was partially supported by the Dirección General de Asuntos del Personal Académico (DGAPA-UNAM IN-207294 and IN-205597) and Consejo Nacional de Ciencia y Tecnología (CONACyT 1005PT).

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needed to fully understand the importance of anatomical studies in discussions of the taxonomic, evolutionary, variability, and diversity of flowering plants, but literature on these topics keeps growing, promoting a more complete concept of the plants of the past and their relationships with extant ones (e.g., Basinger, 1976; Basinger and Rothwell, 1977; Bonde, 1986, 1989; Nishida and Nishida, 1986; Paradkar and Patki, 1987; Stockey, 1987; Erwin and Stockey, 1989; Verma and Upadhyay, 1989; Cevallos-Ferriz and Stockey, 1991; Pigg, Stockey, and Maxwell, 1993; Wheeler and Baas, 1993).

The fossil record of Haloragaceae is based mostly on pollen grains. Its palynological record supposedly goes back to the Upper Cretaceous (Praglowky, 1970; Cronquist, 1981), however, this report has not been widely accepted (Benton, 1993). Nevertheless, all records from the Paleocene to the Pliocene are well supported (e.g., Praglowky, 1970; Gruas-Cavagnetto and Praglowky, 1977; Engel, 1978a, b; Gruas-Cavagnetto, 1978; Rowett and Sparrow, 1994). Megafossils of the family are mainly from the late Tertiary, especially from the Pliocene, such as the fruits of *Proserpinaca* and *Myriophyllum* from Poland (Reid and Reid, 1915, as cited in Praglowky, 1970; Szafer, 1954, as cited in Praglowky, 1970). There are other fossil fruits from the Miocene of several localities in Europe and Siberia that have been referred to *Proserpinaca* (Praglowky, 1970), and from the Oligocene of Central Europe that are related to extant *Myriophyllum* and *Proserpinaca* (Mai, 1985). There is also a report of a four-lobed conic drupe from the Eocene London Clay, named *Holoragicya quadrilocularis* Reid and Chandler (Reid and Chandler, 1933). Finally, from the Upper Eocene of Yugoslavia *Hippuridella stacheana* Edwards was interpreted as related to the extant genus *Hippuris*, which now has been removed from Haloragaceae and placed in its own family (Orchard, 1975; Cronquist, 1981).

The Cretaceous plant material from Huepac, Sonora, allows the reconstruction of an aquatic freshwater plant in which the anatomical structure and morphological characters contribute to a detailed comparison between fossil and extant plants. The understanding of similarities and differences between the fossil and extant plants supports the recognition of two taxa within Haloragaceae, based on reproductive organs, *Tarahumara sophiae* gen. et sp. nov. Hernández-Castillo and Cevallos-Ferriz, and the other based on vegetative organs, *Obispocaulis myriophylloides* gen. et sp. nov. Hernández-Castillo and Cevallos-Ferriz, and suggests a greater diversity in the family during the Cretaceous-Tertiary.

MATERIALS AND METHODS

The fossil plants were collected from a continental volcanic sedimentary deposit known as the Huepac chert locality interpreted as the uppermost member of the Tarahumara Formation (Amaya-Martínez and González, 1993; Jacques-Ayala et al., 1993; Ricalde-Moreno and Cevallos-Ferriz, 1993; Roldán-Quintana, 1993). Its geographic extent ranges from northern (Huepac and Teguachi) to southern (Obispo canyon) Sonora (Fig. 1). The Huepac chert locality is 12.5 km northeast of the town of Huepac, in the central part of the state of Sonora, Mexico, between 29°10'–13' N latitude and 110°6'–9' W longitude. The volcanic-sedimentary sequence in southern Sonora is dated by the U-Pb method as 70 million years (m.y.) (McDowell et al., 1994). The sequence is composed of rhyolitic rocks towards the base and alternating cycles of

limestone, stromatolitic limestone, and chert towards the top of the section (Fig. 1).

The Huepac chert was deposited in a freshwater lacustrine environment, where the fossil material was preserved as silica permineralizations. The fossil plants are represented by detached and often fragmentary organs, mainly of angiosperms (Cevallos-Ferriz and Ricalde-Moreno, 1995), but algae are frequent (Chacón-Baca and Cevallos-Ferriz, 1995; Beraldi-Campesi, Chacón-Baca, and Cevallos-Ferriz, 1997), and fungi are associated with the plant organs.

Some 350 slides were prepared by thin section and peel techniques modified for hydrofluoric acid (Joy, Willis, and Lacy, 1956). Anatomical and morphological observations of the fossil material were made with an Olympus SZH stereoscopic microscope and camera lucida and an Olympus BH-2 light microscope.

The reproductive and vegetative organs were identified by consulting the literature, using the computerized key, MEKA 1.3 (Duncan and Meachan, 1987), and the FAMEX databases (Murguía and Villaseñor, 1993), as well as direct observation of herbarium specimens and fresh material in extant populations. Natural populations of *Myriophyllum heterophyllum* Michx. and *M. aquaticum* (Vellozo) Verdc. were examined from the second and third lagoons of the Zempoala Lagoons National Park, Morelos, Mexico. When similarity with a particular taxon was noticed, this and allied plants were surveyed. The collection of the National Herbarium of Mexico (MEXU) was especially useful at this stage (Table 1). Herbarium material used for histological techniques was treated with standard histological methods (Johansen, 1940), embedded in a plastic resin (JB-4) for ultramicrotome sectioning, and stained with toluidine blue in a 5% water solution. Standard palynological techniques were applied to three chert samples.

All the fossil and extant material used in this study is deposited in the Paleobotanical Collection of the Paleontological Museum of the Instituto de Geología, UNAM (National Autonomous University of Mexico).

SYSTEMATICS

Class—Magnoliopsida

Subclass—Rosidae

Order—Haloragales

Family—Haloragaceae

Tribe—Myriophylleae

Genus—*Tarahumara* Hernández-Castillo et Cevallos-Ferriz gen. nov.

Species—*Tarahumara sophiae* Hernández-Castillo et Cevallos-Ferriz gen. et sp. nov.

Holotype—Paleontological Collection of the Instituto de Geología, Universidad Nacional Autónoma de México. Specimen LPB 3434.

Locality—Huepac chert locality, Sonora, Mexico, located between 29°10'–13' N latitude and 110°6'–9' W longitude.

Etymology—The generic name refers to the geological formation from which the plant was collected. The specific epithet honors the excellent technical work of Mrs. Sofía Espinosa Vázquez in the Paleobotanical Laboratory of the Instituto de Geología, UNAM.

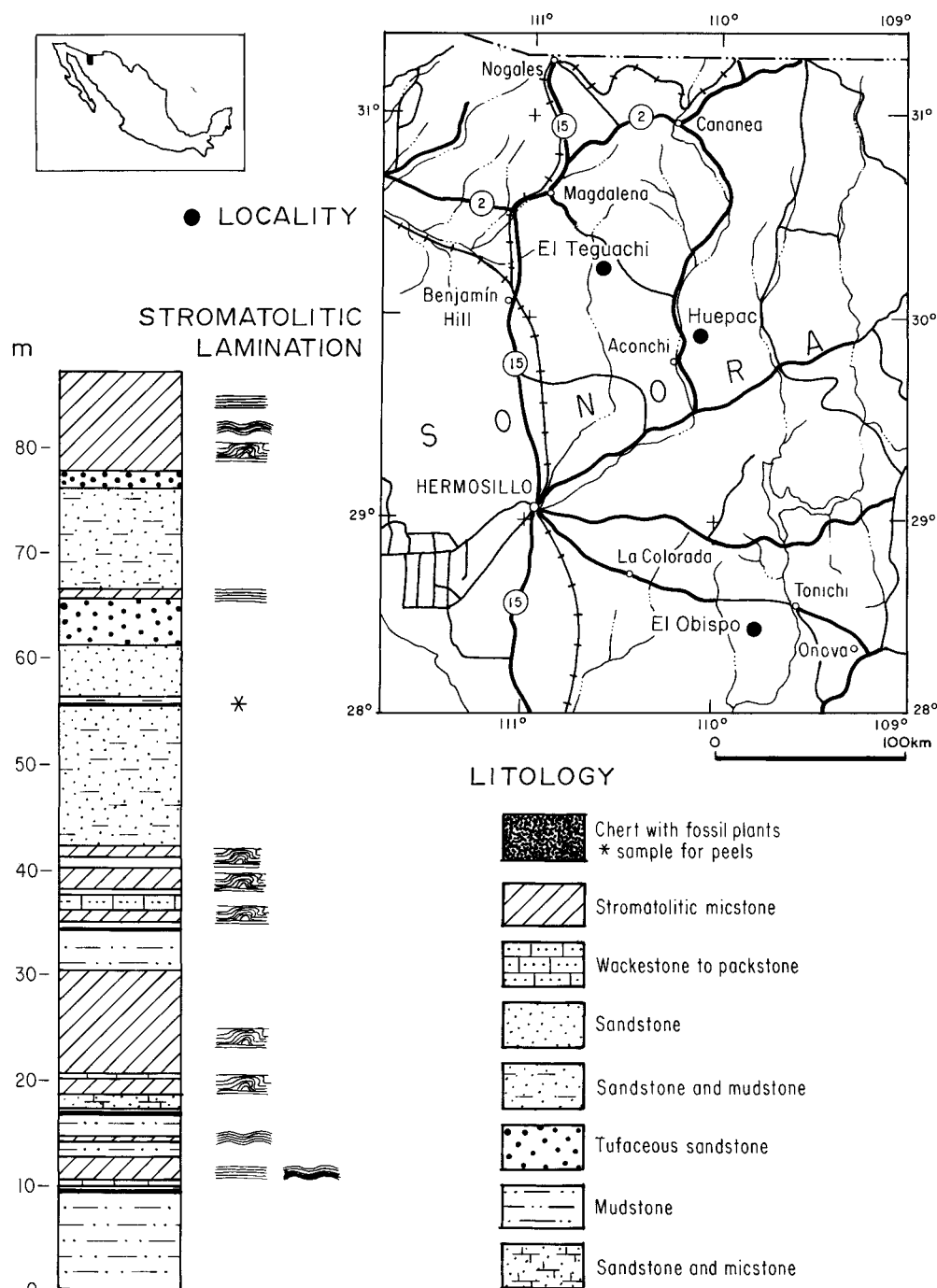


Fig. 1. Location of fossiliferous outcrops of the Tarahumara Formation, Upper Cretaceous (above), and stratigraphic column of the type locality in Huepac (bottom), courtesy of C. Jacques-Ayala.

Diagnosis—Inflorescence/inflorescence similar to a dichasium, composed of a main axis with verticillate secondary axes in the base and opposite secondary axes toward the apex; individual flowers are verticillate and axilar in the first two verticils and terminal in the opposite secondary axes. Flower small, unisexual, actinomorphic, epiginous, and syncarpous (at least in its basal part); gynoecium of four carpels, united at their bases and fused to the basal part of the floral cup; each carpel with a

single anatropous, pendulous ovule. Fruit small, globose to claviform; four-carpelate with one seed per carpel, at maturity schizocarpic; single-layered exocarp with obloid to botuliform cells; mesocarp with several layers of polyhedral nearly isodiametric parenchyma cells; endocarp of five to six layers of nearly rectangular sclerenchymatous cells. Seed pyriform, anatropous with two integumentary zones; outer integumentary zone composed of ellipsoidal cells, inner integumentary zone with crushed

TABLE 1. List of Haloragaceae species from the National Herbarium of Mexico (MEXU) used in comparison with the fossil material. Asterisks indicate taxa analyzed histologically.

Taxa	Collected from	Catalog number (MEXU)
<i>Gunnera insignis</i> (Oerst) A. DC.*	Nicaragua	661 467
<i>Gunnera killipiana</i> Lundell*	Veracruz, Mexico	263 985
<i>Gunnera mexicana</i> Brandegees*	Veracruz, Mexico	209 815
<i>Gunnera talamancana</i> Weber-Mora	Costa Rica	163 581
<i>Gunnera wendlandii</i> Reibe ex Schindll.	Costa Rica	790 117
<i>Halorrhagis trigonocarpa</i> F. Muell.	Australia	597 421
<i>Myriophyllum aquaticum</i> (Vellozo) Verdcourt*	North Carolina	594 756
	Guanajuato, Mexico	306 104
	Jalisco, Mexico	170 818
	State of Mexico, Mexico	594 775
	State of Mexico, Mexico	420 170
	State of Mexico, Mexico	409 971
	Oaxaca, Mexico	428 671
<i>Myriophyllum brasiliense</i> Camb.	Georgia, USA	126 533
	North Carolina, USA	134 263
<i>Myriophyllum exalbescens</i> Fern.	Quebec, Canada	143 946
	Minnesota, USA	773 100
<i>Myriophyllum heterophyllum</i> Michx.*	Hidalgo, Mexico	537 593
	Massachusetts, USA	298 724
	Morelos, Mexico	597 626
	Morelos, Mexico	597 618
	North Carolina, USA	147 099
	North Carolina, USA	134 209
	Texas, USA	414 846
	Veracruz, Mexico	324 859
	Veracruz, Mexico	324 860
	Michoacan, Mexico	497 263
<i>Myriophyllum hippurides</i> Nutt.	State of Mexico, Mexico	170 817
	Morelos, Mexico	768 712
<i>Myriophyllum humile</i> (Raf.) Morong. form <i>capillaceum</i> (Torr.) Fern.	Massachusetts, USA	123 215
<i>Myriophyllum laxum</i> Shuttlew. ex Chapman	North Carolina, USA	134 197
<i>Myriophyllum quitense</i> H.B.K.	State of Mexico, Mexico	357 838
	State of Mexico, Mexico	343 269
<i>Myriophyllum spicatum</i> L.	Arizona, USA	537 346
<i>Myriophyllum spicatum</i> L. spp. <i>exalbescens</i> (Fern.) Hult	Arizona, USA	807 330
<i>Myriophyllum tenellum</i> Bigel	Wisconsin, USA	146 949
<i>Myriophyllum verticillatum</i> L.	Minnesota, USA	691 038
	Quebec, Canada	50 713
<i>Proserpinaca palustris</i> L.*	Florida, USA	398 950
	North Carolina, USA	173 153
	Tennessee, USA	669 409
	Wisconsin, USA	165 224
<i>Proserpinaca pectinata</i> Lam.	Texas, USA	122 892
	North Carolina, USA	399 231
	North Carolina, USA	181 562
<i>Proserpinaca platycarpa</i> Small	Florida, USA	600 470

rectangular cells. Reproductive axes in transverse section with an epidermis of rectangular cells, cortex with two regions, the outer one composed of isodiametric, compactly arranged, parenchyma cells, the inner one with rectangular to isodiametric thin-walled cells, sometimes arranged in radial rows. Protoxylem with tracheary elements and annular thickenings, metaxylem composed of tracheary elements with helical thickenings, secondary xylem diffuse porous, small vessel elements with circular intervacular pits and oblique scalariform end walls, axial parenchyma one or two seriate composed of erect cells. Pith composed of large, polyhedral, parenchyma cells, and small, isodiametric, thin-walled cells, usually with dark contents.

Description—Reproductive (infructescence/inflorance and isolated flowers/fruits) organs are known for this plant. The flowers are 2.2 (1.55–2.51) mm in length including the style and stigma and are 1.5 (1.10–1.80) mm in width (Figs. 2–3). They are composed of a floral cup that surrounds four apocarpic carpels (Figs. 4–5), which are fused to each other toward their base (Fig. 2) and to the floral cup up to two-thirds of its length (Figs. 2–3, 6). In the floral cup three anatomical zones are recognized (Fig. 7). The outer zone (outer epidermis) is composed of small rectangular cells with a mean diameter of 11 (8–13) \times 13 (11–17) μ m in longitudinal section. The middle zone (mesophyll) is composed of four to five layers of rectangular to polyhedral cells, 26 (17–

35) \times 13 (8–26) \times 24 (16–31) μm in diameter. The inner zone (inner epidermis) is similar to the outer epidermis; however, towards the base of the floral cup it does not develop, allowing the fusion of the mesophylls of the carpels and floral cup (Fig. 7).

Individual carpels tend to be triangular with rounded edges in transverse section (Figs. 4–6), pyriform in longitudinal section, have their own style and stigma, and are composed of three distinct cell zones (Figs. 2–3). The outer epidermis is composed of a single layer of thick-walled, oblong to botuliform cells, with dark contents, that are 36 (26–50) \times 29 (22–45) \times 43 (25–65) μm in size (Figs. 8–9). The middle zone, or mesophyll, is formed by several layers of polyhedral, thin-walled parenchyma cells, 17 (10–23) \times 16 (12–20) \times 15 (12–20) μm . Included in this tissue are eight vascular bundles composed of tracheary elements with helical thickenings that are oriented parallel to the long axis of the carpel (Figs. 8–9). The inner epidermis is composed of a single layer of thick-walled cubical to rectangular cells, 8 (5–11) \times 7 (4–10) \times 9 (7–10) μm (Fig. 8). In the distal zone of each carpel is the style with a V-shaped stigma, composed of the same tissues of the ovary (Fig. 10). However, some cells along the inner margin of the mesophyll are slightly more elongated in longitudinal section and are closely packed (Fig. 10).

An anatropous, pendulous ovule is pyriform in longitudinal section (Figs. 2–3, 11) and turbinate in transverse section (Figs. 4–6), with a mean length of 1.2 (0.85–1.25) mm and a mean width of 3.75 (3.0–4.75) mm. A short funiculus, 200 μm in length and 62 μm in width, has a single vascular bundle that is surrounded by thin-walled polyhedral cells and located toward the distal zone of the ovary. The micropyle is located on the distal part of the ovule, close to the hilum, and the two integumentary zones form a micropylar tube (Figs. 11–12). Opposite the micropyle is the chalazal zone where a discoid structure composed of rectangular to almost square cells, 5 (5–7.5) \times 6 (5–7.5) μm in longitudinal section, with rounded edges, suggests the presence of a hypostase (Figs. 11, 13). The outer integumentary zone is composed of a single layer of thin-walled ellipsoidal cells, 35 (25–45) \times 26 (22–30) \times 28 (24–30) μm . The inner integumentary zone is rarely preserved, and when it is, it appears as a squashed membrane composed of rectangular cells that are difficult to observe (Fig. 14).

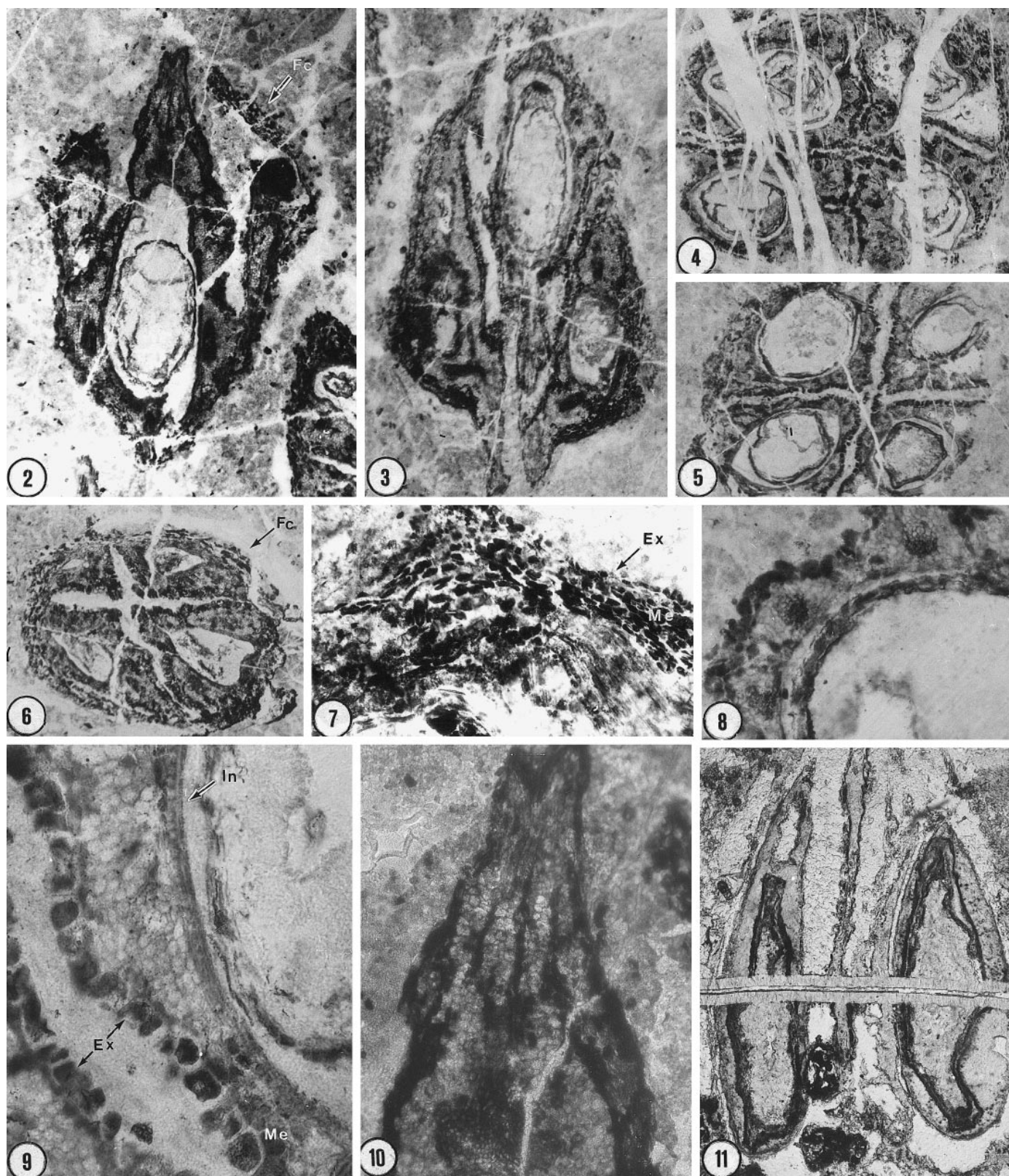
The mature fruit before splitting into mericarps (Fig. 15) is 2.5 (2.3–2.5) mm in length, 1.7 (1.6–1.7) mm in width, and globose to claviform, with its base wider than the apex (Fig. 16). A single specimen has an air space below the carpels, in the area where the carpels and the floral cup should be fused (Fig. 16). The pericarp is composed of three zones, exocarp, mesocarp, and endocarp (Figs. 16–17), which are very similar to the three zones of the ovary. The exocarp is composed of a single layer of thick-walled, botuliform cells, 36 (22–48) \times 30 (20–46) μm in longitudinal section, with dark contents (Fig. 17). The mesocarp is composed of thin-walled polyhedral cells, 16 (10–23) \times 15 (12–20) μm in longitudinal section, with dark contents (Fig. 17). The endocarp is composed of a single layer of sclerified rectangular cells, 24 (15–30) \times 15 (10–25) μm in longitudinal section (Fig. 18). The main difference between the ovary and the ma-

ture fruit is observed in the inner layers of the fruit, where the endocarp and the inner layers of the mesocarp become sclerified after reaching larger dimensions, 24 (15–30) \times 15 (10–25) μm in longitudinal section (Fig. 19). A single specimen with poorly preserved mature seeds has some embryonic polyhedral to circular cells, 17 (15–25) \times 15 (12–17) μm in longitudinal section, preserved close to the chalazal zone (Figs. 20–21).

The inflorescence/infructescence is similar to a dichasium. It is composed of a main axis (peduncle) with verticillate secondary axes toward the base (Figs. 22–23) and opposite secondary axes toward the apex (pedicels) (Fig. 24). The verticillate and opposite axes are each associated with a bract; however, their position in the main axis has not been observed in a single specimen. Its reconstruction is based on the different diameters of the axis and their anatomical characteristics. The peduncle of the inflorescence/infructescence has a length of >15 mm and a diameter of 2–3 mm (Figs. 22–23, 26). Its internodes are spaced \sim 6 mm (only seen in two specimens; Fig. 26). Pedicels are broken so their total length cannot be observed, however they reach an observable length of 0.5–1.0 mm and have a diameter of 0.4 (0.4–0.6) mm (Fig. 27). Both axes, peduncle and pedicel, become slender toward their apex, reaching 0.4 mm in diameter (Fig. 28). The individual flowers are axillary and verticillate if located on the first two whorls (Fig. 23) and terminal if they are in the opposite secondary axes (Fig. 25).

The peduncle, as seen in transverse section, has an epidermis composed of rectangular cells with dark contents, which are 27 (25–32) \times 12 (11–15) μm (Fig. 29). Its cortex can be divided in two zones based on cell shape and arrangement (Fig. 29–30). The outer cortex is three to four cell layers thick and is composed of isodiametric, thin-walled cells, 28 (22–40) \times 32 (25–37) μm . The inner cortex is 10–13 cells thick and composed of isodiametric to rectangular cells, 51 (35–75) \times 49 (40–62) μm , with larger randomly arranged oval-shaped cells, 90 (70–145) \times 74 (42–95) μm (Fig. 30). Sometimes this inner cortex is arranged in a radial direction with some large intercellular spaces suggesting the presence of aerenchyma (Fig. 31). The protoxylem is composed of long tracheary elements with annular thickenings, 11 (8–14) μm in diameter (Fig. 33). The metaxylem elements are slightly wider, 14 (12–17) μm , and shorter. Their lengths were not measured due to poor preservation of their limits. A central pith is composed of two types of thin-walled cells, which tend to be isodiametric in transverse section and rectangular in longitudinal section (Figs. 32, 34). The most conspicuous cells have a diameter of 48 (30–70) μm , while the second type of cells are smaller, usually with dark contents, and have a diameter of 16 (12–23) μm (Fig. 34).

All axes have little development of secondary tissues (Figs. 26, 35). Secondary xylem is diffuse porous and has uni- and biseriate rays (Fig. 32). Vessel elements are 66 (42–76) μm in length and 16 (8–20) μm in diameter, with one or two rows of small to medium size, 4 (2–5) μm , rounded intervacular pits. When in two rows they tend to be opposite (Fig. 36). The end walls have oblique scalariform plates with a mean of 11 (4–16) bars (Fig. 37). Rays in tangential section are 248 (145–248) μm high and composed of fusiform and rectangular cells,



Figs. 2-11. Flower of *Tarahumara sophiae* gen. et sp. nov. **2.** Longitudinal section showing floral cup, central carpel with style, stigma, ovule, and two lateral carpels. LPB 3206, $\times 35$. **3.** Longitudinal section showing three carpels with one ovule each. LPB 3269A, $\times 32$. **4.** Transverse section near the base, showing four carpels almost fused. LPB 3551, $\times 36$. **5.** Transverse section near the apex, showing free carpels. LPB 3333, $\times 30$. **6.** Transverse section near the base, showing fusion of floral cup to the carpels. LPB 3226, $\times 27$. **7.** Longitudinal section of the floral cup, showing external epidermis and mesophyll. LPB 3201, $\times 106$. **8.** Transverse section of carpel, showing external and internal epidermis and mesophyll with vascular bundles. LPB 3315, $\times 105$. **9.** Transverse section of carpel, showing cellular components of external epidermis, mesophyll and internal

which in radial section correspond to erect cells (Fig. 35). Secondary phloem, in transverse section, is composed of packages of circular cells separated by wide rays composed of rectangular thin-walled cells (Fig. 38). In the packages two types of thin-walled cells are distinguishable. The larger ones (sieve elements?) have a diameter of 19 (18–20) μm , a length of 77 (50–85) μm , and dark contents (Fig. 39). In contrast, the smaller cells have a diameter of 12 (10–15) μm and a length of 60 (55–65) μm (Fig. 39). Some parenchyma cells are dispersed within the packages. Between the secondary xylem and phloem a region composed of three layers of rectangular thin-walled cells represents the cambial zone, with the middle layer corresponding to the vascular cambium (Fig. 39).

Although male flowers have not been observed, isolated pollen grains similar to those of Haloragaceae have been recovered from chert samples containing the described female reproductive structures (Figs. 40–41). They are psilate, tetrazonoporate, and 20–21 μm in diameter, suggesting an oblate-spheroidal shape. The exine is 1 μm thick; the four pores are separated by a distance of at least 10 μm , and the aperture of these pores is \sim 2 μm (Fig. 40). Unfortunately, their small number and light color suggest they may be contaminants. Further palynological studies are needed to confirm their association with the new reproductive structures.

Genus—*Obispocaulis* Hernández-Castillo et Cevallos-Ferriz gen. nov.

Species—*Obispocaulis myriophylloides* Hernández-Castillo et Cevallos-Ferriz gen. et sp. nov.

Holotype—Paleontological Collection of the Instituto de Geología, Universidad Nacional Autónoma de México. Specimen LPB 842.

Locality—Obispo chert locality, located between 28°3'–6' N latitude and 109°6'–8' W longitude, but also present in the Huepac Chert locality.

Etymology—The generic name refers to the locality where the material was collected. The specific epithet refers to the extant genus with the most similar stem anatomy.

Diagnosis—Stem epidermis composed of semi-obloid cells with thin cuticle; outer and inner cortex of polyhedral parenchyma cells; middle cortex composed of radially elongated lacunae limited by biseriate chains of parenchyma cells connecting the inner and outer cortex (aerenchyma); endodermis with thick-walled radial walls; primary xylem composed of tracheary elements, some

vessels, and parenchyma cells. Verticillate ensheathing leaves with an epidermis of ellipsoidal thin-walled cells; mesophyll of four to six layers of polyhedral to isodiametric parenchyma cells; no vascular bundles have been observed.

Description—Only transverse, and poorly preserved oblique, sections are available. Fragile stems, 0.75–2.3 mm in diameter with verticillate leaves (Fig. 42), have an epidermis composed of semi-obloid cells, 25 (17–35) \times 15 (12–20) μm (Fig. 43). Its outer cortex is four to eight layered, composed of thin-walled parenchyma cells, 28 (20–37) \times 24 (20–27) μm (Fig. 43). The inner cortex is composed of three or four layers of parenchyma, thin-walled cells, similar to those of the outer cortex, 21 (15–25) \times 18 (14–23) μm (Fig. 43). The middle cortex is composed of aerenchyma. The lacunae are limited by one or two layers of thin-walled parenchyma cells, arranged in chains of \sim 7 cells that unite the outer and inner cortex. Individual lacunae are \sim 365 (350–380) μm in length (Fig. 43). The endodermis is single layered, composed of rectangular thin-walled cells, 21 (16–25) \times 13 (10–20) μm , with thickenings in their radial walls (Fig. 44). Primary xylem is composed of tracheary elements, 17 \times 15 μm in diameter. In some cases it is possible to see in the central part of the stele four to five vessel elements, 70 \times 80 μm to 87 \times 90 μm in diameter (Fig. 44).

In transverse section, the shape of the stems is circular when these are isolated. However, when they are grouped with other stems or leaves the shape varies from circular to elliptical (Fig. 45). When grouped there are two or three stems and almost the same number of leaves. One of these stems is always larger than the others (Fig. 46).

Epidermal cells of the leaves are dome shaped, 25 (17–27) \times 15 (13–20) μm (Fig. 43). The mesophyll is composed of 4–5 layers of hexagonal cells, 25 (20–26) \times 15 (15–20) μm , and no vascular bundles have been observed (Fig. 43).

DISCUSSION

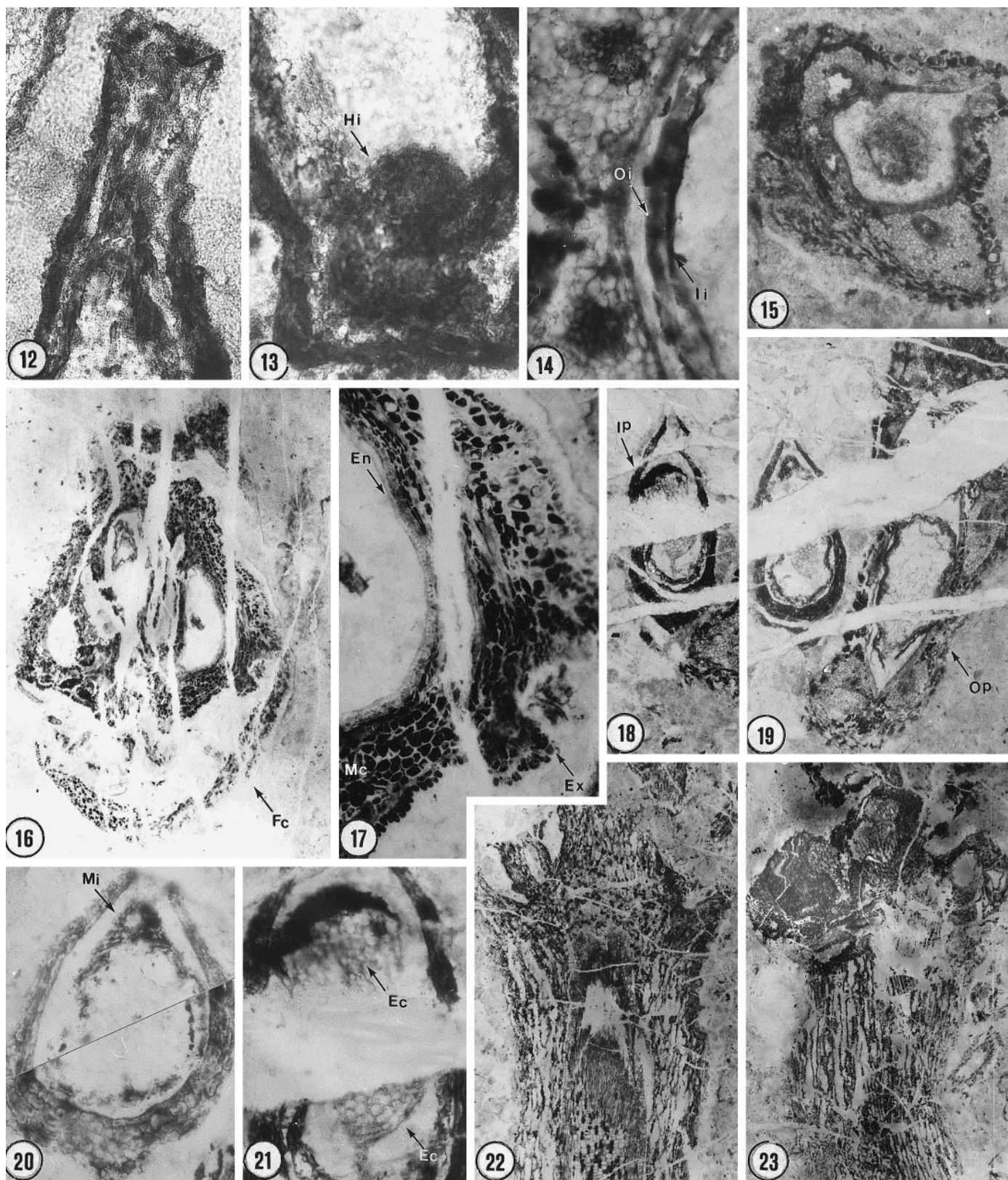
The plant organs described above have been treated as two distinct taxa because they are not in organic connection. However, their occurrence in the same locality, the fact that they have characters found in the same family, and that only one type of each plant organ assignable to the family has been collected in the locality, strongly suggest that they may belong to the same taxon. Therefore, they will be discussed as representing a single plant type.

Although the actinomorphic and epigynous characters of the fossil flowers can be found in Rosaceae, Cunoniaceae, Rhizophoraceae, Hippuridaceae, Gunneraceae, and Rubiaceae (Duncan and Meachan, 1987; Murguía and

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epidermis. LPB 3333, \times 143. **10.** Longitudinal section of style and V shaped stigma. LPB 3206, \times 111. **11.** Longitudinal section of fruit showing two seeds. LPB 3508, \times 41.

Figure Abbreviations: Air space (As), Bract (B), vascular cambium (C), embryonic cells (Ec) epidermis (E), endodermis (Ed), endocarp (En), external epidermis (Ep), exocarp (Ex), floral cup (Fc), hypostase (Hi), inner integument (Ii), internal epidermis (In), inner pericarp (Ip), leaves (L), mesocarp (Mc), mesophyll (Me), micropyle (Mi), outer integument (Oi), outer pericarp (Op), Phloem (P), rays (R), secondary axes (Se), vessel elements (V), xylem (X).



Figs. 12–23. Ovule, fruit, and inflorescence/inflorescence of *Tarahumara sophiae* gen. et sp. nov. **12.** Longitudinal section, showing micropylar tube area. LPB 3508, $\times 200$. **13.** Longitudinal section, showing chalazal zone and hypostase. LPB 3508, $\times 200$. **14.** Transverse section, showing outer and inner integuments. LPB 3315, $\times 218$. **15.** Transverse section of free mericarp. LPB 3504, $\times 63$. **16.** Longitudinal section of fruit showing basal air space and floral cup. LPB 3437, $\times 35$. **17.** Longitudinal section, showing pericarp layers with dark contents: endocarp, mesocarp, and exocarp. LPB 3413, $\times 60$. **18.** Longitudinal section of seed showing internal pericarp with sclerified endocarp and internal layers of the mesocarp.

Villaseñor, 1993), only Haloragaceae have organs with similar anatomy and morphology to those of the fossil material (Table 2). Haloragaceae typically have four carpels, each with one anatropous pendulous ovule and one seed per carpel. Rosaceae, Cunoniaceae, Rhizophoraceae, and Rubiaceae may have four carpels, but usually have more than one ovule per carpel. Furthermore, Rubiaceae have axile placentation like Cunoniaceae and Rhizophoraceae, and the latter also have a nectary disk. Rosaceae also have two to many ovules per carpel, and placentation in most cases is quite different (axile, marginal, etc.). These four families have fruits either with more than four or less than two seeds, and sometimes they are ornamented with hairs, wings, etc., unlike the fruits and seeds of *Tarahumara sophiae*. Furthermore, anatomical comparisons between *T. sophiae* and these families show the strongest similarities with the Haloragaceae (Netolitzky, 1926; Kirchheimer, 1957; Dickinson, 1975; Corner, 1976; Cronquist, 1981).

The other families in Table 2 (Hippuridaceae, Gunneraceae, and Haloragaceae) have solitary, unisexual, epigynous flowers with one anatropous, apical, and pendulous ovule per carpel. Although they share these characters with *T. sophiae*, there are differences in the number of carpels. Hippuridaceae and Gunneraceae have fewer than four carpels per flower. Anatomical comparison of the fruits and seeds of these two families with those of *T. sophiae* further demonstrate their differences (Netolitzky, 1926; Corner, 1976; Cronquist, 1981; Cook, 1990). Therefore, the characters of the fossil reproductive structures are found only in Haloragaceae.

The flowers of *Tarahumara sophiae* are similar to those of extant Haloragaceae in morphology and anatomy. They share a reduced perianth composed of four carpels with one anatropous, pendulous ovule per carpel and an inferior ovary. For example, in the female flowers of *Lauremburgia*, *Proserpinaca*, and *Myriophyllum*, the petals are normally absent or are rudimentary, and sometimes sepals are absent or they are caducous (Orchard, 1975, 1981; Orchard and Keighery, 1993). Although sepals, petals, or tepals have not been observed in the flowers of *T. sophiae*, it is assumed that the floral cup is composed of at least one of these perianth elements. The presence of a four-carpellate and four-seeded gynoecium is common in Haloragaceae. In genera like *Myriophyllum*, *Meziella*, and *Haloragodendron* these characters are normal, however in other genera the four-carpellate ovary does not always have four locules with one seed per carpel. For example, *Gonocarpus* has a reduction in its ovary evidenced by the presence of two or three locules, in *Haloragis* two, three or four locules can be found; and *Glyschocaryon* has a single locule with four ovules.

Reproductive anatomical characters are not well known for some members of the family. Although anatropous, pendulous, and bitegmic ovules are described

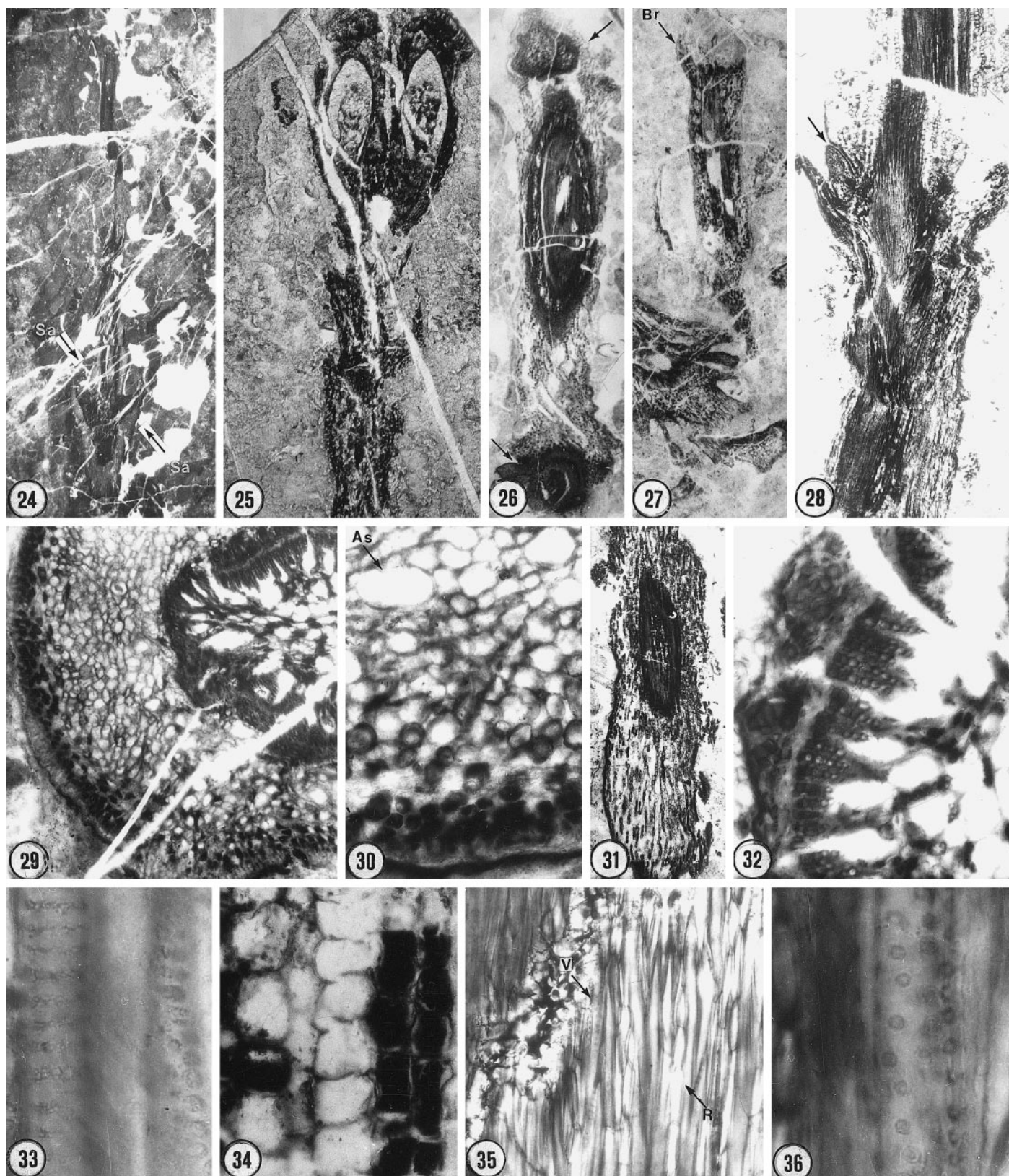
for Haloragaceae, it seems that these characters have been observed only in some species of *Myriophyllum*, *Haloragis*, and *Lauremburgia* (Nagaraj and Nijalingappa, 1967; Corner, 1976; Cronquist, 1981); therefore, information for the rest of the genera in the family is needed. Even so, *T. sophiae* is known to have the same characters as described for the extant plants. A funiculus, which unites the anatropous and pendulous ovule/seed to the carpel near to the micropyle, has been observed for this plant. Furthermore, the ovule has some modified cells in the chalazal zone that form a structure similar to a hypostase, and the integuments are distinguished by an outer layer with tabular thin-walled cells, while the rest of the integumentary zones appear at maturity as a crushed membrane. This zone of crushed cells is present in the Haloragaceae of Corner (1976), who described the seed coats as nonmultiplicative and reduced to an exotesta composed of tabular thin-walled cells, with the remainder of the testa and the tegmen crushed.

Further similarities between *Tarahumara sophiae* and Haloragaceae are seen in fruitlet anatomy. According to Cook (1990) and Orchard (1985), mature extant fruits of Haloragaceae are always schizocarpic nuts or nutlets. However, *T. sophiae* has the endocarp and some inner layers of the mesocarp sclerified, while the rest of the mesocarp and the exocarp are composed of thin-walled cells, being closer to a drupe. Since little anatomical information is available for reproductive organs of the family Haloragaceae (Netolitzky, 1926; Nagaraj and Nijalingappa, 1967; Orchard, 1975; Corner, 1976), we prepared histological slides of some extant fruits. Fruit anatomy in extant *Myriophyllum heterophyllum* Michx. and *M. aquaticum* (Vellozo) Verdc. (Figs. 47–51) is similar to that found in *T. sophiae*, in that only the innermost layers (endocarp and inner layers of mesocarp) of the fruit become sclerified. Although definition of fruit types is sometimes complicated, following Roth (1977) it can be said that nuts are typically characterized by having all their tissues sclerified; nutlets have a sclerified endocarp, a partly sclerenchymatous mesocarp, and a sclerified single-layered exocarp; and drupes are characterized by having, typically, an endocarp and sometimes the inner layers of the mesocarp sclerified, with a thin-walled single-layered exocarp. Even if different definitions for these fruit types were used, what is important for this discussion is that anatomically the fruits of extant Haloragaceae and *T. soffii* are very close to each other.

The genus *Gunnera* has recently been removed from Haloragaceae (Orchard, 1975). However, it was the only taxon in the family sensu lato in which the fruit was described as a drupe. The anatomy of the fruits of *Gunnera* is comparable with that of the extant *Myriophyllum*, as well as with *T. sophiae*. However, detailed anatomical comparison demonstrates some differences between these

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LPB 3551, ×29. **19.** Longitudinal section of two seeds showing external parenchymatous pericarp. LPB 3548, ×33. **20.** Longitudinal section, showing micropyle. LPB 3548, ×100. **21.** Longitudinal section, showing closer view of embryonic cells (arrow). LPB 3551, ×114. **22.** Longitudinal section of the base of the inflorescence/infructescence, showing verticil with secondary axes. LPB 3625, ×14. **23.** Longitudinal section of the base, showing verticil with axillary flowers/fruits. LPB 1–10C, ×9.5.



Figs. 24–36. Inflorescence/infructescence of *Tarahumara sophiae* gen. et sp. nov. **24.** Longitudinal section of the apical zone, showing position of opposite secondary axes. LPB H1, $\times 0.6$. **25.** Longitudinal section of a secondary axis, showing apical flower. LPB 3434, $\times 25$. **26.** Oblique/longitudinal section of the base, showing distance between internodes (arrows) and secondary growth. LPB 7-HLM, $\times 14$. **27.** Longitudinal section of the intermedial zone of the main axis, showing bracts. LPB 3627, $\times 9$. **28.** Longitudinal section of apical part of secondary axis, showing a bract and a bud (arrow). LPB 9-HLM, $\times 25$. **29.** Transverse section of the middle zone of the main axis. LPB 6-HLM, $\times 66$. **30.** Transverse section of

taxa. The shape, number, and size of their endocarp and mesocarp cell layers are different (Figs. 52–53).

Fossil flowers and fruits of *Tarahumara sophiae* are similar to those of the Tribe Myriophylleae where the ovary is differentiated into four separated carpels (Orchard and Keighery, 1993). Differences between the two extant genera of this tribe, *Meziella* and the more abundant *Myriophyllum*, are evident in the mature fruit. *Myriophyllum* has a fruit that splits into four mericarps at maturity, whereas in *Meziella* the fruits do not split into mericarps. The mature carpels of the Haloragaceae are in most cases free from any specialized structure. However, in *Meziella* the carpels are surrounded by persistent, long sepals that are fused to form a terminal corona (Orchard and Keighery, 1993). The presence of this structure in *Meziella* resembles the floral cup of *Tarahumara sophiae*, which surrounds the four-apocarpic-syncarpic carpels. Floral cups have never been reported for the family, but the size and appearance of the terminal corona of *Meziella* are similar to that found in the fossil flowers (see Orchard and Keighery, 1993).

Differences in the apocarpic and/or syncarpic condition of the ovary are observed between the flowers and fruits of fossil and extant members of Tribe Myriophylleae. Extant species of this tribe are always syncarpic with all their carpels fused to each other to different degrees. They may have carpels fused to each other by only one of their edges. Normally the areas of fusion are located toward the central zone of the flower or fruit. They may have carpels fused to each other only by one of their edges, or they may be fused in the basal part of the lateral walls of the carpel, as in *Myriophyllum heterophyllum* Michx. and *M. aquaticum* (Vellozo) Verdc. (Figs. 47–49). *Tarahumara sophiae* is syncarpic only at the base of its carpels, where the outer epidermis of each carpel is not present, and the mesophyll of each carpel becomes fused with that of the neighbor carpel, while toward the distal zone of the fossil flowers the carpels become apocarpic.

The development of the fossil flowers into fruits is similar to that observed in *Myriophyllum*. The process begins with the sclerification of the single-layered endocarp, followed by the same process in the inner part of the mesocarp. The fossil fruits have a single-layered, thin-walled endocarp, a parenchymatous mesocarp, and a single-layered exocarp. After fertilization, the young fruits of *T. sophiae* have two layers of clearly sclerified cells, one corresponding to the endocarp and the other to the innermost layer of the mesocarp. As fruits mature the number of sclerified cell layers increases to five or six. Because sclerified cells do not divide, the new sclerified layers correspond to the inner part of mesocarp. As sclerification proceeds, the thin-walled parenchymatic cells of outer zone of the mesocarp increase in number. These

parenchyma cells sometimes become darker in color. While this color change may be due to fruit ripening, most probably it is due to the activity of fungi in the fruits. This phenomenon has been studied in the permineralized material of the Princeton Chert, British Columbia, Canada (R. A. Stockey, University of Alberta, personal communication, 1997). The exocarp remains single layered and its cells thin walled as in the flowers.

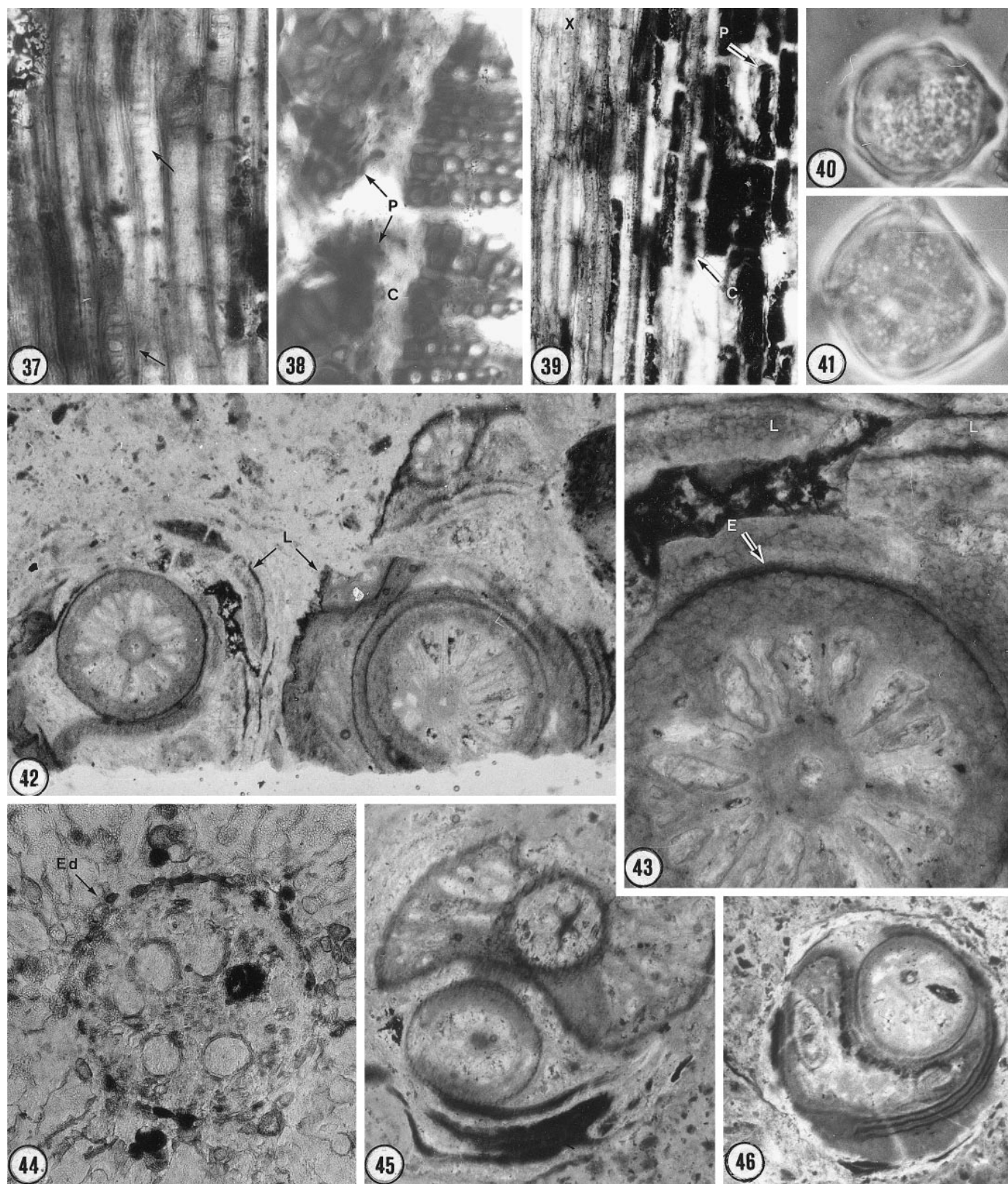
The floral cup also changes as the endocarp and part of the mesocarp become sclerified. It increases in size by cell multiplication with the cell types maintaining their characteristics. However, as cell layers increase in number the shape of the floral cup changes. Its form in mature fruits is globose with two small ornamentations in the apex.

General morphology of the inflorescence/infructescence is based on the interpretation of various axes and its reconstruction using anatomical characteristics. The inflorescence/infructescence is composed of a main axis with secondary axes. Associated with each secondary axis is a bract. In the base of the main axis there are two nodes with verticillate secondary axes, each with flowers/fruits in the axils. This verticillate pattern is not continuous along the main axis. The upper part of the inflorescence has secondary axes with opposite disposition and flowers attached to their apical part. Inflorescences/infructescences with more than one branching order are considered compound inflorescences (Weberling, 1989), and those with their flower/fruit in the apical zone of the opposite branches represent a dichasium.

A dichasium, and more often the compound dichasium, is the basic unit of the indeterminate inflorescences/infructescences in Haloragaceae (Orchard, 1975). However, the inflorescence of *Haloragodendron* is a simple determinate dichasium. In most genera like *Haloragis*, *Glischrocharyon*, *Laurembergia*, and *Proserpinaca*, the second-order branches of the dichasia are alternate, and only in *Haloragodendron* are these opposite. However, not all taxa have this kind of inflorescence (e.g., *Myriophyllum*, *Gonocarpus*, and *Meziella*). Most species of *Myriophyllum* have verticillate axillary flowers; however, some species have a simple dichasium like *M. filiforme* Benth., *M. papillosum* Orchard, and *M. glomeratum* Schindler (Orchard, 1985). From the third verticil on, *Tarahumara sophiae* has a terminal simple dichasia with opposite branches resembling those of extant *Haloragodendron*. However, it is important to remark that the first two nodes have verticillate axile flowers, resembling the position of the flowers of almost all extant species of *Myriophyllum*. Due to preservation, it is not possible to know whether some of the branches with flowers in apical position represent, in fact, the apical zone of the main axis, and thus,

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the middle zone of main axis, showing epidermis, external cortex, and intercellular spaces (air spaces) in the internal cortex. LPB 7-HLM, 93. **31.** Oblique/transverse section of the basal part of main axis, showing aerenchyma. LPB 16-HLM, ×18. **32.** Transverse section of main axis, showing secondary phloem and xylem, and pith. LPB 5-HLM, ×143. **33.** Longitudinal section showing primary xylem. LPB 9-HLM, ×1100. **34.** Longitudinal section of pith with two types of cells and dark contents. LPB 2–19, ×200. **35.** Tangential section showing vessel elements and fusiform rays. LPB 7-HLM, ×400. **36.** Longitudinal section of the secondary xylem, showing vessel elements with rounded intervacular opposite pits. LPB 9-HLM, ×1100.



Figs. 37–41. Inflorescence/infructescence of *Tarahumara sophiae* gen. et sp. nov., and fossil pollen grains. **37.** Longitudinal section of secondary xylem, showing scalariform perforation plates in vessel elements (arrow). LPB 7-HLM, $\times 480$. **38.** Transverse section showing phloem packages, xylem, and between them the vascular cambium zone. LPB 5-HLM, $\times 320$. **39.** Longitudinal section showing secondary xylem, zone of the vascular cambium, and secondary phloem. LPB 2–14, $\times 400$. **40.** Pollen grain polar view showing symmetry, type, and disposition of pori. LPB 2416, $\times 1100$. **41.** Pollen grain polar view showing ornamentation and two pori. LPB 2426, $\times 1100$. **42–46.** *Obispocaulis myriophylloides* gen. et sp. nov. **42.** Transverse section, showing two stems surrounded by ensheathing leaves. LPB 842, $\times 27$. **43.** Transverse section of stem and leaves, showing

it is not possible to state whether this is a determinate or indeterminate inflorescence.

The anatomy of main and secondary axes of the inflorescence/infructescence is similar. It consists of a single-layered epidermis. The cortex is composed of several layers of thin-walled polyhedral to isodiametric parenchyma cells. It can be divided into an outer and an inner cortex. The outer cortex is characterized by the presence of a compact tissue, while the inner cortex is less dense. The outer cortex always has the same characteristics throughout the inflorescence/infructescence; in contrast, the inner cortex varies depending on the position along the main axis. It tends to form an aerenchyma towards the proximal zone of the inflorescence/infructescence. The aerenchyma is formed by the lysis of some cells, which give place to radially arranged lacunae. The limiting cells of the lacunae increase their size by the lysis of the anticlinal walls of neighboring cells and their fusion through the periclinal walls. The stele is composed of a pith surrounded by primary and secondary xylem. Primary xylem is composed of tracheary elements with annular and helical thickenings. Secondary xylem is composed of vessels with scalariform perforation plates and fusiform rays. Pith cells are parenchymatic and thin walled. Two kinds of cells are recognized based on size. Because the Haloragaceae include several aquatic genera like *Proserpinaca* and *Myriophyllum*, among others, different kinds of aerenchymatous stems have been reported (Ogden, 1974); however, information about the inflorescence axis anatomy is unknown. Nevertheless, the presence of wood with simple perforation plates in Haloragaceae is reported for several shrubby and tree-like species of *Haloragis*, *Haloragodendron*, *Gonocarpus*, and *Glyschrocaryon*, and normally these woody parts are reported for the basal zones of the plants (Orchard, 1975; Cronquist, 1981).

Further support for the haloragaceous affinity of the fossil plant from the Tarahumara Formation is given by the presence in the same locality of stems with a well-developed aerenchyma that closely resembles those of extant Haloragaceae. This plant organ is easily recognizable and is clearly distinct from the same organs of the plants of the families discussed above. The stems have been collected also and are more abundant in the Huepac locality.

Although the vegetative stems lack organic connection with the reproductive structures discussed above, they are typical of aquatic plants. These stems can be found isolated, or in groups of two or three, and are surrounded by ensheathing leaves. The presence of more than one stem in certain zones of these axes where stems ramify resembles the condition in the nodes of extant genera in the Haloragaceae. The anatomy of these fossil stems is very characteristic and similar to those of submerged stems of the genus *Myriophyllum* (Fig. 53; see Ogden, 1974). The fossil stems are characterized by having an epidermis, a single circle of large lacunae separated by

radially arranged chains of parenchyma cells connecting the inner and outer cortex, a well-developed endodermis, and a nonlacunate central stele with tracheids and some vessels. Among aquatic or subaquatic plants there are some genera with similar aerenchyma in their stems, but their architecture is quite different from that observed in *Obisipocaulis myriophylloides*. For example, in these genera the stem may be composed of a central stele with one or more xylem canals, a lacunate stele, and a highly lacunate aerenchyma (e.g., *Ruppia*, *Zannichella*, *Najas*), while others have few interlacunar vascular bundles (e.g., *Potamogeton*), or are highly lacunate with several interlacunar vascular bundles (e.g., *Sagittaria*, *Nuphar*), and sometimes with a central stele divided in two, three, or four separated vascular bundles (e.g., *Brasenia*, *Cabomba*; see Ogden, 1974). However, there are some aquatic plants with a stem anatomy more similar to that of *O. myriophylloides*, like *Proserpinaca*, *Gratiola*, and *Utricularia*. They share the large circle of lacunae separated by radially arranged chains of parenchyma cells that connect the inner and outer cortex, the endodermis, and a nonlacunate central stele. Nevertheless, these genera differ in having a cortex with two circles of lacunae and a more complex stele with secondary growth surrounding a large pith (e.g., *Proserpinaca*), a shallow outer cortex with uniseriate parenchyma strands, and often an inconspicuous endodermis (e.g., *Gratiola*). Others have a thin-walled cortical endodermis and a central stele composed only of tracheids, as in *Utricularia* (Ogden, 1974).

Extant Haloragaceae have opposite, alternate, or whorled leaves. They may be simple or pinnatifid, and bimorphic with pectinately divided submerged leaves and sessile or petioleted, and entire, ovate, or lanceolate aerial leaves (Orchard, 1979; Cook, 1990). In contrast, *Obisipocaulis myriophylloides* has adpressed leaves that surround almost the entire diameter of the stems. The submerged leaves, at least in *Myriophyllum heterophyllum* Michx., have one to several air spaces in their mesophyll (Fig. 54); in contrast, leaves of *O. myriophylloides* have a compact mesophyll of isodiametric parenchyma cells.

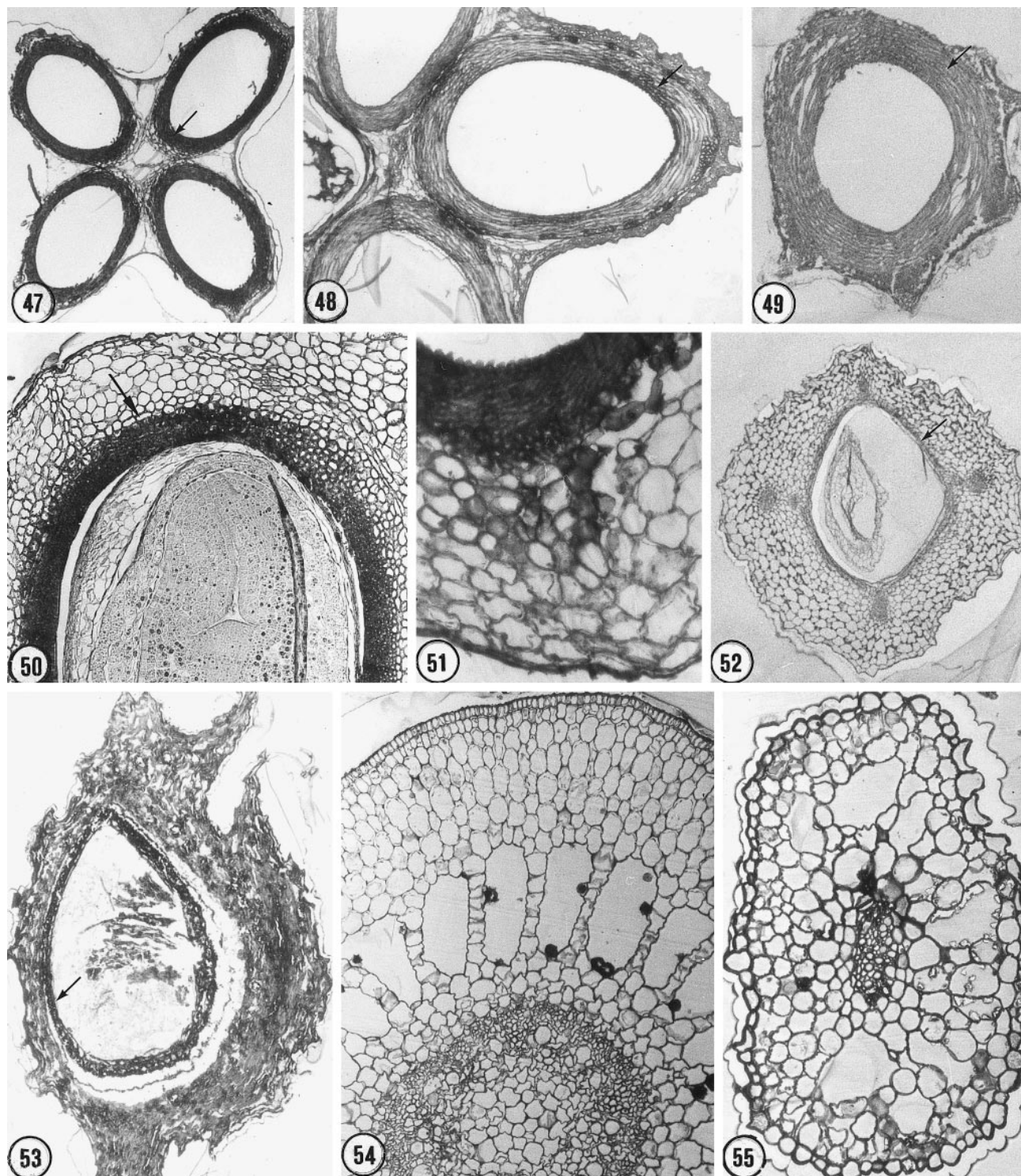
Although confirmation of the relationship of the pollen with the flowers/fruits is needed, it is important to discuss some similarities with the pollen grains of extant plants. Among extant plants of Haloragaceae, *Haloragis* and *Myriophyllum* have pollen grains that resemble those associated with the fossil plant. *Haloragis* pollen grains are paraisopolar or occasionally isopolar, radially symmetrical, peritectate, typically 4–5 colpate (80%) or 4–5 porate (20%), crassimarginate, and frequently aspidote. The polar length is 15–31 μm and varies from suboblate (80%) to oblate (20%) and rarely oblate-spheroidal. *Myriophyllum* has pollen grains that are isopolar, radially symmetrical, peritectate, colpate (25%), 3, 4, 5-porate (25%), or colpate and porate (50%), usually aspidote, crassimarginate, with a polar axis between 16 and 35 μm , an equa-

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epidermis, outer and inner cortex, and aerenchyma. LPB 842, $\times 90$. **44.** Transverse section showing endodermis and central stele with some vessel elements. LPB 33A, $\times 112$. **45.** Transverse section showing a central stem with "U" shape and a smaller one surrounded by leaves. LPB 835, $\times 53$. **46.** Transverse section showing arrangement of main stem, ramifications, and ensheathing leaves. LPB 219, $\times 26$.

TABLE 2. Character comparison between *Tarhumara sophiae* and extant related families.

Family	Habit	Flowers	Inflorescences	Ovary	Carpels	Ovules per carpel	Placentation	Ovule	Type of fruit	Number of seeds
Rosaceae	Terrestrial	Perfect, unisexual	Solitary flowers, spikes, raceme, etc.	Hypogynous, epigynous, perigynous	1 to 5 or more	1, 2, or many more	Axile, apical, marginal, free central	Anatropous to hemitropous or campitropous	Follicles, drupe achene, pome	1, 2, or many
Cunoniaceae	Terrestrial	Perfect, rarely unisexual	Panicles, raceme, and rarely unisexual	Hypogynous, rarely epigynous	2 or less often 3-5	1 or 2, or more	Apical-axile, basal, central	Apotropous	Capsule, or seldom nutlike or drupaceous	2, 4, or many
Rhizophoraceae	Aquatic	Perfect, seldom unisexual	Solitary, rarely cymes, racemes	Hypogynous to epigynous	2 to 5, rarely 6	2, seldom 4, or more	Apical-axile, pendulous	Anatropous to hemitropous	Baccate, capsular	1 to many
Rubiaceae	Terrestrial	Perfect, rarely unisexual	Cymes, rarely solitary flowers	Epigynous	2 seldom 3 to 5 or more	1 to many more	Axile, free central, apical, basal	Anatropous to hemitropous	Capsule, berry, drupe, or dry indehiscent schizocarp	2 to many
Hippuridaceae	Aquatic	Perfect, rarely unisexual	Solitary flowers	Epigynous	1	1	Apical	Anatropous	Achene or drupalet	1
Gunneraceae	Aquatic	Unisexual seldom perfect	Panicle	Epigynous	2 fused	1	Apical pendulous	Anatropous	Drupe	1
Haloragaceae	Aquatic	Perfect, unisexual	Dichasium, solitary flowers, and spikes	Epigynous	1 to 4	1	Apical pendulous	Anatropous	Nuts and schizocarpic nutlets	1-4
<i>Tarhumara sophiae</i>	Aquatic	Unisexual	Dichasium and axillary flowers	Epigynous	4	1	Apical pendulous	Anatropous	Drupaceous and schizocarpic	4



Figs. 47–55. Extant species of *Myriophyllum* and *Gunnera*. **47.** Transverse section of *Myriophyllum heterophyllum* Michx. showing pericarp and four pyrenes with partially sclerified mesocarp (arrow). LPB 1-MHC, $\times 50$. **48.** Transverse section of *M. farwellii* Morong, with partially sclerified mesocarp (arrow). LPB 2-MHC, $\times 100$. **49.** Transverse section of mericarp in *M. aquaticum* (Vellozo) Verdc. showing partially sclerified mesocarp (arrow) LPB 3-MHC, $\times 66$. **50.** Longitudinal section of young fruit of *M. heterophyllum* Michx. showing sclerified endocarp and inner mesocarp, and parenchymatous outer mesocarp (arrow). LPB 4-MHC, $\times 67$. **51.** Longitudinal section of *M. heterophyllum* Michx. showing inner mesocarp with sclerenchyma. LPB 4-MHC, $\times 173$. **52.** Longitudinal section of *Gunnera insignis* (Oerst) A. DC. showing inner sclerified (arrow) and outer parenchymatous pericarp. LPB 5-MHC $\times 33$. **53.** Longitudinal section of *Gunnera mexicana* Brandege showing sclerified endocarp and inner mesocarp (arrow). LPB 6-MHC, $\times 50$. **54.** Stem, transverse section of *Myriophyllum mexicanum* (Morong) Novelo showing epidermis, cortex with aerenchyma, and the central stele. LPB 7-MHC, $\times 133$. **55.** Transverse section of *Myriophyllum mexicanum* (Morong) Novelo leaf, showing epidermis, mesophyll with air spaces, and vascular bundle. LPB 8-MHC, $\times 120$.

torial diameter of 20–40 μm , and a suboblate shape (99%). The fossil pollen grains could be related to one of these genera, but unfortunately the number of pollen grains recovered from the rock is not sufficient to fully demonstrate their relationship to the flowers.

The new plant from the Tarahumara Formation (*Tarahumara sophiae* + *Obispocaulis myriophylloides*) represents an extinct taxon with a mosaic of characters that can be found today in two or three extant genera (*Myriophyllum*, *Meziella*, and *Haloragodendron*) of the Haloragaceae. Documenting this situation is important since the history of the family based on the fossil record alludes to the presence of fruits and pollen grains that have been referred to extant taxa. The new fossil plant (*T. sophiae* + *O. myriophylloides*) broadens the morphology of reproductive and vegetative structures among Haloragaceae.

Morphological and anatomical comparisons between the extant and fossil Haloragaceae suggest that this new plant had an aerial inflorescence/infructescence and branched rhizomatous stems, surrounded by ensheathing leaves. Due to the secondary growth and different stages of aerenchyma development in the base of the inflorescence/infructescence, as well as leaf architecture, reconstruction of the fossil plant (*T. sophiae* + *O. myriophylloides*) argues for an aquatic plant with both an aerial and an aquatic stem. Its small size and anatomical organization suggest that this was a herbaceous plant that grew along the shores of the freshwater environments of the Upper Cretaceous Tarahumara Formation. Most probably, this aquatic plant was erect, using the rhizomatous system as an anchoring mechanism, while the aerial parts were floating at the water surface. Furthermore, the air space in the base of the fruits of *Tarahumara sophiae* was probably an aid for dispersal. Being a sub-aquatic plant, its fruits were dropped as a single unit into the water, as in extant *Meziella*. While fruits were a single unit, the air space probably served as a flotation chamber, facilitating buoyancy and dispersal from the parent plant. Later these fruits were separated into four distinct mericarps, as in *Myriophyllum*. The drupaceous condition of the mericarps of *Tarahumara sophiae* is probably related to the environment. In extant *Myriophyllum mattogrossense* Hoehne fruits can be hard or succulent depending on the submerged or aerial development of the fruit (Orchard and Kasselman, 1992). If fruits grow out of the water they have a hard fruit wall, but if they develop inside the water they become succulent or fleshy.

The Haloragaceae belong to a series of families (e.g., Araceae, Pandanaceae, and Musaceae) that based on their extant distribution are thought to have originated in Gondwana, but which have their oldest, or some of their oldest, fossil records in Laurasia. It may be that these families actually originated in Gondwana, or near to the border of these two paleocontinents, and then diversified in the Northern Hemisphere during the Cretaceous and Tertiary. This would explain the presence of fruits and pollen grains similar to those of extant Haloragaceae during the Tertiary of North America and Europe. However, modern genera may have evolved subsequently. Thus, caution is necessary when trying to relate these reports to extant taxa within the family. It is premature to say when the extant genera appear in the fossil record of the Northern Hemisphere. However, if the idea of a Southern Hemisphere origin for the family, based on extant plants, is correct, many of the lower Ter-

tiary records may represent extinct taxa, like the fossil plant of the Huepac chert (*T. sophiae* + *O. myriophylloides*).

Unfortunately, comparison of compression/impression fossils with permineralized ones is difficult, and further discussion on this idea will have to wait for additional whole-plant reconstructions. The new plant from the Tarahumara Formation confirms that morphological variability in the Haloragaceae was greater in the Cretaceous than in the present (Praglowky, 1970; Cronquist, 1981; Orchard, 1985; Benton, 1993).

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