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On Some Aberrations of Extant Horsetails (*Equisetum* L.) and the Origin of the Family Equisetaceae

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Abstract—Aberrations of the extant species *Equisetum hyemale* L. are described. In one type of aberrations, the strobili are laterally disposed on short secondary shoots, thus resembling the arrangement of strobili in Mesozoic members of *Equisetites* and *Neocalamites* (Equisetaceae). Other types of aberrations in fertile organs of the extant horsetails are also analyzed. These aberrations repeat characters of the Paleozoic (Permian) genera *Equisetinostachys, Paracalamitina,* and *Sendersonia* (Tchernoviaceae). Reduction of both vegetative and reproductive organs in members of the Tchernoviaceae leading to the morphological patterns characteristic of the modern horsetails is traced.

Key words: *Equisetum*, Tchernoviaceae, aberrations, Permian, evolution.

INTRODUCTION

In the summer of 1998, the author collected several shoots of the extant *Equisetum hyemale* (Pl. 13) in the Ulyanovsk Region (right bank of the Volga River, 10 km upstream of the town of Tetyushi, in the vicinity of the village of Monastyrskoe, near the mouth of the Monastyrskii Gully, Fig. 1). Although the herbarium collected includes rare normal shoots (Pl. 13, fig. 1), the population was dominated by aberrant specimens with strobili disposed not on the main axis but on several lateral shoots (Pl. 13, figs. 2, 3). Subsequent visits to this site did not revealed any aberrant horsetails in the population.

The shoots of *Equisetum hyemale* studied are 50–80 cm in total length and 4 cm in width. The lengths of the internodes vary from 38 to 65 mm. The stems being studied are mostly devoid of lateral shoots as is typical of this species. However, in aberrant specimens the uppermost node bears two or three short lateral shoots, each of which is terminated by a strobilus. The main shoot also ends with a terminal strobilus, which is typically better developed than the strobili of the lateral shoots. This strobilus of the main shoot (hereinafter called the axial strobilus) is 12–16 mm long and a maximum of 4–5 mm wide, whereas the maximal length of the lateral strobili is 10 mm and their average length and width do not exceed 7 and 3 mm, respectively. The length of the lateral shoots (excluding the length of their strobili) is 4–7 mm. Each lateral branch has one to three nodes with whorls of leaves fused into leaf sheaths, which are identical in general outline to the normal leaf whorls on the main shoot of this species (Pl. 11, fig. 4). The leaf whorls increase in size toward the strobilus. The leaf whorl of the lateral shoot that is nearest to the strobilus is hypertrophied and three times greater than the lowest whorl (Pl. 13, fig. 2).

A similar arrangement of strobili on lateral shoots is known in Mesozoic members of *Equisetites* Sternberg and *Neocalamites* Halle. Solitary strobili that terminate

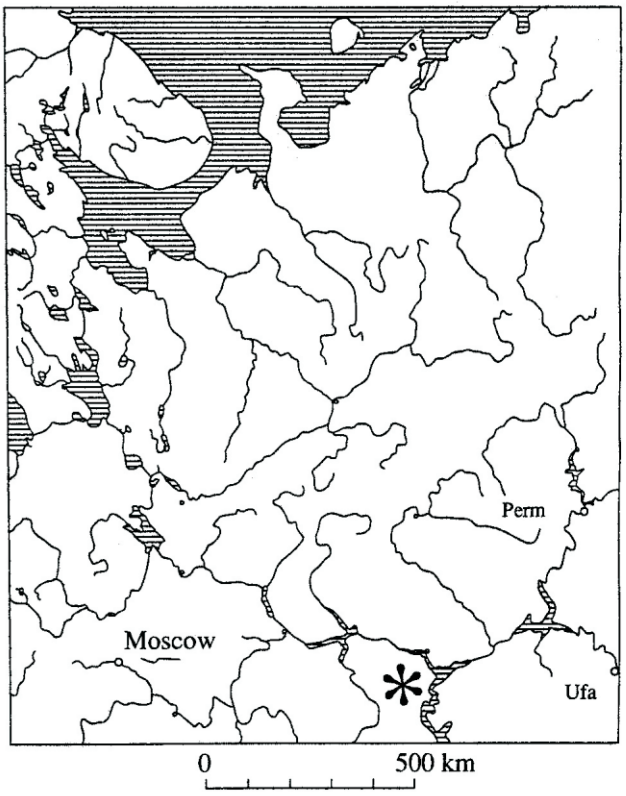


Fig. 1. Sketch map showing the geographical position of the Monastyrskii Gully (asterisk).

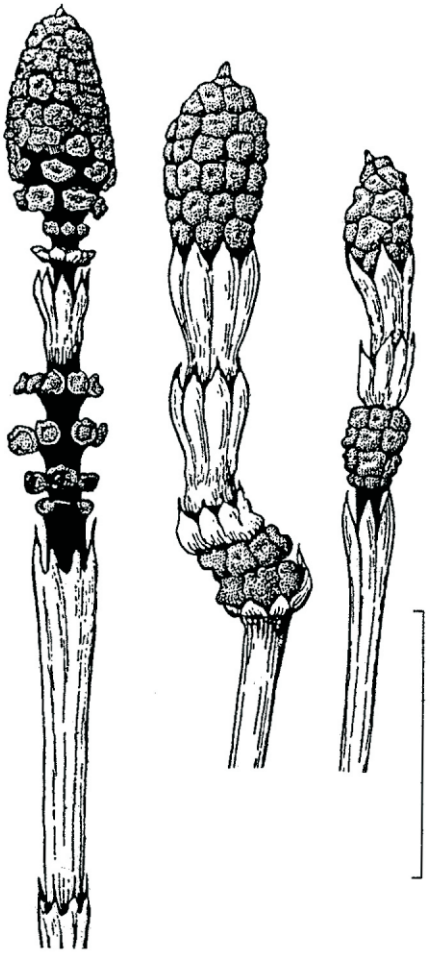


Fig. 2. Aberrant shoots of the extant *Equisetum* sp. (*E. "debile"* s. Kashyap) with fertile zones morphologically identical to the fertile zones in *Equisetinostachys* Rasskasova (modified after Kashyap, 1930). Scale bar 1 cm.

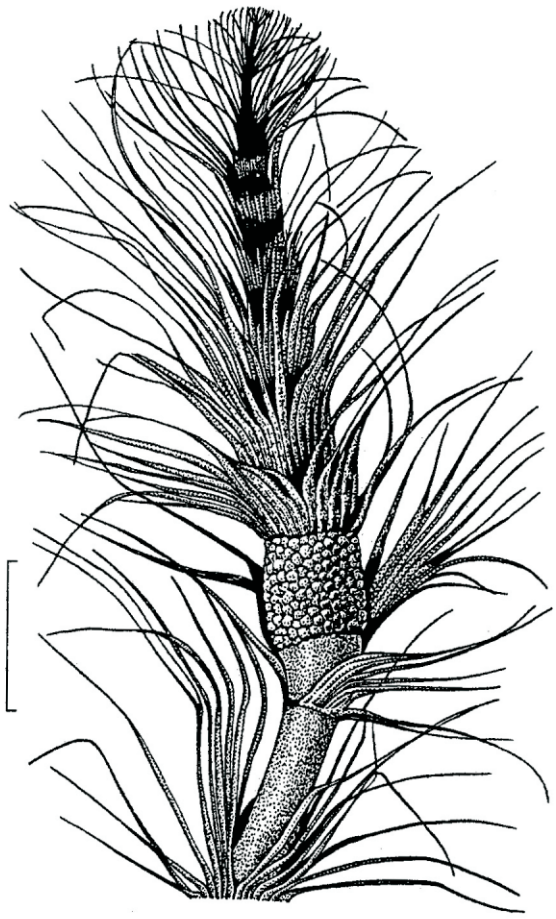


Fig. 3. Aberrant shoot of the extant species *Equisetum telmateia* (modified after Tschudy, 1939, generalized drawing after photograph). Scale bar 1 cm.

lateral shoots like in the specimens of *E. hyemale* under description are reported in *Neocalamites* aff. *carrerei* (Zeiller) Halle 1958 from the coal-bearing Triassic deposits of the Chelyabinsk Basin (Vladimirovich, 1958; *Fundamentals* ..., 1963; Fig. 4d). Another similar arrangement of strobili (but with three strobili on each shortened lateral shoot) was recorded in *Equisetites arenaceous* (Jager) Schenk (Frentzen, 1934; Kelber and van Konijnenburg-van Cittert, 1998). As the aberrant specimens of *E. hyemale* from the Monastyrskii Gully (Pl. 11, fig. 2), *E. arenaceous* also shows a hypertrophy of the leaf whorl closest to the strobilus (Kelber and van Konijnenburg-van Cittert, 1998, pl. II, figs. 5, 7, text-fig. 11).

ABERRATIONS IN THE EXTANT SPECIES OF *EQUISETUM* L.

Extant members of *Equisetum* L. are known to have aberrant specimens with the strobili divided into several fertile zones (Figs. 2, 3). Such structures greatly resemble the reproductive organs of the Permian genus *Equisetinostachys* Rasskasova (Rasskasova, 1961). Occasionally, the upper fertile zone in *Equisetum* might bear a bunch of sterile leaves corresponding to the terminal "tuft" of *Equisetinostachys*.

Explanation of Plate 13

Morphology of vegetative and reproductive organs of *Equisetum hyemale* L. (Monastyrskii Gully).

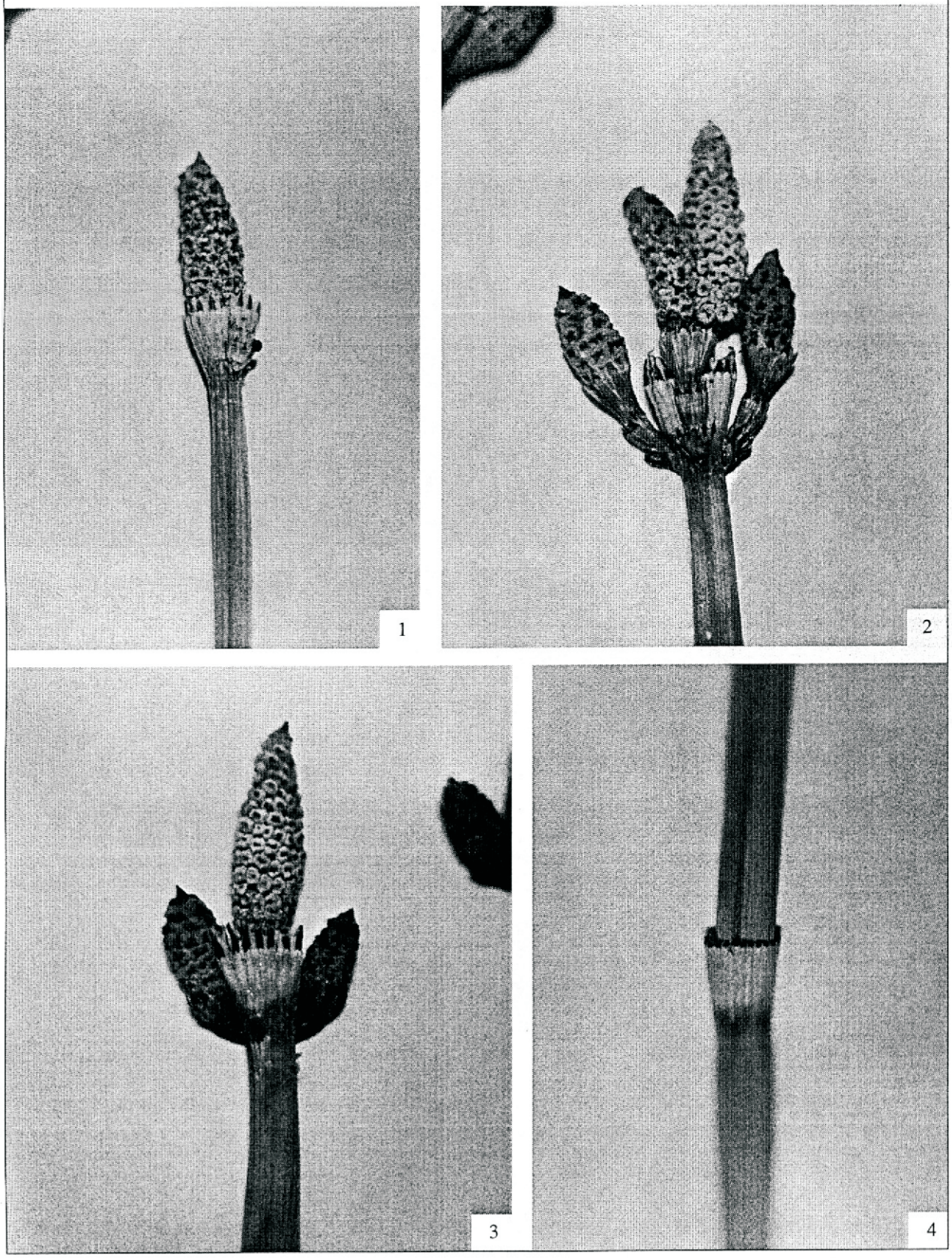
Fig. 1. Shoot with a well-developed terminal axial strobilus, a developing lateral shoot is seen at the right, ×2.

Fig. 2. Aberrant shoot with three lateral branches bearing terminal strobili, ×2.

Fig. 3. Aberrant shoot with a well-developed axial strobilus and two weaker developed strobili on the lateral branches, ×2.

Fig. 4. Well-developed leaf sheath with reduced free parts of the leaves, ×2.

Plate 13



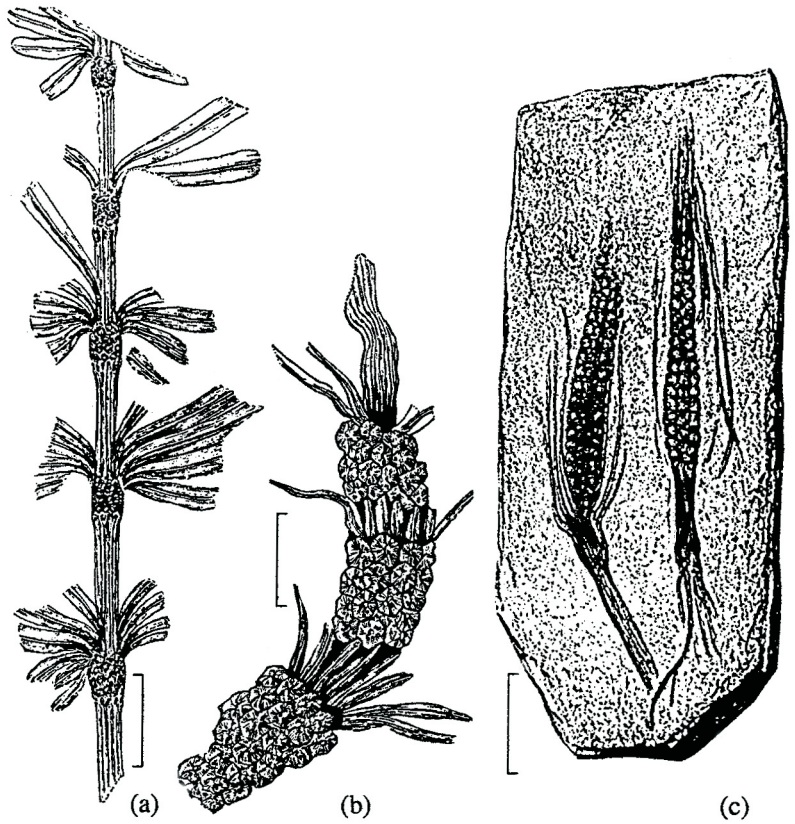


Fig. 4. Main types of reproductive organs of Permian members of the Tchernoviaceae: (a) fertile zones on reproductive shoots of *Annulina neuburgiana* (Radcz.) Neub., described by Zalessky (1934a) as *Phyllotheca bardensis* Zalessky (?=*Stephanostachys borealis* Neub. nom. dub., this taxon was presented by Neuburg (1964) as gen. et sp. nov. but was not validly published according to the International Code of Botanical Nomenclature), Krasnaya Glinka locality, Kungurian stage, middle Fore-Urals; (b) fertile zones on a reproductive shoot of *Equisetinostachys* sp. (*Phyllotheca peremensis* Zalessky, 1934a), Chekarda-1 locality, supposedly layer no. 10, Kungurian Stage, middle Fore-Urals; (c) "quasistrobili" of *Paracalamitina striata* (Schmalh.) Zalessky emend. Naug. (after Schmalhausen, 1879; the same specimen is reproduced in Zalessky, 1918, pl. XVII, fig. 7), Ufimian Stage, Pechora Region of Fore-Urals. Scale bar 1 cm.

Explanation of Plate 14

Vegetative and reproductive morphology of the members of the family Tchernoviaceae from the Permian of Fore-Urals.

Fig. 1. *Phyllotheca campanularis* Zalessky emend. Naug., a whole plant with leafed shoots (leaf sheaths are clearly seen) and roots, GIN, no. 3773(11)/103(89), ×2.5.

Fig. 2. *Equisetinostachys* sp., three fertile zones, a terminal sterile "tuft" (upper leaf whorl) is visible, GIN, no. 2009/53, ×2.

Fig. 3. *Paracalamitina striata* (Schmalhausen) Zalessky emend. Naug., a terminal fertile zone ("quasistrobilus") with a whorl of sterile leaves on the top, GIN, no. 4846/117, ×2.5.

Fig. 4. *Paracalamitina striata* (Schmalhausen) Zalessky emend. Naug., a distal shoot fragment with two large, well-developed cylindrical leaf sheaths, GIN, no. 4846/95, ×2.

Fig. 5. *Paracalamitina striata* (Schmalhausen) Zalessky emend. Naug., a proximal shoot fragment with one short leaf sheath, GIN, no. 4846/112, ×2.5.

Fig. 6. *Phyllotheca campanularis* Zalessky emend. Naug., a fragmentary shoot, the free parts of the leaves of the upper whorls are significantly larger than those of the lower whorls, GIN, no. 3773/346a, ×3.

Fig. 7. *Paracalamites decoratus* (Eichwald) Zalessky, a basal part of the shoot, GIN, no. 4031/3, ×1.

Fig. 8. *Phyllotheca campanularis* Zalessky emend. Naug., a shoot showing two orders of branching, GIN, no. 3773/400a, ×2.2.

Fig. 9. *Paracalamites* sp., middle part of a shoot, ribs in opposition in the nodes are clearly visible, GIN, no. 4856/69, ×2.

Fig. 10. *Paracalamites* sp., a shoot fragment, nearly every rib shows a longitudinal keel, formed by rodlike sclerenchymatous plates covering conducting bundles, GIN, no. 4856/27, ×2.

Localities: (7) Chernaya Gora, Sylva River, Artinskian, Perm Region, middle Fore-Urals; (10) Mesyagutovo, Grib, Artinskian, Bashkiria, southern Fore-Urals; (1, 8) Chekarda-1, layer no. 7, Kungurian, Perm Region, middle Fore-Urals; (2) Chekarda-1, layer no. 10, Kungurian, Perm Region, middle Fore-Urals; (9) Novyi Bugalysh, Kungurian, Bashkiria, southern Fore-Urals; (3–5) Kozhim, layer no. 103 (outcrop no. 2012), Ufimian, Komi Republic, Pechora Region of Fore-Urals. All specimens are stored at the Geological Institute of the Russian Academy of Sciences (GIN), see Naugolnykh (1998) for details concerning the collections studied.

Plate 14

For instance, development of the shoot over the strobilus is known in aberrant forms of the extant species *Equisetum telmateia* Ehrh. (Kashyap, 1930; Tschudy, 1939). Thus, this strobilus represents a fertile zone situated on an internode. Strobili terminated by tufts of sterile leaves and specimens with fertile zones (shoot proliferating through the strobilus) were described and depicted by Milde (1851). Terminal bunches of leaves are known in *Equisetum arvense* f. *campestre* (Milde, 1851, text-figs. 3, 6), fertile zones are known in *E. inundatum* (Milde, 1851, text-figs. 15–17), *E. telmateia* (Milde, 1851, text-fig. 21), and *E. limosum* (Milde, 1851, text-fig. 43).

An arrangement of strobili on lateral shoots similar to that in *Sendersonia matura* Meyen et Mensh. was recorded in *Equisetum telmateia* (Westwood, 1989). Fertile zones with proliferation are occasionally present on the lateral shoots of this horsetail (Westwood, 1989, text-figs. 1, 2).

It is the author's opinion that the aberrations in modern horsetails resembling reproductive organs of the Tchernoviaceae (*Paracalamitina, Equisetinostachys*, and *Sendersonia*) support a direct phylogenetic relation between the Equisetaceae and the Angaran members of the Tchernoviaceae.

VEGETATIVE AND REPRODUCTIVE MORPHOLOGY OF THE PERMIAN SPHENOPHYTES OF THE TCHERNOVIACEAE

The shoots of Angaran members of the Tchernoviaceae as well as other sphenophytes (Division Equisetophyta=Sphenophyta, Arthropsida) are divided into nodes and internodes. The shoots are arthrostelic, with longitudinal ribs, opposite in nodes (Pl. 14, figs. 7, 9, 10). There is a cylindrical cavity in the shoot center. Pith casts of tchernoviaceous shoots are conventionally assigned to the formal genus *Paracalamites* Zalessky, although several species of this genus are definitely described on the basis of impressions or even compressions of shoots (Neuburg, 1948; Khakhlov, 1964). As a rule, the width of tchernoviaceous shoots does not exceed 3–4 cm. Nevertheless, specimens with a trunk width no less than 10 cm are also known (*Paracalamites robustus* Zalessky and *P. decoratus* Zalessky), thus indicating that the height of the plants is at least 5–6 m.

Unlike the shoots of calamites (Calamostachyales), the conducting bundles in tchernoviaceous shoots transverse the shoot nodes without alternation. Immediately under the longitudinal ribs that run on the shoot surface over the conducting bundles, there are narrow radical sclerenchymatous plates, which provide additional mechanical strength to the shoots (Pl. 14, fig. 10). Similar sclerenchymatous plates are characteristic of the shoots of the extant *Equisetum*.

Leaf remains of the Tchernoviaceae are traditionally assigned to the formal genus *Phyllotheca* Brongniart (Pl. 14, figs. 1, 4–6, 8). They are leaf whorls with well-developed leaf sheaths (leaf bases connected by their margins). The leaf sheaths of the Tchernoviaceae are virtually identical to those of *Equisetum* (Pl. 13, fig. 4). Some species (*Phyllotheca turnaensis* Gorelova, *Ph. stenophylloides* Zalessky, *Ph. campanularis* Zalessky emend. Naug., and *Phyllotheca* sp.; Zalessky, 1937, 1939; Meyen, 1971; Naugolnykh, 1998) occasionally show hypertrophied sheaths that enter one into another and form the so-called cone-in-cone structure (Pl. 14, fig. 1). In case of coalescent sheaths, the conducting bundles of the leaf whorls might coincide with the shoot arthrostele; this phenomenon is typical of the Equisetaceae (Filin, 1978). Leaves of the Tchernoviaceae with relatively small leaf sheaths and flattened leaf whorls are attributable to *Annulina* Neuburg and *Umbellaphyllites* Rasskasova.

Reproductive organs of Angaran members of the Tchernoviaceae are described as the genera *Tschernovia* (*Tchernovia*) Zalessky (established on the basis of isolated sporangiophores), *Equisetinostachys* Rasskasova (Fig. 4b), and *Sendersonia* Meyen et Menshikova. The reproductive morphology is also known for *Paracalamitina* Zalessky emend. Naug. (Naugolnykh, 2002).

Equisetinostachys sp., a typical member of this genus, comes from the Kungurian of Fore-Urals (Figs. 4b, 5a, Pl. 14, fig. 2: Naugolnykh, 1998, text-fig. 15A). Similar compound sporangiophores were originally described as *Phyllotheca peremensis* Zalessky and *Phyllotheca macrostachya* Zalessky (Zalessky, 1934a).

In general aspect, reproductive organs of this plant resemble strobili of the extant horsetail. The strobili are compact aggregations of small pedicellate peltate shields with sporangia suspended to the lower side of the shield. The shields of immature strobili tightly contact by the margins. As the strobili mature, the pedicels of shields lengthen, the margins bend upwards and move apart, and the spores release from the sporangia and are dispersed by wind or water. Unlike the solitary strobilus of the extant *Equisetum* terminating the shoot, the reproductive organs of *Equisetinostachys* consisted of several fertile zones that formed a complex multilevel structure, which was segmented by whorls of sterile leaves. The reproductive organs of *Equisetinostachys* were located directly on the plant shoot and did not form true specialized strobili.

Another member of the family Tchernoviaceae, *Paracalamitina striata* (Schmalh.) Zalessky emend. Naug., is known from younger deposits of Fore-Urals (Intinskaya Formation and its analogues, Ufimian Stage). Originally, the name *Paracalamitina striata* was applied only to the remains of the covering of large shoots of sphenophytes with ribs in opposition in the nodes (Zalessky, 1934b). Neuburg (1964) supposed the relationship between the reproductive organs of *Tschernovia striata* Neub. and leaves of *Phyllotheca striata* Schmalh. Recently, all these remains have been found

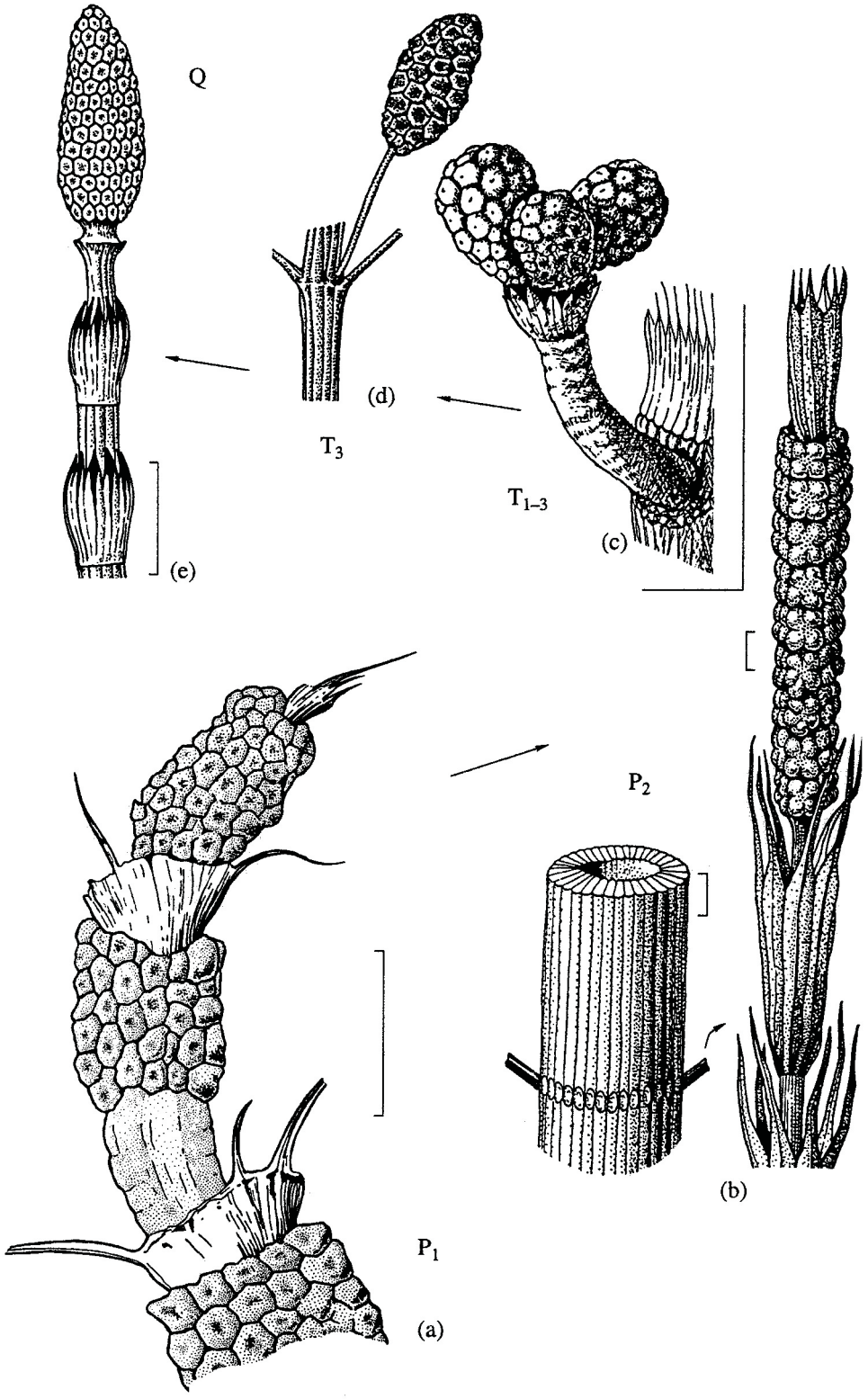


Fig. 5. Morphogenetic trend in the evolution of members of the families Tchernoviaceae and Equisetaceae: (a) *Equisetinostachys*; (b) *Paracalamitina striata*, note a shoot fragment with scars of branches at the left and a terminal fertile zone ("quasistrobilus") at the right; (c) *Equisetites arenaceous* (modified after Frentzen, 1934); (d) *Neocalamites* aff. *carrerei* (modified after Vladimirovich, 1958); and (e) *Equisetum arvense*. Scale bar is 1 cm in (5a), (5b, left), (5d), and (5e) and 2 mm in (5b, right).

in organic connection and now there is no reason to use different names for the parts of the same plant (Naugolnykh, 2002).

The reproductive organs of *Paracalamitina striata* have retained active terminal meristems. At the apices of the fertile zones (="quasistrobili"), a bunch of sterile leaves persists. However, compared to *Equisetinostachys*, the number of fertile zones is restricted to one or, occasionally, two zones. *Sendersonia matura* Meyen et Mensh. from the Uskatskaya Formation of the Kuznetsk Basin is one more sphenophyte of the Permian age with incipient reduction of fertile zones on lateral shoots (Meyen and Menshikova, 1983).

PHYLOGENETIC RELATIONSHIPS OF THE EQUISETACEAE

The extant *Equisetum* is known to have aberrations with the terminal meristem retaining its activity even after the complete development of the strobilus, thus enabling the shoot to proliferate. Such aberrant reproductive organs are virtually identical to the fertile zones of the Permian members of *Equisetinostachys* or *Paracalamitina* (depending on the number of repeatedly appearing fertile zones on the shoots).

It is worth noting that in the extant members of *Equisetum* aberrant proliferating reproductive organs typically appear on lateral shoots. They do not terminate the main shoot as normal strobili do. This peculiarity unites such aberrant horsetails with the Permian sphenophytes of the family Tchernoviaceae (*Equisetinostachys, Paracalamitina*, and *Sendersonia*). Such recapitulation of latent primitive genes transforms extant aberrant horsetails into much-reduced (several dozen times) copies of their Permian precursors.

Comparing the plants discussed above and ranging them from ancient to younger species, we can see a clear morphogenetic trend showing general reduction in both reproductive and vegetative organs. The plants diminish in size from the members of *Paracalamitina*, which are 3–4 m in height, to the extant horsetails, the majority of which do not exceed 60–70 cm. Reproductive organs persist only on the shoot apex. Numerous fertile zones are reduced to a single zone in which the terminal meristem is inactive (this fertile zone transforms in a strobilus, Fig. 5).

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