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# Lower Cretaceous Palynological Assemblages of the Levashi Formation in the Aimaki Section of Central Dagestan

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**Abstract**—We present the results of the study of higher plant spores and pollen in a section of the Levashi Formation near the village of Aimaki. The Hauterivian and Barremian palynological associations were defined on the basis of changes in the taxonomic content of terrestrial plant spores and pollen. The associations are comparable with Hauterivian and Barremian assemblages of various regions of the Caucasus with respect to the composition of major groups and individual taxa. A transition in the vegetation was noted, from the coniferous palynological association of the Hauterivian to a fern association in the Barremian. The predominance of hygrophilous ferns and the presence of lycophytes and representatives of Taxodiaceae and Sphagnopsida in the Barremian (which were nearly absent in the Hauterivian), accompanied by a significant decrease in thermophilic Cheirolepidiaceae and other conifers, indicate a change in climate characterized by an increase in humidity and a decrease in temperature.

*Keywords*: Central Dagestan, spores, pollen, Hauterivian, Barremian, biostratigraphy

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## INTRODUCTION

The palynological study of the Lower Cretaceous deposits of the Caucasus began in the 1960s (Yaroshenko, 1960, 1965; Kuvaeva et al., 1964; Aliyev et al., 1976; Danilenko, 1973) and has subsequently continued (Danilenko and Lisunova, 1994; Aleksandrova et al., 2010; Smirnova and Smirnova, 2012). The majority of these works are dedicated to the study of palynological assemblages from the faunistically characterized Lower Cretaceous deposits of various regions of the Caucasus.

Neocomian deposits of the Aimaki section, situated in Central Dagestan (Fig. 1), do not have macrofaunal remains. As a result, it was studied palynologically to establish its age on the basis of the taxonomic composition of its palynomorphs. The study of specimens from the Levashi Formation, primarily containing terrigenous deposits, revealed diverse miospores and microphytoplankton represented by dinocysts, prasinophytes (*Pterospermella*, *Leiosphaeridia*), green algae (*Schizosporis*, *Schizophacus*, *Tasmanites*), and acritarchs. Associations of higher plant spores and pollen, characteristic of the Hauterivian and Barremian, were identified. Because of the unsatisfactory preservation of palynomorphs, many taxa are given in open nomenclature.

## MATERIALS AND METHODS

The material for this study was collected in 2008 from the Levashi Formation of the Aimaki section by G.N. Aleksandrova, E.A. Shcherbinina, and Yu.O. Gavrilov from the Geological Institute of the Russian Academy of Sciences during fieldwork in Central Dagestan.

Sixty palynological samples were subjected to chemical treatment based on the method adopted by the Laboratory of Paleofloristics of the Geological Institute, Russian Academy of Sciences. The samples were treated with 10% HCl to dissolve carbonates, followed by a 5% solution of $Na_2HPO_4OH$ to remove clay minerals during further elutriation. To isolate the palynomorphs, the remaining sample sediment was separated by centrifugation in a heavy liquid with a density of 2.25 (KI + CdI salt solution). The macerate was treated with HF to remove silicate minerals. The treated material was collected in tubes and filled with glycerin for further study and storage. Miospores were studied under a Reichert Zetopan (Austria) light microscope. Palynomorphs were photographed under an Axiostar plus (Carl Zeiss, Germany) light microscope fitted with a Canon Power Shot A640 camera. Materials studied are housed at the Laboratory of Paleofloristics of the Geological Institute, Russian Academy of Sciences, Moscow.

The majority of samples contained a small number of poorly preserved miospores which were almost completely uninformative. Representative spectra of spores and pollen of higher plants and microphytoplankton were identified in 21 samples. Characteristic taxa are shown in Plates I–V.

Both geochronological ranges and floral content were included in establishing palynological associations. These associations are classified according to the method of determining ecological groups of spores and pollen proposed in a previous work (Abbink et al., 2004).

## LITHOLOGY

The section studied is located in the central part of the village of Aimaki of the Gergebil district of the Republic of Dagestan, 0.5 km south of the mosque. From bottom to top (Fig. 2):

Bed 1. Limestone bioclastic, brown, dense, compact, forming a slope face. Thickness around 2.5 m.

Bed 2. Above an indistinct contact, siltstone yellowish gray, argillaceous, indistinctly bedded, with unevenly distributed siliciclastics. Thickness around 4.8 m. Sample 401/08, 2 m above the base of the bed.

Bed 3. Above a distinct, even contact, siltstone gray, very dense, compact, forming a ledge. Thickness around 0.03–0.05 m. Sample 402/08 in the middle of the bed.

Bed 4. Siltstone dark gray, dense. At the base (0.5 m) with thin layers of thinly laminated dark gray argillite, with small sulfide nodules. Toward the top, the amount of arenaceous material increases. Bed 4 is gradually overlain by Bed 5. Thickness around 1 m. Sample 403/08, 0.5 m above the base of the bed.

Bed 5. Siltstone (clayey sandstone) brownish gray, argillaceous, dense, with small-sized lumpy jointing, fine-grained, strongly bioturbated, with serpulids at the top. Thickness around 0.6 m.

Bed 6. Above a distinct contact, dark gray argillite, becoming siltstone up the section. 2.2 m above the base, a clayey layer with numerous pyrite nodules. In the upper part of the bed, the siltstone has lumpy jointing, with considerable bioturbation, traces up to 0.015 m in diameter. Thickness around 4.8 m. Sample 404/08, 2.2 m above the base of the bed.

Bed 7. Above a conformable straight contact, argillaceous siltstone, becoming denser and more massive up the bed. Thickness around 5.7 m. Sample 405/08, 0.2 m above the base of the bed; Sample 406/08, 5 m above the base of the bed.

Bed 8. The siltstone is gradually replaced by sandstone, dark gray, fine-grained, argillaceous, strongly bioturbated, with irregular distribution of arenaceous material. Thickness around 2 m.

Bed 9. Sandstone yellowish gray, indistinctly bedded, very compact, forming a ledge in the slope, strongly bioturbated, fissured. Thickness around 1.65 m. Sample 407/08, 0.5 m above the base of the bed.

Bed 10. At the base, sandstone argillaceous, dark gray, with black stains of argillaceous material (0.3 m); overlain by dark gray silt, lumpy, bioturbated (0.6 m); at the top of the bed, rusty colored ferruginous sandstone, compact, indistinctly bedded, bioturbated (40 cm); with serpulids along the top. Thickness around 1.3 m. Sample 408/08, 0.8 m above the base of the bed.

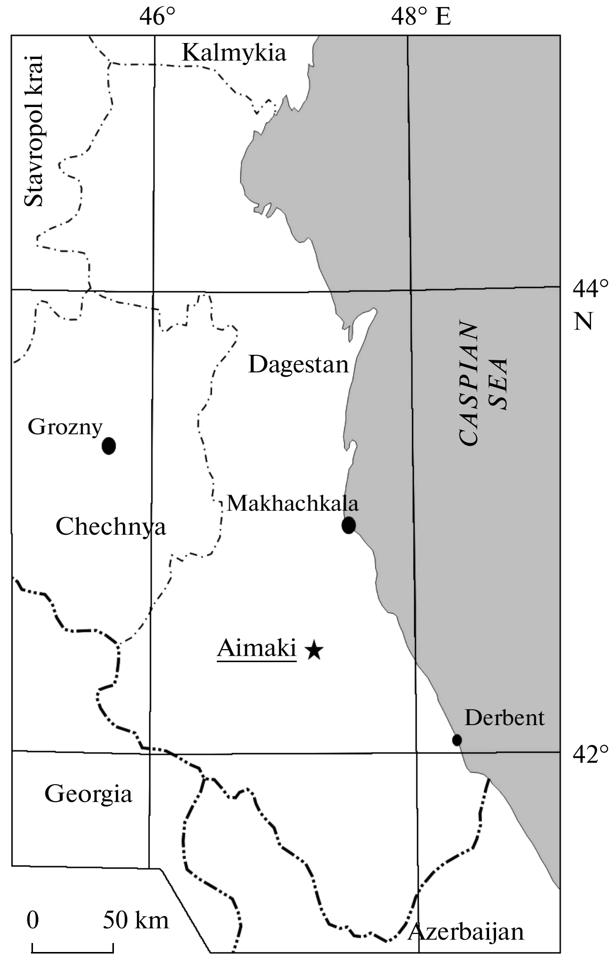



**Fig. 1.** Location of the Aimaki section.

Bed 11. The sandstone is gradually overlain by dark gray, fissured argillite, with poorly preserved sulfide nodules. The middle part of the bed (about 1.5 m) is covered. Thickness around 3.6 m. Sample 409/08, at the base of the section; Sample 410/08, 1 m above the base of the bed; Sample 411/08, 3.2 m above the base of the bed.

Bed 12. Frequent alternation of dark gray, thinly laminated argillite and gray, strongly bioturbated sandstone. Thickness around 0.4 m.

Bed 13. The alternation member is gradually overlain by very densely alternating dark gray thinly laminated argillite and gray lumpy sandstone, inconsistently thick, strongly bioturbated. Thickness around 8.6 m. Sample 412/08, 3 m above the base of the bed; Sample 413/08, 2.3 m below the top of the bed.

Bed 14. Above a distinct contact, siltstone gray, dense, ferruginous, strongly bioturbated. At the top a layer (0.15 m) with numerous oyster shells. Thickness around 0.8 m. Sample 414/08, 0.5 m above the base of the bed.

Bed 15. The previous bed is gradually overlain by siltstone dark gray, weakly ferruginous, in the middle of the bed with a layer of flattened sideritic nodules. Thickness around 0.4 m. Sample 415/08, 0.1 m below the top of the bed.

Bed 16. The previous bed is overlain along a pocket-like contact by a bed of sandstone yellowish gray, medium to fine-grained, lumpy, dense, forming a ledge on the slope, with numerous oyster shells. Thickness around 0.2 m.

Bed 17. Siltstone dark gray, dense, unbedded, with pyritic nodules. Thickness around 1.2 m.

Bed 18. A bed of siderite (?) dark gray, strong, with distinct ledge on the wall, ferruginous on the surface. Thickness around 0.01–0.012 m. Sample 416/08, in the middle of the bed.

Bed 19. Argillite dark gray, soft, silty, with sulfide nodules. Thickness around 2.1 m. Sample 417/08, 0.6 m below the top of the bed.

Bed 20. Siltstone dark gray, dense. Thickness around 1.3 m.

Bed 21. The previous bed is gradually overlain by yellowish gray, medium to fine-grained, lumpy, dense sandstone, forming a ledge in the wall, with numerous oyster shells. Thickness around 0.22 m. Sample 418/08, in the middle of the bed.

Bed 22. Argillite dark gray, indistinctly horizontally bedded, silty at the top and at the base. Thickness around 5.7 m. Sample 419/08, in the middle of the bed.

Bed 23. Argillite gray, horizontally bedded, ferruginous along the bedding planes. Thickness around 0.7 m. Sample 420/08, in the middle of the bed.

Bed 24. Sandstone yellowish gray, dense, lumpy, indistinctly bedded, at the base massive, with large oyster shells. A bed of oyster coquina lies at the top of the bed. This bed forms a massive marking horizon in the section. Thickness around 2.6 m. Sample 421/08, in the middle of the bed.

Bed 25. Argillite dark gray, indistinctly horizontally bedded, silty at the base and at the top. Thickness around 1.5 m. Sample 422/08, 1.3 m above the base of the bed.

Bed 26. Argillite gray, horizontally bedded, ferruginous along the bedding planes. Thickness around 0.5 m.

Bed 27. Sandstone yellowish gray, medium-grained, with crushed oyster shells, forming a ledge in the wall. Thickness around 0.25 m. Sample 450/08, in the middle of the bed.

Bed 28. Siltstone in the lower part of the bed (around 1.8 m) more strongly argillaceous, in the upper part strongly bioturbated, dense, with sulfide nodules at the top. Thickness around 3.4 m. Sample 451/08, 1.8 m above the base of the bed; Sample 452/08, 2.3 m above the base; Sample 453/08, at the top of the bed.

Bed 29. Clay silty, soft, up the section becoming arenaceous siltstone, with a horizon of carbonate nodules at the top. Thickness around 2.5 m.

Bed 30. Clay gray. Thickness 0.3 m. Sample 454/08, in the middle of the bed.

Bed 31. Siltstone gray. Thickness around 3 m.

Bed 32. Arenaceous siltstone dense. Thickness around 0.3 m.

Bed 33. Siltstone gray. Thickness around 1.5 m.

Bed 34. Arenaceous siltstone dense, with fragments of oyster shells. Thickness around 0.15–0.4 m. Sample 455/08, in the middle of the bed.

Bed 35. Siltstone gray. Thickness around 1.3 m.

Bed 36. Siltstone gray, argillaceous. Thickness around 0.4 m. Sample 456/08, in the middle of the bed.

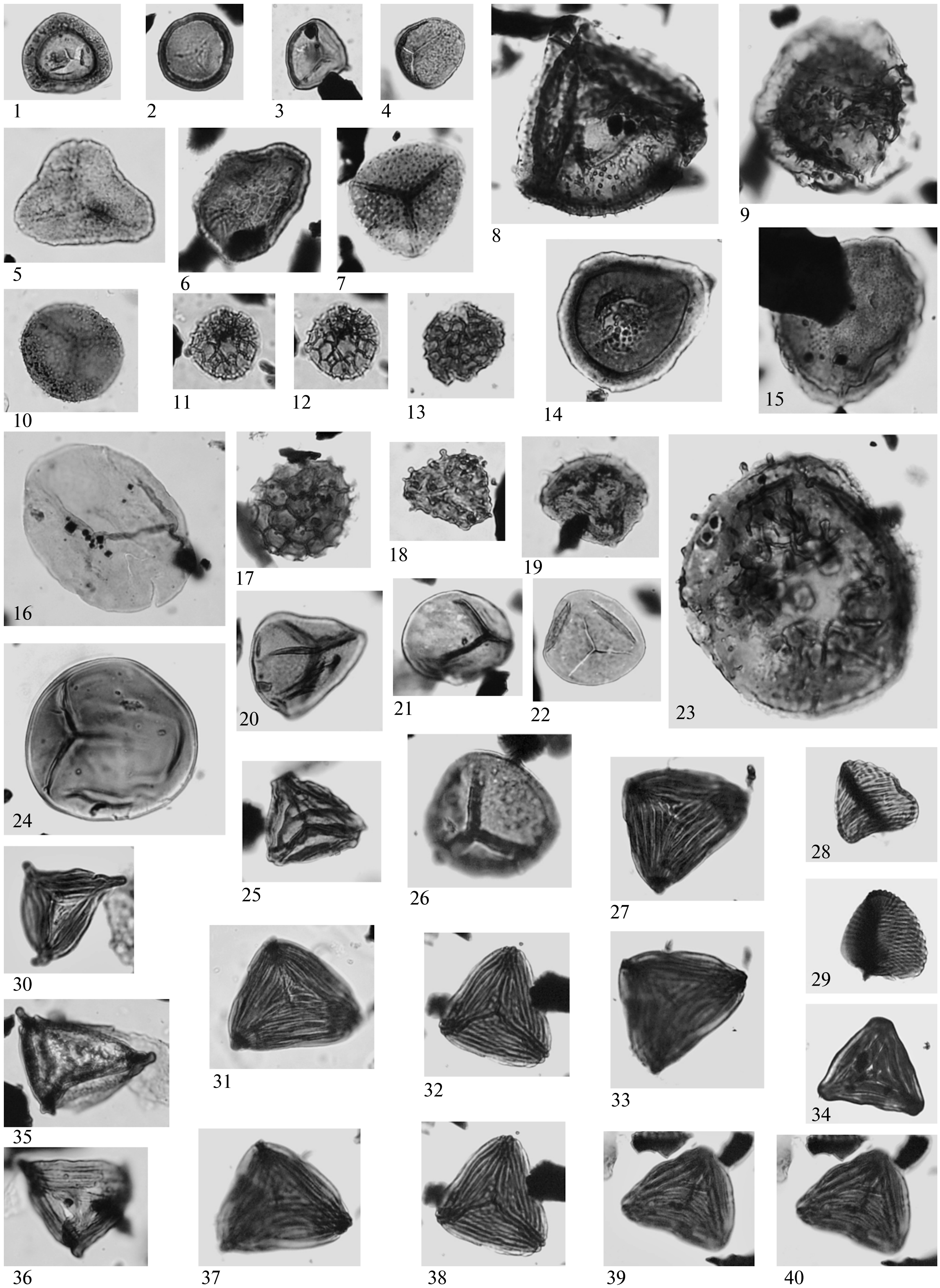
Bed 37. Siltstone gray, interbedded with three denser layers. Thickness around 2.2 m.

Bed 38. Siltstone gray, with increased clay content at some levels, with a bed of fine-grained dense sandstone of inconsistent thickness with many traces of bioturbation. Thickness around 5.9 m.

**Plate I.** Levashi Formation palynomorphs. All sizes are ×500.

(1) *Cingutriletes clavus* (Balme) Dettmann, sample 464; (2) *Cingutriletes pocockii* (Burger) Burden et Hills, Sample 403; (3) *Stereisporites antiquasporites* (Wils. et Webst.) Dettmann, sample 420; (4) *Foraminisporis dailyi* (Cookson et Dettmann) Dettmann, Sample 406; (5, 6) *Foraminisporis asymmetricus* (Cookson et Dettmann) Dettmann: (5) Sample 403, (6) Sample 415; (7) *Sestrosporites pseudoalveolatus* (Couper) Dettmann, Sample 412; (8) *Aequitriradites* sp., Sample 415; (9) *Aequitriradites spinulosus* (Cookson et Dettmann) Dettmann, Sample 401; (10) *Foraminisporis wonthaggiensis* (Cookson et Dettmann) Dettmann, Sample 409; (11, 12) *Lycopodiumsporites* sp., Sample 403; (13) *Lycopodiumsporites austroclavatidites* (Cookson) Potonie, Sample 412; (14) *Cooksonites variabilis* Pocock, Sample 401; (15) *Aequitriradites* sp., Sample 412; (16) *Triporoletes simplex* (Cookson et Dettmann) Playford, Sample 406; (17) *Lycopodiumsporites crassatus* Singh, Sample 403; (18) *Neoraistrickia truncata* (Cookson) Potonie, Sample 403; (19) *Ceratosporites pocockii* Srivastava, Sample 464; (20, 21, 26) *Biretispotites potoniaei* Delcourt et Sprumont: (20) Sample 403, (21) Sample 415, (26) Sample 464; (22) *Todisporites minor* Couper, Sample 403; (23) *Couperisporites* sp., Sample 401; (24) *Todisporites major* Couper, Sample 401; (25) *Cicatricosisporites hughesi* Dettmann, Sample 412; (27, 31, 33, 37) *Cicatricosisporites australiensis* (Cookson) Potonie, Sample 414; (28, 29) *Cicatricosisporites tersus* (Kara-Murza) Pocock: (28) Sample 401, (29) Sample 415; (30, 36) *Anemia macrorhyza* (Mal.) Bolch.: (30) Sample 401, (36) Sample 464; (32, 38) *Cicatricosisporites australiensis* (Cookson) Potonie, Sample 412; (34) *Cicatricosisporites pseudotripartitus* (Bolchovitina) Dettmann, Sample 458; (35) *Appendicisporites unicus* (Markova) Singh, Sample 465; (39, 40) *Anemia exilioides* (Mal.) Bolchovitina, Sample 464.

Plate I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Bed 39. Silty clay, with a layer of carbonate nodules in the middle part. Thickness around 1.5 m. Sample 457/08, in the middle of the bed.

Bed 40. Siltstone gray, becoming denser at the top. Thickness around 1.7 m.

Bed 41. Siltstone gray, argillaceous, up the section becoming fine-grained sandstone. Thickness around 2.4 m.

Bed 42. Siltstone gray, argillaceous, up the section becoming fine-grained sandstone. Thickness around 5 m.

Bed 43. Siltstone gray, argillaceous, up the section becoming fine-grained sandstone, with ovoid weathering. Thickness around 2.3 m.

Bed 44. Siltstone gray, with a small admixture of argillaceous material, up the section becoming dense, bioturbated sandstone. Thickness around 1.8 m.

Bed 45. Siltstone gray. Thickness around 0.6 m. Sample 458/08, at the base of the bed.

Bed 46. Calcareous concretionary lenses.

Bed 47. Siltstone gray. Thickness around 1 m.

Bed 48. Siltstone gray, in the lower part argillaceous, toward the top becoming more strongly arenaceous and dense. Thickness around 2.2 m. Sample 459/08, 0.6 m below the top of the bed.

Bed 49. Siltstone gray, in the lower part argillaceous, toward the top becoming more strongly arenaceous and dense. Thickness around 1.5 m.

Bed 50. Siltstone gray, in the lower part argillaceous, toward the top becoming more strongly arenaceous and dense. Thickness around 1.3 m.

Bed 51. Siltstone gray, in the lower part argillaceous, toward the top becoming more strongly arenaceous and dense. Thickness around 3.3 m.

Bed 52. Siltstone gray, in the lower part argillaceous, toward the top becoming more strongly arenaceous and dense. Thickness around 1.7 m.

Bed 53. Siltstone gray, in the lower part argillaceous, toward the top becoming more strongly arenaceous and dense. Thickness around 1.5 m.

Bed 54. Siltstone gray, at the top overlain by a bed of fine-grained sandstone. Thickness around 2 m. Sample 460/08, 0.5 m above the base; Sample 461/08, 0.5 m below the top of the bed.

Bed 55. Siltstone gray, at top overlain by a bed of fine-grained sandstone. Thickness around 1 m.

Bed 56. Siltstone gray, with three layers of fine-grained sandstone. Thickness around 5.5 m. Sample 462/08, 2 m below the top; Sample 463/08, 1.5 m below the top of the bed.

Bed 57. Siltstone gray, with infrequent irregularly shaped dense structures, probably mounds.

Bed 58. Argillaceous dark gray siltstone, silty at the base. Thickness around 2.5 m. Sample 464/08, at the base of the bed; Sample 465/08, 0.7 m above the base; Sample 466/08, at the top of the bed.

Bed 59. Sandstone fine-grained. Thickness around 0.6 m.

Bed 60. Argillaceous bioturbated siltstone. Thickness around 0.3 m.

Bed 61. Fine-grained sandstone. Thickness around 3 m. Sample 467/08, in the middle of the bed.

Bed 62. Composed of seven layers of sandstone, divided by interbeds of siltstone. Thickness around 4.8 m. Sample 468/08, 0.7 m below the top of the bed.

Bed 63. Sandstone fine-grained, indistinctly bedded. Thickness around 4 m. Sample 469/08, in the middle of the bed.

Bed 64. Sandstone fine-grained, dense, monolithic. Thickness around 3 m.

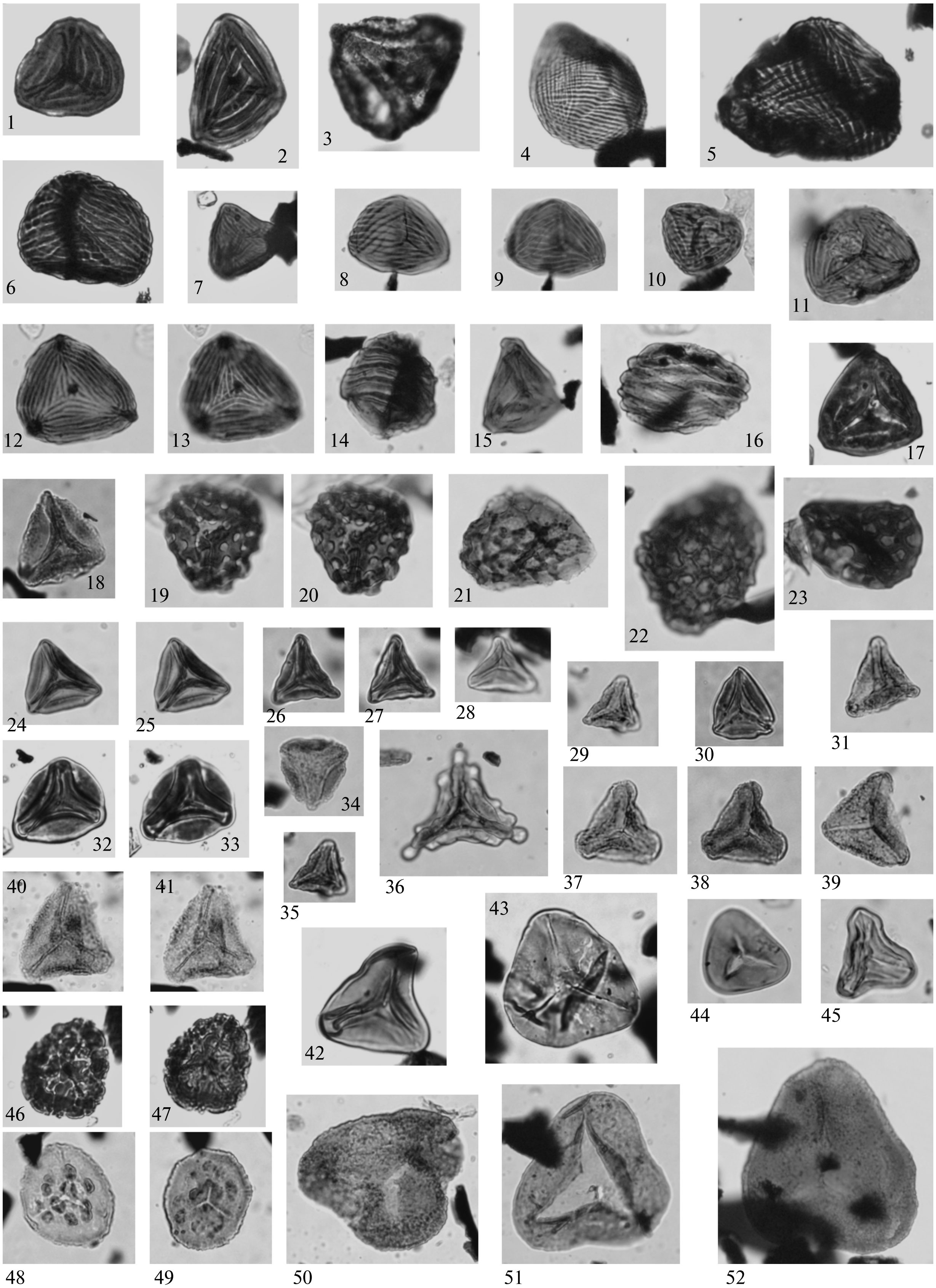
Bed 65. At the base, siltstone (0.3–0.5 m); above, layers of sandstone, relatively monolithic at the top. The bed forms a large ledge in the wall. Thickness around 5.5–6 m. Sample 470/08, in the upper part of the bed.

Bed 66. Argillite light gray, silty, fissured, with scattered sulfide nodules and malacofauna. The argillite at the base is strongly arenaceous, almost siltstone. The contact with the underlying bed is covered along the slope. Thickness around 1.7 m. Sample 442/08, 1 m below the top of the bed; Sample 443/08, 0.2 m above the base of the bed.

**Plate II.** Levashi Formation palynomorphs. All sizes are ×500.

(1, 2) *Cicatricosisporites spiralis* Singh: (1) Sample 415, (2) Sample 450; (3) *Cicatricosisporites perforatus* (Markova) Döring, Sample 401; (4) *Cicatricosisporites minutaestriatus* (Bolchovitina) Pocock, Sample 464; (5) *Cicatricosisporites imbricatus* (Markova) Singh, Sample 464; (6) *Cicatricosisporites mediostriatus* (Bolchovitina) Pocock, Sample 403; (7) *Cicatricosisporites minor* (Bolchovitina) Pocock, Sample 403; (8–11) *Cicatricosisporites* spp.: (8, 9, 11) Sample 401, (10) Sample 409; (12, 13) *Plicatella crimensis* (Bolchovitina) Dörhöfer, Sample 464; (14) *Contignisporites cooksonii* Dettmann, Sample 420; (15) *Distaltriangulisporites* sp., Sample 412; (16) *Contignisporites multimuratus* Dettmann, Sample 456; (17) *Distaltriangulisporites perplexus* Singh, Sample 464; (18, 31, 37–41) *Ornamentifera* spp.: (18, 31, 37, 38) Sample 403, (39) Sample 454, (40, 41) Sample 439; (19, 20) *Klukisporites foveolatus* Pocock, Sample 403; (21) *Klukisporites granulatus* (Pocock) Burden et Hills, Sample 409; (22, 23) *Klukisporites pseudoreticulatus* Couper: (22) Sample 403, (23) Sample 465; (24–27) *Gleicheniidites senonicus* Ross: (24, 25) Sample 406, (26, 27) Sample 409; (28) *Gleicheniidites laetus* Bolchovitina, Sample 415; (29, 35) *Gleicheniidites radiatus* Bolchovitina, Sample 412; (30) *Gleicheniidites minor* Döring, Sample 403; (32, 33) *Gleicheniidites carinatus* Bolchovitina, Sample 464; (34) *Gleicheniidites rasilis* Bolchovitina, Sample 420; (36) *Clavifera triplex* Bolchovitina, Sample 420; (42) *Dictyophyllidites harrisii* Couper, Sample 420; (43) *Cyathidites australis* Couper, Sample 403; (44) *Cyathidites minor* Couper, Sample 406; (45) *Cyathidites concavus* (Bolchovitina) Dettmann, Sample 401; (46, 47) *Antulsporites distaverrucosus* (Brenner) Arch. et Gamerro, Sample 403: (46) distal side, (47) proximal side; (48, 49) *Stoverisporites lunaris* (Cooks. et Dett.) Burger: (48) Sample 415, (49) Sample 403; (50–52) *Concavissimisporites punctatus* (Delc. et Sprum.) Brenner: (50) Sample 464, (51) Sample 403, (52) Sample 412.

Plate II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Bed 67. Argillite dark gray, silty, fissured, unbedded, with scattered sulfide nodules and fragments of malacofauna shells. At the base, the ferruginous horizon is very dense, with conchoidal fracture (around 0.2 m). Thickness around 5 m. Sample 437/08, 1 m below the top of the bed; Sample 438/08, 1.9 m below the top of the bed; Sample 439/08, 2.9 m below the top; Sample 440/08, 3.9 m below the top; Sample 441/08, at the base of the bed.

Bed 68. Sandstone yellowish greenish gray, strong, with sulfide nodules, small pebbles, at the base indistinctly bedded, at the top strongly bioturbated, lumpy. Thickness around 0.05–0.06 m.

Bed 69. Argillite dark gray, silty, dense, fissured, unbedded with poorly preserved scattered sulfide nodules. Thickness around 6 m. Sample 431/08, 1 m below the top of the bed; Sample 432/08, 2 m below the top of the bed; Sample 433/08, 3 m below the top; Sample 434/08, 4.1 m below the top; Sample 435/08, 0.85 m above the base of the bed.

Bed 70. Sandstone dark gray, very dense, with lumpy fracture, bioturbated. Thickness around 0.5 m. Sample 430/08, in the middle of the bed.

Bed 71. Argillite gray, weakly silty, unbedded. Thickness around 1.8 m. Sample 428/08, 0.5 m below the top of the bed; Sample 429/08, at the base of the bed.

Bed 72. Siltstone greenish gray, dense, with lumpy jointing, strongly bioturbated. At the top with a horizon of flattened oval septarian nodules, up to 0.2 m in diameter. Thickness around 3 m. Sample 427/08, in the middle of the bed.

Bed 73. Argillite dark gray, with sulfide nodules, more densely packed at the base of the bed. Thickness around 1.1 m. Sample 425/08, 0.3 m below the top of the bed; Sample 426/08, 0.1 m above the base.

Bed 74. Above a distinct contact, sandstone gray, medium- to fine-grained, dense. At the base, with a horizon (0.2 m) in the weathered state, light yellowish, with siliceous variegated weakly rounded pebbles and gravel, with numerous ammonites and belemnites. Thickness around 0.65 m. Sample 424/08, in the middle of the bed.

## PALYNOLOGICAL CHARACTERIZATION

Associations are assigned to the Hauterivian and Barremian on the basis of the changes in taxonomic content of pollen and spores of land plants. It is important to note that most of the miospore species encountered have a broad stratigraphic range, so the association characterization is based on the changes in the proportions of particular groups (Table 1). Establishment of palynological associations is based on identifying the distribution of spores and pollen over the section and the comparison with the palynological assemblages of the Lower Cretaceous of the Caucasus, Crimea, and other regions.

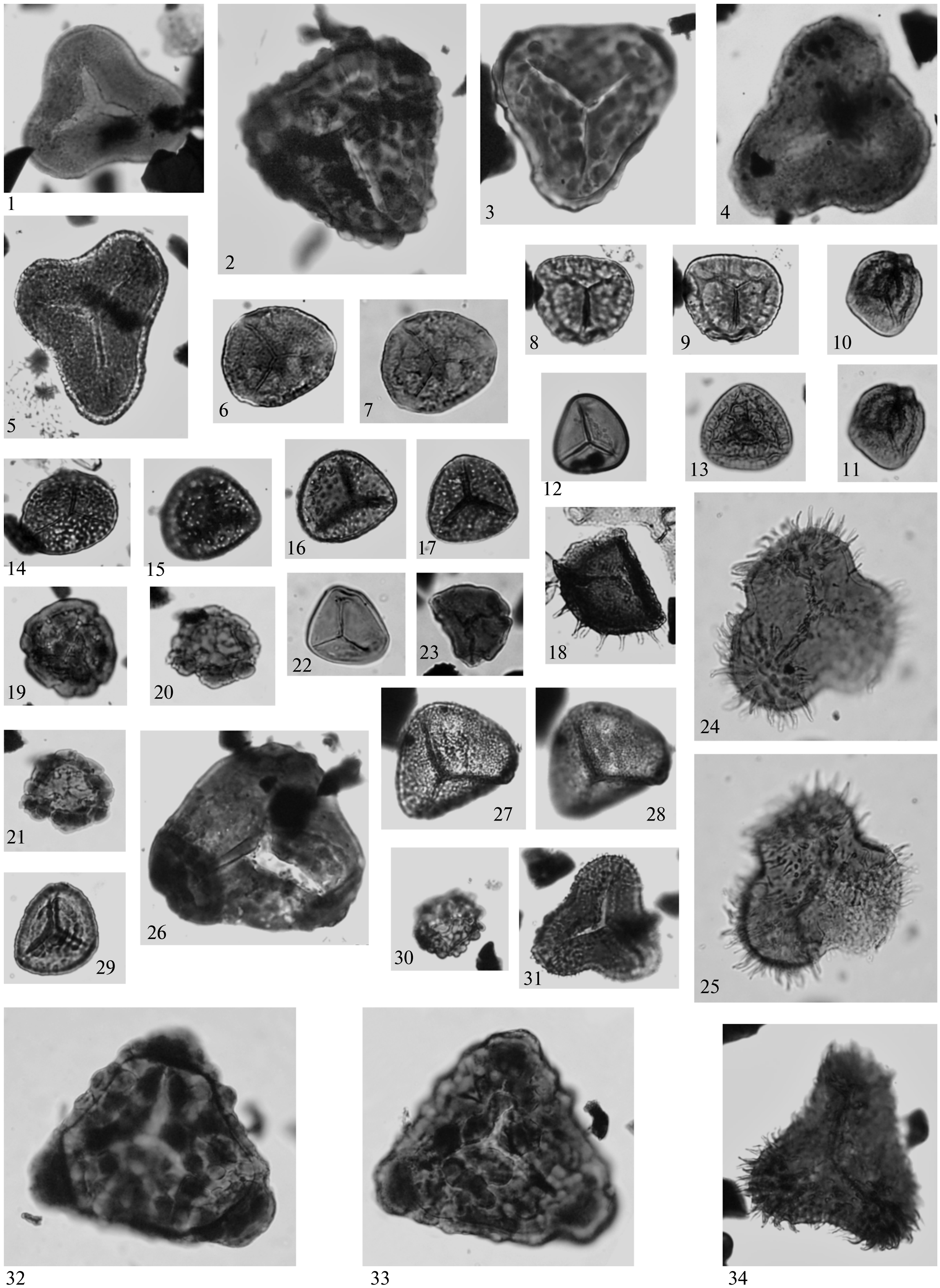
The Hauterivian palynological association of *Trilobosporites canadensis* and *Cicatricosisporites spiralis* was isolated from the lower part of the Levashi Formation at a specimen level of 401/08-458/08 (Fig. 2). The prevalence of gymnosperm pollen (up to 77%) over spores is characteristic of this higher plant palynomorph association. *Classopollis* (family Cheirolepidiaceae) pollen predominates (sometimes up to 50%). Disaccites pollen (*Alisporites*, *Cedripites*, *Podocarpidites*) constitutes up to 30%. Pollen closely related to Taxodiaceae plays a role (up to 20%)—*Perinopollenites*, *Exesipollenites*, *Spheripollenites*—as does that of Araucariaceae (up to 10%)—*Araucariacites*, *Callialasporites*. The pollen of *Cycadopites*, *Ephedripites*, and *Eucommiidites* is also present.

Relatively diverse pteridophyte, lycophyte, and bryophyte spores constitute a smaller part of the assemblage. Gleicheniaceae and Schizaeaceae play major roles (23 and 17%, respectively) amongst the pteridophytes. Within Gleicheniaceae, *Gleicheniidites* spp. and *G. senonicus* are constantly present in large numbers, *Clavifera triplex* and *Ornamentifera* spp. are fewer, and *Gleicheniidites radiatus*, *G. rasilis*, *G. carinatus*, and *G. minor* are rarer still. Schizaeaceae spores are more diverse; amongst them, the ridged *Cicatricosisporites* forms are prevalent: *C. australiensis*, *C. imbricatus*, *C. minutaestriatus*, *C. mediostriatus*, *C. hughesi*, *C. minor*, *C. spiralis*, *C. tarsus*, *C. pseudotripartitus*, *Anemia* cf. *exilioides*, and *Plicatella jansonii*. *Klukisporites*, *Contignisporites*, and *Distaltriangulisporites* species are prominent. Species of *Trilobosporites*, *Concavissimisporites*, *Impardecispora*, and *Pilosisporites* are also found. These genera are assigned

**Plate III.** Levashi Formation palynomorphs. All taxa magnified ×500.

(1) *Concavissimisporites asper* (Bolchovitina) Pocock, Sample 412; (2) *Concavissimisporites macrotuberculatus* (Kara-Murza) Bondarenko, Sample 412; (3) *Concavissimisporites informis* Döring, Sample 401; (4) *Concavissimisporites* sp., Sample 412; 5) *Concavissimisporites variverrucatus* (Couper) Brenner, Sample 412; (6–9, 13) *Coronatispora valdensis* (Couper) Dettmann: (6, 7) Sample 450, (8, 9) Sample 409, (13) Sample 406; (10, 11) *Staplinisporites caminus* (Balme) Pocock, Sample 464; (12, 22) *Deltoidospora hallii* Miner: (12) Sample 406, (22) Sample 409; (14) *Foveosporites canalis* Balme, Sample 409; (15–17) *Foveotriletes subtriangularis* Brenner, Sample 414; (18) *Kraeuselisporites hastilobatus* Playford, Sample 415; (19) *Leptolepidites verrucatus* Couper, Sample 420; (20, 21) *Leptolepidites proxigranulatus* (Brenner) Dörhöfer, Sample 412: (20) distal side, (21) proximal side; (23) *Deltoidospora juncta* (Kara-Murza) Singh, Sample 415; (24, 25) *Pilosisporites verus* Delcourt et Dettmann, Sample 401; (26) *Trilobosporites obsitus* Norris, Sample 435; (27, 28) *Microreticulatisporites uniformis* Singh, Sample 462; (29) *Taurocusporites segmentatus* Stover, Sample 406; (30) *Leptolepidites proxigranulatus* (Brenner) Dörhöfer, Sample 420; (31) *Pilosisporites* sp. cf. *P. notensis* Cookson et Dettmann, Sample 439; (32, 33) *Trilobosporites canadensis* Pocock, Sample 401; (34) *Pilosisporites trichopapillosus* (Thiergart) Delcourt et Sprumont, Sample 464.

Plate III



to Lygodiaceae (Falcon-Lang et al., 2007); however, according to other researchers *Concavissimisporites* is closely related to ?Dicksoniaceae/Cyatheaceae, and both *Impardecispora* and *Trilobosporites* are close to ?Dicksoniaceae (Abbink et al., 2004). Within this group of spores, the largest role in the palynological assemblage belongs to *Concavissimisporites* spp., *C. asper*, *C. punctatus*, *C. informis*, *C. macrotuberculatus*, *C. variverrucatus*, *Impardecispora apiverrucata*, and more rarely *Impardecispora gibberula*.

*Trilobosporites* sp., *T. canadensis*, *T. bernissartensis* are less represented and, as with *Cicatricosisporites spiralis*, their distribution is restricted to this association. *T. canadensis* and *C. spiralis* are characteristic of this association. *T. canadensis*, described from the Canadian Neocomian (Pocock, 1962), is widespread in the Berriasian and Valanginian (Burden and Hills, 1989) and is last present in the upper Hauterivian (Falcon-Lang et al., 2007). *T. canadensis* specimens have been found from the Hauterivian deposits of the Northeast Caucasus (Danilenko and Lisunova, 1994) and southern Dagestan (Smirnova and Smirnova, 2012). *C. spiralis*, described from the Albian of Canada (Singh, 1971), is found in Hauterivian deposits (Fensome, 1987).

Amongst the lycophytes, *Lycopodiumsporites* spp., *Sestrosporites pseudoalveolatus*, *Leptolepidites verrucatus*, *L. proxigranulatus*, *Densoisporites* sp., *D. velatus*, *D. circumundatus*, *D. microrugulatus*, *Ceratosporites* sp., and *Foveosporites canalis* are encountered frequently and *Kraeuselisporites hastilobatus* and *Neoraistrickia* sp. are found more rarely. Of those closely related to Dicksonioideae/Cyatheaceae, *Cyathidites* sp., *C. australis*, *C. minor*, *Deltoidospora* sp., *D. hallei*, *Dictyophyllidites* sp., and *D. harrisii* are present. Spores of unclear systematic affiliation are often found, such as those of *Biretisporites potoniaei*, *Stoverisporites lunaris*, *Coronatispora valdensis*, *Microreticulatisporites uniformis*, *Interulobites* sp., *Tappanispora* sp., and more rarely *Undulatisporites* sp. Amongst the bryophytes, *Cingutriletes pocockii*, *Foraminisporis dailyi*, and *F. wonthaggiensis* are most prominent with *Foraminisporis asymmetricus*, *Triporoletes simplex*, *Aequitriradites* spp., *Cooksonites* sp., and *Couperisporites* sp. being rarer. Rare instances of angiosperm pollen (*Tricolpites* sp.) are found in some palynological spectra.

The palynological association of *Trilobosporites canadensis* and *Cicatricosisporites spiralis* established in the Aimaki section correlates with the palynological assemblage of the Concavissimisporites–Classopollis Regional Zone of the Hauterivian of the Northeast Caucasus on the basis of the presence of *T. canadensis*, *Concavissimisporites*, and *Clavifera triplex* spores, *Ornamentifera* species, and abundant *Classopollis* pollen (Danilenko and Lizunova, 1994). The palynological association from the Aimaki section is closely related to the Hauterivian palynological assemblage of southern Dagestan (Smirnova and Smirnova, 2012). They are similar in the prevalence of Gleicheniaceae, the variety of Schizaeaceae, and the contribution of lycophytes such as *Lycopodiumsporites* sp., *Densoisporites velatus*, and *Neoraistrickia* and Dicksonioideae/ Cyatheaceae such as *Cyathidites* and *Concavissimisporites*, and also the presence of *Trilobosporites canadensis* and *Pilosisporites trichopapillosus*. In the pollen, common constituents include *Perinopollenites elatoides*, *Callialasporites dampieri*, and *Cedripites* and *Ephedripites* species. Similarity is also observed in the *Classopollis* pollen content, which is 18–20% in the Hauterivian of southern Dagestan and varies between 20–30% in the Aimaki section, rarely reaching 50%. In the Valanginian of southern Dagestan and other Caucasian sections, this pollen content is 70–90%, which is consistent with its general decrease in deposits younger than the Valanginian. Comparison of the established palynological association with the Hauterivian assemblage of the Crimean Mountains (Kuvaeva and Yanin, 1973) reveals species in common amongst spores of Gleicheniaceae, Schizaeaceae, and Bryophyta and members of Hepataceae such as *Aequitriradites*, *Cooksonites*, and *Couperisporites*, which are characteristic of both regions. It should be noted that the content of Gleicheniaceae and Schizaeaceae is significantly lower in the Crimean Mountains. The similarity of this palynological association to the Hauterivian palynological assemblage of the Central Volga region (Baraboshkin et al., 2001) is based on the large number of Gleicheniaceae species in common and some Dicksonioideae/Cyatheaceae

**Plate IV.** Levashi Formation palynomorphs. All sizes are ×500.

(1) *Impardecispora apiverrucata* (Couper) Venk. et al., Sample 403; (2) *Impardecispora gibberula* (Kara-Murza) Venkatachala et al., Sample 439; (3) *Impardecispora tribotrys* (Dettmann) Venkatachala et al., Sample 464; (4) *Undulatisporites pannuceus* (Brenner) Singh, Sample 414; (5, 6) *Interulobites* sp.: (5) Sample 415, (6) Sample 403; (7) *Interulobites sinuosus* Scott, Sample 415; (8) *Tappanispora reticulata* (Singh) S.K. Srivastava, Sample 464; (9) *Tappanispora scurranda* (Norris) S.K. Srivastava, Sample 420; (10, 11) *Verrucosisporites major* (Couper) Burden et Hills, Sample 425; (12) *Uvaesporites argenteaeformis* (Bolch.) Schulz, Sample 462; (13) *Perinopollenites elatoides* Couper, Sample 415; (14, 15) *Exesipollenites tumulus* Balme, Sample 415; (16) *Abietineaepollenites* sp., Sample 415; (17) *Podocarpidites multesimus* (Bolch.) Pocock, Sample 412; (18) *Alisporites bilateralis* Rouse, Sample 403; (19) *Araucariacites* sp., Sample 403; (20) *Podocarpidites granulates* Singh, Sample 403; (21, 26) Disaccites with features of *Rugubivesiculites* sp., Sample 406; (22) *Cedripites canadensis* Pocock, Sample 431; (23) *Podocarpidites biformis* Rouse, Sample 403; (24) *Cerebropollenites mesozoicus* (Couper) Nilsson, Sample 465; (25) *Schizosporis reticulatus* Cookson et Dettmann, Sample 439; (27) *Cedripites cretaceus* Pocock, Sample 456; (28, 31) *Callialasporites dampieri* (Balme) Dev: (28) Sample 401, (31) Sample 420; (29) *Podocarpidites miniscululs* Singh, Sample 412; (30) *Cedripites* sp., Sample 420; (32) *Inaperturopollenites limbatus* Balme, Sample 456.

Plate IV

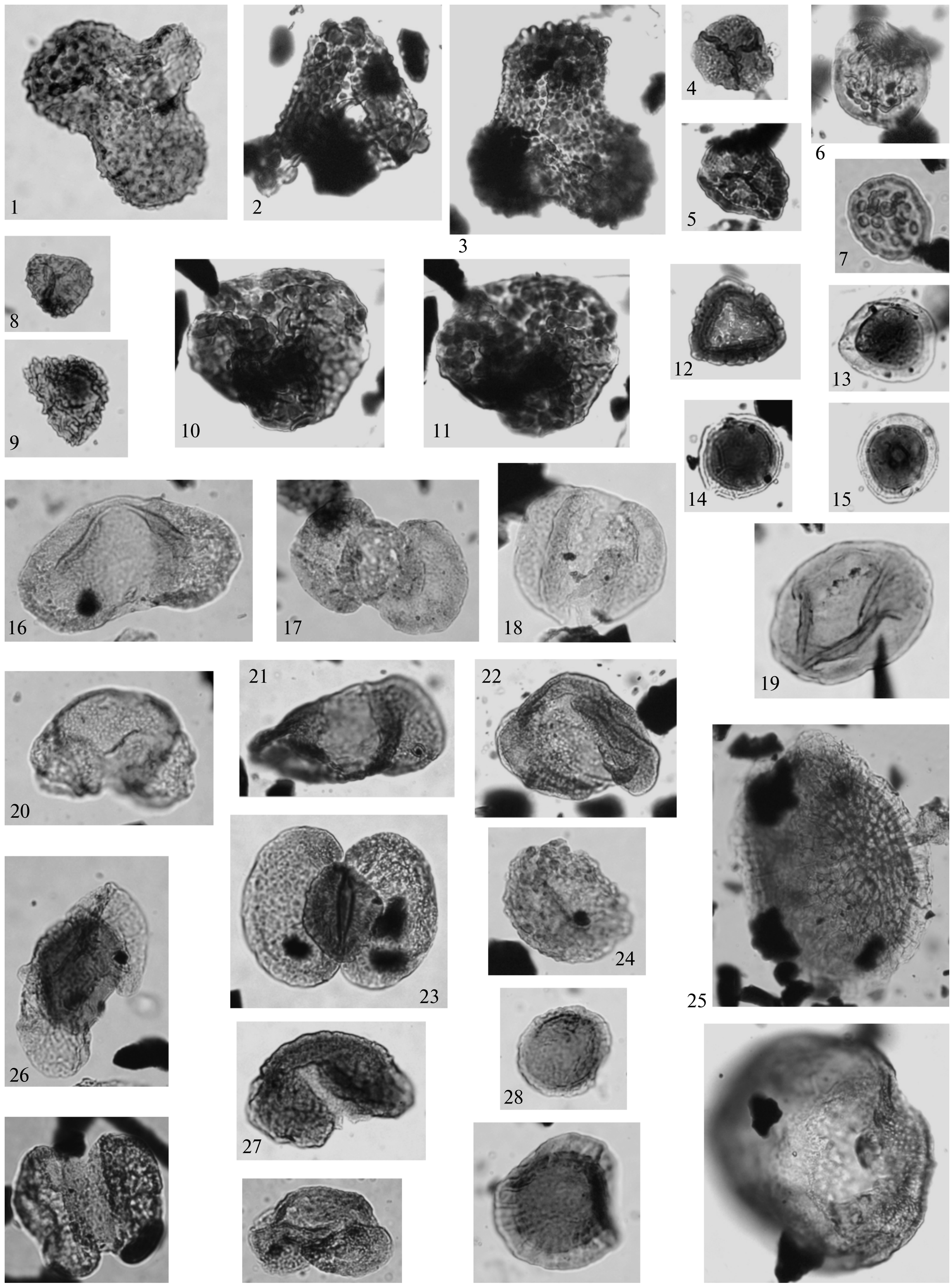

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Plate V

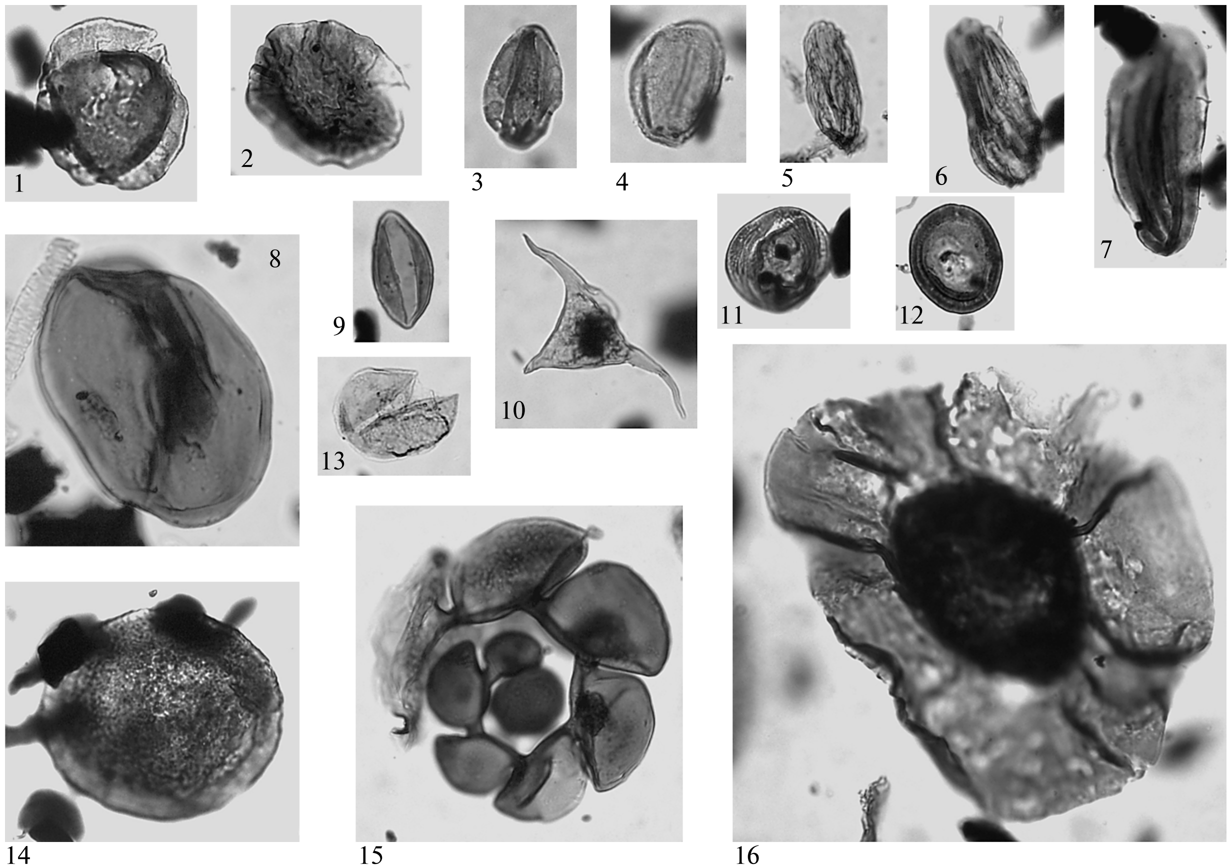


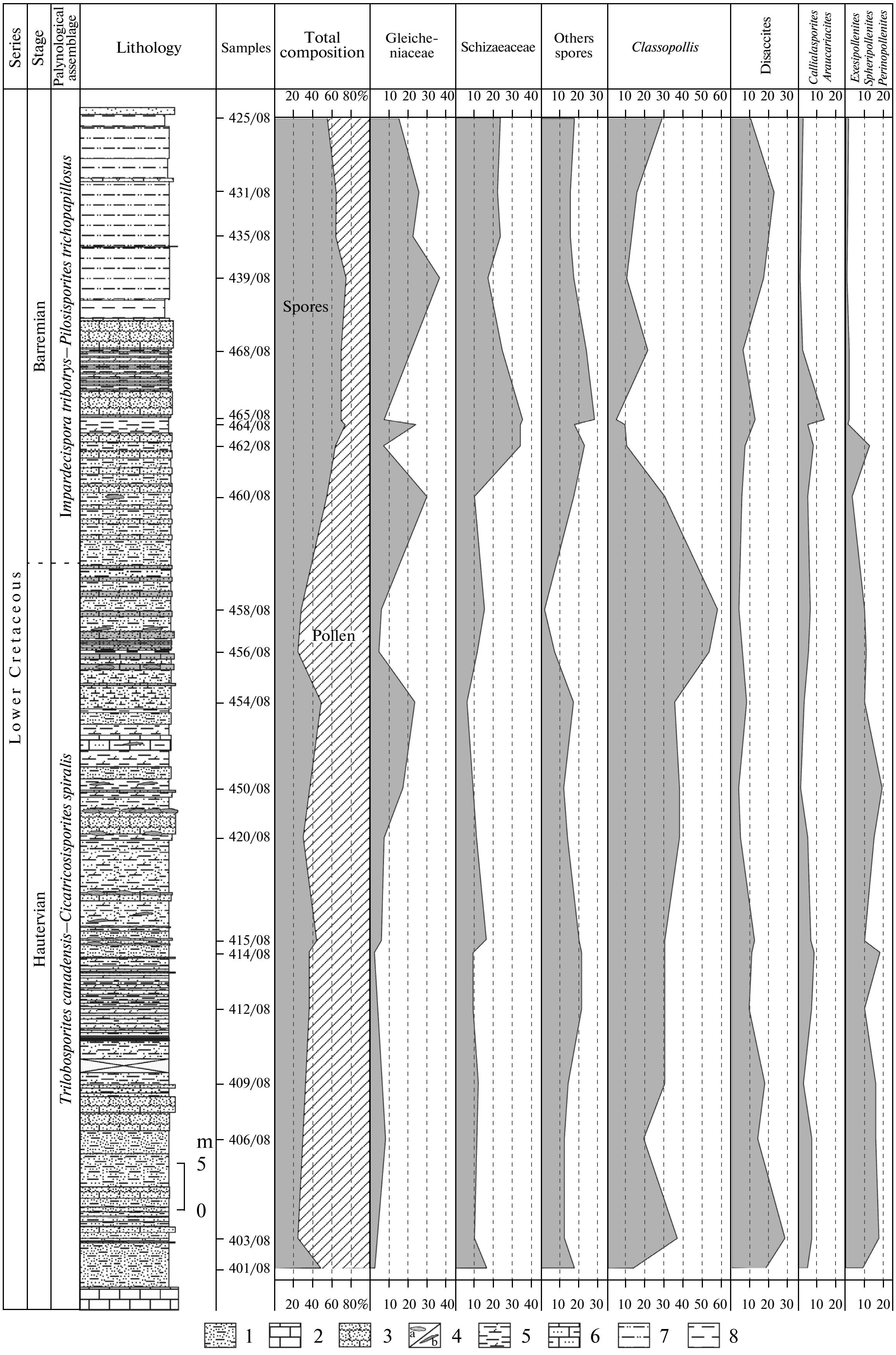

**Plate V.** Levashi Formation palynomorphs. All sizes are ×500.

(1) *Callialasporites trilobatus* (Balme) Dev, Sample 420; (2) *Callialasporites segmentatus* (Balme) Srivastava, Sample 415; (3, 4) *Tricolpites* spp., Sample 456; (5–7) *Ephedripites* spp.: (5) Sample 415, (6) Sample 412, (7) Sample 435; (8) *Araucariacites* sp., Sample 401; (9) *Cycadopites* sp., Sample 415; (10) *Veryachium* sp., Sample 456; (11, 12) *Classopollis* spp.: (11) Sample 468, (12) Sample 450; (13) *Taxodiaceaepollenites hiatus* (Potonie) Kremp, Sample 403; (14) *Tasmanites* sp., Sample 435; (15) microforaminiferal linings, Sample 462; (16) *Pterospermella* sp., Sample 462.

and Lycophyta, as well as on the presence of rare angiosperm pollen samples. The Hauterivian palynological assemblage of the Central Volga region is distinct in dominance of spores over pollen; amongst the spores, Gleicheniaceae are prevalent with a lesser contribution from Schizaeaceae and an extremely low *Classopollis* content, which is characteristic of certain regions of the Russian Platform (Shramkova, 1970; Dobrutskaya, 1973). The dinocyst assemblage of this interval of the Levashi Formation (Yaroshenko and Aleksandrova, 2012) is characterized by the co-occurrence of *Muderongia* spp., *Cribroperidinium* spp., *Batioladinium longicornutum* Alberti, *Gardodinium trabeculosum* (Gocht) Alberti, and *Pseudoceratium pelliferum* Gocht, which is typical of Hauterivian deposits of different regions (Davey, 1979, 1982; Aarhus et al., 1986, 1990; Prössl, 1990; Lebedeva and Nikitenko, 1998; Peshchevitskaya, 2010; etc.).

The Barremian palynological association of *Impardecispora tribotrys* and *Pilosisporites trichopapillosus* was established from the upper part of the Levashi Formation at a sample level of 460/08–425/08 (Fig. 2). Despite the inherited succession of the main miospore taxonomic composition, significant changes in the proportions of the main palynomorph groups are seen in the Barremian association: pteridophyte spores are predominant (up to 76%). Schizaeaceae and Gleicheniaceae play a leading role; their proportion significantly increases (35 and 37%, respectively). Amongst Schizaeaceae, the number of *Appendicisporites unicus*, *Anemia macrorhyza*, *Cicatricosisporites imbricatus*, *C. perforatus*, and *Plicatella crimensis* slightly increases

**Fig. 2.** Lithology and proportions of the major higher plant spore and pollen groups in the Aimaki section. Legend: (1) siltstone, (2) limestone, (3) sandstone, (4a) malacofauna, (4b) nodules, (5) silty clay, (6) arenaceous siltstone, (7) argillite, (8) clay.


Series
Stage
Palynological assemblage
Lithology
Samples
Total composition
Gleiche-niaceae
Schizaeaceae
Others spores
Classopollis
Disaccites
Callialasporites
Araucariacites
Exesipollenites
Spheripollenites
Perinopollenites
Lower Cretaceous
Barremian
Hautervian
Impardecispora tribotrys–Pilosisporites trichopapillosus
Trilobosporites canadensis–Cicatricosisporites spiralis
Spores
Pollen
425/08
431/08
435/08
439/08
468/08
465/08
464/08
462/08
460/08
458/08
456/08
454/08
450/08
420/08
415/08
414/08
412/08
409/08
406/08
403/08
401/08
m
5
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20 40 60 80%
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**Table 1.** Distribution of spore and pollen in the section of the Levashi Formation

| Taxa / Sample no. | 401 | 403 | 406 | 409 | 412 | 414 | 415 | 420 | 450 | 454 | 456 | 458 | 460 | 462 | 464 | 465 | 468 | 439 | 435 | 431 | 425 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cingutriletes clavus* (Balme) Dettmann | | | | | | | | | | + | | | + | × | × | | | + | + | | + |
| *Cingutriletes pocockii* (Burger) Burden et Hills | | × | + | + | × | + | + | + | + | + | + | | × | | + | | | + | + | | |
| *Stereisporites antiquasporites* (Wils. et Webs.) Dettmann | | + | | + | | | + | + | | | | | + | | | | | + | + | | |
| *Aequitriradites spinulosus* (Cooks. et Dett.) Dettmann | + | | | | + | | | | | | | | | | | | + | | | | |
| *Aequitriradites* sp. | | | | | + | | + | + | | | + | | | | | | | | | | |
| *Cooksonites variabilis* Pocock | + | | + | | | | | + | + | | | | | | | | | | | | |
| *Couperisporites* sp. | + | | | | + | | + | | + | | | | + | | | | + | | | | |
| *Foraminisporis asymmetricus* (Cooks. et Dett.) Dettmann | | + | × | | + | | + | | | | + | | | | | | | | | | + |
| *Foraminisporis dailyi* (Cooks. et Dett.) Dettmann | | × | × | + | + | + | + | ◑ | | + | + | | + | | × | + | + | + | | | |
| *Foraminisporis wonthaggiensis* (Cooks. et Dett.) Dettmann | + | + | + | + | × | + | × | × | | | + | | | + | + | | + | + | + | + | |
| *Triporoletes simplex* (Cooks. et Dett.) Playford | | + | + | | + | + | | + | + | | | + | | | | | | | | | |
| *Staplinisporites caminus* (Balme) Pocock | | | + | | | | | | | | | | | | + | | | | | | |
| *Lycopodiumsporites austroclavatidites* (Cookson) Potonie | | | | × | + | | | | | | | | | | | | | | | | |
| *Lycopodiumsporites* spp. | + | + | + | | × | + | + | + | + | + | × | × | + | + | × | + | + | ◑ | + | + | × |
| *Lycopodiumsporites crassatus* Singh | + | + | | | | | | | | | | | | | | | | | | | + |
| *Sestrosporites pseudoalveolatus* (Couper) Dettmann | + | + | ◑ | + | × | + | × | + | | + | + | + | + | | + | + | + | + | + | + | |
| *Leptolepidites verrucatus* Couper | | + | + | + | + | | | × | + | + | + | | × | | + | | + | + | + | | |
| *Leptolepidites proxigranulatus* (Brenner) Dörhöfer | | + | | | + | + | × | + | | + | × | × | + | | | | | | | | |
| *Kraeuselisporites hastilobatus* Playford | | + | | | | | + | + | | | | | | | | | | | | | |
| *Foveosporites canalis* Balme | | | + | + | + | | | | | | | | | | | + | + | | + | | |
| *Ceratosporites* spp. | + | + | + | | + | + | × | × | + | + | + | + | | | + | + | × | | + | | |
| *Densoisporites circumundulatus* (Brenner) Playford | | | + | | | + | | | | | | | | | | | | | | | |
| *Densoisporites microrugulatus* Brenner | | + | + | | | + | + | + | | | | + | | | + | | | | | | |
| *Densoisporites velatus* Weyland et Krieger | + | + | + | + | | | | | | + | | | | | | + | | | | + | |
| *Neoraistrickia truncata* (Cookson) Potonie | | + | | | | | | | | | | | + | | | | | | | | |
| *Biretisporites potoniaei* Delcourt et Sprumont | ◑ | ◑ | ◑ | ◑ | + | ◑ | × | + | + | ◑ | × | × | + | + | ◑ | ◑ | + | + | + | × | + |
| *Todisporites major* Couper | + | | | | | | | + | | | | | | | | | | | | | |
| *Todisporites minor* Couper | | + | + | | + | | + | | | | | | | | | | | | | + | |
| *Appendicisporites unicus* (Markova) Singh | | | | | | | | | | | + | | | | + | + | | + | | | |
| *Anemia macrorhyza* (Mal.) Bolch. | + | | | | | | | | + | | | + | | | + | | + | | | + | + |
| *Cicatricosisporites australiensis* (Cookson) Potonie | | | | | + | + | | | + | | | | | + | | | | | | | |
| *Anemia exilioides* (Mal.) Bolch. | | + | | | | + | | | + | | | | | + | + | | | + | | | |
| *Cicatricosisporites hughesi* Dettmann | + | | + | | + | | | + | | + | | | | + | | + | | | | | |

**Table 1.** (Contd.)

| Taxa / Sample no. | 401 | 403 | 406 | 409 | 412 | 414 | 415 | 420 | 450 | 454 | 456 | 458 | 460 | 462 | 464 | 465 | 468 | 439 | 435 | 431 | 425 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cicatricosisporites imbricatus* (Markova) Singh | | | + | | | + | × | | | + | + | + | + | + | + | | + | × | + | + | |
| *Cicatricosisporites mediostriatus* (Bolch.) Pocock | | + | | + | × | | × | | | + | | | | | | | + | + | | | + |
| *Cicatricosisporites minor* (Bolch.) Pocock | | + | + | | | | × | | | | | | | | | + | | | | | |
| *Cicatricosisporites minutaestriatus* (Bolch.) Pocock | × | ◑ | | | + | | | ◑ | × | × | × | + | × | × | + | + | + | | + | | ◑ |
| *Cicatricosisporites perforatus* (Markova) Döring | + | | | | | | | | | + | + | × | + | + | + | + | + | + | + | + | + |
| *Cicatricosisporites pseudotripartitus* (Bolch.) Dettmann | | | | | | | + | + | | + | | + | | | | + | | | | | |
| *Cicatricosisporites spiralis* Singh | + | | + | + | | | + | | + | | | | | | | | | | | | |
| *Cicatricosisporites tersus* (K.-M.) Pocock | + | | | | | | + | | | | | | | | | | | | | | |
| *Cicatricosisporites* spp. | × | | ◑ | ◑ | + | × | ◑ | ◑ | ◑ | × | ◑ | ● | ◑ | ◑ | ● | ◑ | ◑ | ● | ◑ | ◑ | ◑ |
| *Plicatella crimensis* (Bolch.) Dörhöfer | | | | | | | | | + | | | | | | × | | | | | | |
| *Plicatella jansonii* (Pocock) Dörhöfer | + | | | | | | | | | | | | + | | | | | | | | |
| *Contignisporites cooksonii* Dettmann | | | | + | + | | + | × | + | + | | | | | | | | | | | + |
| *Contignisporites* sp. | + | | + | + | | | | | | | | | + | + | | | + | | + | + | |
| *Contignisporites multimuratus* Dettmann | | + | | | | | | | | + | + | | + | | + | | | | | | |
| *Distaltriangulisporites perplexus* Singh | + | | | | | | + | + | | | | | | + | × | | | | | + | |
| *Distaltriangulisporites* sp. | + | | | | + | | | | | | | | | | | | | | | | + |
| *Klukisporites foveolatus* Pocock | + | + | | | + | | + | + | | | | | | | | + | | | | + | + |
| *Klukisporites* spp. | | | × | + | + | | + | + | + | + | + | + | | + | | + | | + | + | + | |
| *Klukisporites granulatus* (Pocock) Burden et Hills | | | | + | | | | | | | | | | | | | | | | | |
| *Klukisporites pseudoreticulatus* Couper | + | + | | | | | | + | | | | | | | + | + | | | | | + |
| *Gleicheniidites* spp. | × | + | ◑ | | × | | × | ◑ | × | ● | | | + | | ◑ | + | ◑ | ◑ | + | | |
| *Gleicheniidites carinatus* Bolch. | | | | | | | | | | | + | | | | × | | | | | | |
| *Gleicheniidites radiatus* Bolch. | | | | | + | | | | + | + | | | | | + | | + | | | | |
| *Gleicheniidites rasilis* Bolch. | | | | + | | | | + | + | + | + | | | + | + | | | + | | | |
| *Gleicheniidites minor* Döring | | + | | | | | | | | | | | | | | | | | | | |
| *Gleicheniidites senonicus* Ross | + | ◑ | ◑ | ◑ | × | + | ◑ | | ◑ | ◑ | × | + | ◑ | × | | × | ◑ | ◑ | × | ◑ | ◑ |
| *Clavifera triplex* Bolch. | + | | × | + | + | + | + | ◑ | ● | ● | ◑ | × | ◑ | + | ● | + | × | ● | + | ◑ | × |
| *Ornamentifera* spp. | | + | × | | + | + | | ◑ | × | × | × | ◑ | ▲ | ◑ | + | + | ◑ | ● | ◑ | ● | ◑ |
| *Cyathidites australis* Couper | + | × | + | | | ◑ | | | | | + | + | | | + | + | | | | | |
| *Cyathidites concavus* (Bolch.) Dettmann | + | | | | | | | | | | | | | | | | | | | | |
| *Cyathidites* spp. | ◑ | + | ◑ | + | × | | + | + | ◑ | × | × | | + | ◑ | ◑ | × | ◑ | ◑ | + | + | × |
| *Cyathidites minor* Couper | | | + | | | | + | ◑ | | | | | | | | | | | | | |
| *Stoverisporites lunaris* (Cookson et Dettmann) Burger | + | × | + | + | + | | + | × | + | | | + | | | + | | | | | | |
| *Dictyophyllidites* sp. | | × | ◑ | + | + | + | | × | ◑ | | | | × | + | ◑ | | | × | + | + | + |

**Table 1.** (Contd.)

| Taxa / Sample no. | 401 | 403 | 406 | 409 | 412 | 414 | 415 | 420 | 450 | 454 | 456 | 458 | 460 | 462 | 464 | 465 | 468 | 439 | 435 | 431 | 425 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Dictyophyllidites harrisii* Couper | | | + | | | + | + | + | | | | | | | | | | | | | |
| *Antulsporites distalverrucosus* (Brenner) Arch. et Gamerro | | + | | | | | | | | | | | | | + | | | | + | | |
| *Concavissimisporites* spp. | × | × | + | × | + | | + | × | + | + | × | + | × | × | ◑ | ◑ | | + | + | + | |
| *Concavissimisporites* asper (Bolch.) Pocock | + | + | | + | + | × | × | + | + | | + | + | | | | | + | | | × | + |
| *Concavissimisporites informis* Döring | + | + | | + | | | | | | | | | | | | | | | | | |
| *Concavissimisporites punctatus* (Delc. et Sprum.) Brenner | | + | + | | + | + | × | + | + | | | | + | | × | | × | | + | | |
| *Concavissimisporites macrotuberculatus* (K.-M.) Bondarenko | + | | | + | + | + | | | | | | | | | + | | | | | | |
| *Concavissimisporites variverrucatus* (Couper) Brenner | | | + | + | + | + | × | | + | | | | × | + | + | × | + | | | + | |
| *Coronatispora valdensis* (Couper) Dettmann | | + | + | × | | | | + | + | + | + | + | | × | + | + | | | | + | + |
| *Deltoidospora* sp. | | | + | | + | × | + | × | | + | | + | | | | + | + | | + | | |
| *Deltoidospora hallii* Miner | | | + | × | + | + | | + | | | × | | × | | + | + | | + | | | + |
| *Deltoidospora juncta* (K.-M.) Singh | | | + | + | | | + | | | | | | | | | | | | | + | + |
| *Foveotriletes subtriangularis* Brenner | | + | | + | + | + | | | + | | | | | | + | × | | + | | + | + |
| *Microreticulatisporites uniformis* Singh | | + | | + | + | | + | + | + | | + | + | | × | + | | + | | | + | + |
| *Pilosisporites verus* Delcourt et Dettmann | + | | + | + | + | + | + | ◑ | + | | + | + | | + | + | + | + | + | | | |
| *Pilosisporites trichopapillosus* (Thiergart) Delc. et Sprum. | + | + | × | + | + | + | + | × | + | | | | + | ◑ | ◑ | ◑ | + | ◑ | ◑ | ◑ | ◑ |
| *Pilosisporites* spp. | + | + | + | + | × | | × | × | + | | + | | | × | + | + | + | + | | × | |
| *Taurocusporites segmentatus* Stover | | | + | | | | | | | | | | | | | | | + | | | |
| *Trilobosporites* sp. | + | | | + | + | + | + | | | | | | | | | | | | | | |
| *Trilobosporites bernissartensis* (Delc. et Sprum.) Venk. et al. | + | | + | + | | | | | | | | | | | | | | | | | |
| *Trilobosporites obsitus* Norris | | | | | | | | | | | | | | | | | | | + | | |
| *Trilobosporites canadensis* Pocock | + | | | | | | | | | | | | | | | | | | | | |
| *Impardecispora humilis* Delcourt et Sprumont | | | | | | | | | | | | | | | | + | | | | | |
| *Impardecispora apiverrucata* (Couper) Venk. et al. | + | + | | + | | + | + | + | + | + | | | | | + | + | + | | + | + | + |
| *Impardecispora gibberula* (K.-M.) Venk. et al. | | | + | | + | | | | | | | | | | | | | + | | + | |
| *Impardecispora tribotrys* (Dettmann) Venk. et al. | | | | | | | | | | | | | | | + | | | | + | | |
| *Undulatisporites fossulatus* Singh | | | + | | | | | + | | | | | | | + | | | | | | |
| *Undulatisporites pannuceus* (Brenner) Singh | | | | | | + | | | | | | | | + | | | | | | | + |
| *Interulobites* sp. | | + | | | | + | + | | + | + | | | + | + | | | | | | | |
| *Interulobites sinuosus* Scott | | + | | | + | + | + | | | + | | | | | | | | | | | |
| *Tappanispora reticulata* (Singh) S.K. Srivastava | | | | + | + | + | + | + | | | | | + | | + | | | | | | |
| *Tappanispora scurranda* (Norris) S.K. Srivastava | | | | | + | | | × | + | + | | | | | + | | | | + | | |
| *Verrucosisporites major* (Couper) Burden et Hills | | | | | | + | + | | | | | | | + | | + | | | + | + | + |
| *Uvaesporites argenteaeformis* (Bolch.) Schulz | | | | | | | | | | | | | | + | | | | | | | |

**Table 1.** (Contd.)

| Taxa / Sample no. | 401 | 403 | 406 | 409 | 412 | 414 | 415 | 420 | 450 | 454 | 456 | 458 | 460 | 462 | 464 | 465 | 468 | 439 | 435 | 431 | 425 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Vitreisporites* sp. | | | | | | | | + | | | | | | | | | | | + | | |
| *Cycadopites* sp. | | × | + | + | × | | + | × | | + | × | + | + | + | + | | + | + | | | |
| *Araucariacites* sp. | + | × | × | + | × | | | ◑ | + | | ◑ | × | + | ◑ | × | × | | | | | |
| *Callialasporites dampieri* (Balme) Dev | × | ● | ◑ | ◑ | ◑ | ◑ | ◑ | ◑ | + | ◑ | ◑ | × | ◑ | × | ◑ | ◑ | + | + | | + | + |
| *Callialasporites segmentatus* (Balme) S.K. Srivastava | | | + | + | + | | + | + | | | + | + | | | | | | | | | |
| *Callialasporites trilobatus* (Balme) Dev | | | | | | | | + | | | | | + | | | | | | | | + |
| *Abietineaepollenites* sp. | | + | × | | | | + | | | | | + | | | | | | | | | |
| *Parvisaccites radiatus* Couper | × | ◑ | ◑ | + | × | | | × | + | + | + | + | | | + | | + | ◑ | | × | + |
| *Podocarpidites biformis* Singh | | + | | | | | | | | | | | | + | | | | | | + | |
| *Podocarpidites ellipticus* Couper | ◑ | + | ◑ | | | | | | | | | | + | | | | | | | | |
| *Podocarpidites* sp. | + | | + | + | | + | × | × | × | + | × | + | + | + | | + | | | | ◑ | + |
| *Podocarpidites granulatus* Singh | | + | | | + | | | | | | | | | | | + | | | | | |
| *Podocarpidites minisculus* Singh | | × | | | + | | | | | | | | | | | | | | | | |
| *Podocarpidites multesimus* (Bolch.) Pocock | | + | | | + | | | | | | | | | | | | | | | | |
| *Alisporites* sp. | | + | | | ◑ | | | | | + | | | | | | | | | | | |
| *Alisporites bilateralis* Rouse | + | × | ◑ | | ◑ | + | + | ◑ | | | | | | | | | + | | | | × |
| *Cedripites canadensis* Pocock | | | ◑ | + | + | + | | + | | + | | | | | ◑ | | | | | + | |
| *Cedripites cretaceus* Pocock | | | | | × | | | + | | | + | | | | | | | + | | | |
| *Disaccites* | ● | ◑ | ● | ● | ● | ◑ | ● | ▲ | ◑ | ◑ | ● | × | ◑ | ◑ | ● | ◑ | × | ▲ | ● | ● | ◑ |
| *Ephedripites* spp. | | | | | + | + | + | + | | | × | + | | | + | | + | + | + | + | + |
| *Classopollis* spp. | ● | ■ | ▲ | ■ | ■ | ▲ | ■ | ■ | ■ | ■ | ■ | ■ | ▲ | ◑ | ● | × | ● | ● | ◑ | ● | ▲ |
| *Eucommiidites troedssonii* Erdtman | + | + | + | + | + | | + | × | | + | | | | | | | | | | | |
| *Perinopollenites elatoides* Couper | + | + | ◑ | + | ◑ | + | ◑ | ◑ | | | | | + | | + | | + | | | | |
| *Exesipollenites tumulus* Balme | ◑ | ● | ▲ | ◑ | ◑ | + | ◑ | ▲ | ▲ | ● | ▲ | ◑ | ◑ | ◑ | + | + | | | | | + |
| *Spheripollenites* sp. | × | ● | ● | ▲ | | ● | ◑ | ◑ | ● | × | × | + | | ◑ | | + | | | | | |
| *Cerebropollenites mesozoicus* (Couper) Nilsson | | | | | | | | | | | | | | + | + | + | + | + | + | + | + |
| *Inaperturpollenites* spp. | × | ● | ◑ | ◑ | × | | ▲ | | | ◑ | ◑ | | | | | | | | | | ◑ |
| *Taxodiaceaepollenites* sp. | | + | | | | | | | | | ◑ | × | + | + | × | + | | | | | |
| *Tricolpites* sp. | | | | | | | | | | | + | + | + | | + | | | | | | |
| *Schizosporis reticulatus* Cookson et Dettmann | + | | | | | | + | | | | | | | | | | | + | | + | |
| *Schizophacus spriggii* (Cookson et Dettmann) Pierce | + | | + | | | | | | | | | | | | | | | | ◑ | | |
| *Schizophacus* spp., *Leiosphaeridia* sp. | × | ● | ◑ | + | × | + | ◑ | ▲ | × | ● | ◑ | × | | × | | × | × | ◑ | + | × | ◑ |
| *Tasmanites* sp. | | | | | | | | | | | | | | | | | | + | + | + | |

+ 1–4 specimens
× 5–9 specimens
◑ 10–24 specimens
● 25–49 specimens
▲ 50–100 specimens
■ >100 specimens

in the constant presence of *Klukisporites*. A slight increase in the quantity of *Concavissimisporites variverrucatus* is seen, while the constant Hauterivian species *C. macrotuberculatus*, also known from the Hauterivian deposits of the Ust-Yenisei region (Peshchevitskaya, 2010), loses its significance in this association. One of the features of this association is the inclusion of *Impardecispora tribotrys*, *I. humilis*, and *Trilobosporites obsitus*, which were not encountered in the previous association. It should be noted that, while the appearance of the first two taxa is confined to the early Barremian, the stratigraphic range of *T. obsitus* encompasses the Valanginian and Hauterivian (Burden and Hills, 1989). Another feature is the sharp increase in the quantity of *Pilosisporites* spores, particularly of *P. trichopapillosus*, known from the Berriasian (Burden and Hills, 1989). However, *Pilosisporites* species are known to be characteristic of the Barremian of different regions (Yaroshenko, 1965; Danilenko, 1973; Kuvaeva and Yanin, 1973; Shevtsova, 1973; Smirnova and Smirnova, 2012). A variety of *Pilosisporites* species are constantly present in the Barremian of Western Siberia, where they are an important indicator for age determination (Peshchevitskaya, 2010). Apart from the many *P. trichopapillosus*, which are also found together with *P. verus* in the Hauterivian, *Pilosisporites notensis*, found in the Barremian of Australia (Burger, 1973), plays a notable role. This exemplifies the wide geographic distribution of many taxa. The co-occurrence of the dinocysts *Odontochitina operculata* (Wetzel) Deflandre et Cookson, *Cassiculosphaeridia magna* Davey, *Callaiosphaeridium asymmetricum* subsp. *latum* Heilmann-Clausen, *Pseudoceratium pelliferum*, and *Prolixosphaeridium parvispinum* (Deflandre) Davey, Downie, Sarjeant et Williams was established in this part of the Levashi Formation section (Yaroshenko and Aleksandrova, 2012), which confirms the Barremian age of the palynological association (Heilmann-Clausen and Thomsen, 1995; Oosting et al., 2006).

The quantity of Dicksonioideae/Cyatheaceae spores markedly increases in this association, while Lycophyta spores (*Lycopodiumsporites*, *Sestrosporites*, *Leptolepidites, Foveosporites*, *Ceratosporites*) and Bryophyta spores (*Foraminisporis* spp.) are constant. The Hepataceae spore content, such as of *Aequitriradites*, *Cooksonites*, and *Couperisporites*, slightly decreases. The regular occurrence of Sphagnopsida spores, in particular, of *Cingutriletes clavus*, which is sporadically found in the Hauterivian, is noteworthy. This species is a key taxon for the lower Aptian assemblage of the Northeast Caucasus (Danilenko and Lizunova, 1994) and is predominant in the Aptian deposits of the section in question (Aleksandrova et al., 2010).

The gymnosperm pollen content is poor: the quantity of *Classopollis*, as well as of Pinaceae and Podocarpaceae pollen, significantly decreases. Poorly preserved and often fragmented specimens are attributed to Disaccites. The Araucariaceae and Taxodiaceae content decreases insignificantly. *Cerebropollenites*, which is closely related to Taxodiaceae, is constantly present, while in the Hauterivian it occurs sporadically. There are rare Angiospermae pollen grains identified as *Tricolpites* spp. The appearance of *Tasmanites* is noted, and *Pterospermella*, *Schizosporis*, and fungal spores are traceable.

Analysis of the content of the palynological assemblage indicates that the climate in the Barremian was changing owing to increasing humidity. This is evidenced by the reduction in *Classopollis* and the increasing development of pteridophytes, such as Gleicheniaceae and Schizaeaceae, which at present grow in warm and humid subtropical climatic conditions.

## DISCUSSION

On the basis of the content of the main groups and separate miospore taxa, the established associations are comparable to the Hauterivian and Barremian assemblages of certain regions of the Southeast Caucasus (Kuvaeva et al., 1964), the North Caucasus (Yaroshenko, 1965), the Northeast Caucasus (Danilenko and Lizunova, 1994), and southern Dagestan (Smirnova and Smirnova, 2012).

We should consider the presence of the angiosperm pollen of *Tricolpites* sp. found in Hauterivian and Barremian associations of both the Aimaki section and other regions. *Protoquercus agdjakendensis* pollen described from the Hauterivian of Kazakhstan was assigned to Angiospermae (Bolkhovitina, 1953). Similar specimens from the upper Hauterivian of the Northern Caspian region were assigned to this genus (Shakhmundes, 1971). *Protoquercus* sp., *Tricolpites* sp., and ?*Polyporites* sp. were identified in the Hauterivian–Barremian of the northeastern part of West Siberia (Mchedlishvili, 1971). Angiosperm pollen was found in Hauterivian deposits of the Khatanga Depression and the lower reaches of the Lena River, as well as in the Barremian of the Lena-Olenek region (Peshchevitskaya, 2007).

Previously, the most reliable first representative of angiosperm pollen was considered to be *Asteropollis* pollen from Barremian deposits of Transbaikalia (Vakhrameev and Kotova, 1977). Later, these deposits were dated Hauterivian–Barremian (Krassilov and Bugdaeva, 1996). *Retimonocolpites* and *Clavatipollenites* monocolpate pollen was found in Barremian deposits in the central part of the Atlantic Ocean (Kotova, 1986). *Clavatipollenites* is known from the Barremian of England (Hughes et al., 1979), Gabon and Congo (Doyle et al., 1977), and Portugal (Heimhofer et al., 2007); the Hauterivian of Israel (Brenner, 1996); and the Jurassic of Denmark (Koppelhus, 1991). Angiosperm *Archaefructus* pollen has been studied from the Barremian Yixian Formation in Northeast China (Ge Sun and Dilcher, 2012).

Vakhrameev (1981) placed the appearance of the first angiosperms in the early Barremian—a so-called beginning of the first stage of development of these plants, linked to a fundamental change in terrestrial floras. Krassilov (1997) believes that the first angiosperms appeared significantly earlier—by the Hauterivian–early Barremian. The appearance/presence of angiosperm pollen in the studied material approximately corresponds to this time. This coincides with changes in the Hauterivian and Barremian associations, the development of which involved a quantitative redistribution of major miospore groups. Gymnosperm pollen, with a prevalence of *Classopollis*, dominated the Hauterivian with Disaccites playing an insignificant role, while the Barremian is dominated by pteridophytes, marked by the rise and culmination of development of Schizaeaceae, together with many Gleicheniaceae and associated lycophytes. The significance of *Classopollis* pollen and, especially, Disaccites pollen is greatly reduced.

The Aimaki section associations were studied from marine and coastal-marine deposits, as evidenced by the presence of dinocysts. In the absence of larger floral fossils, spores and pollen are the only objects which indicate the existence of terrestrial vegetation—both coastal and from further removed regions. Terrestrial vegetation can only be assessed by correlating dispersed miospores with taxa classified on the basis of complete plants, using previously published data. (Bolkhovitina, 1953, 1961, 1968; Vakhrameev, 1981, 1988, 1990; Krassilov, 1972, 1977, 1997; Abbink et al., 2004; Balme, 1957, 1995; Couper, 1958; Dettmann, 1963; Falcon-Lang et al., 2007; Pocock, 1962, 1964; Singh, 1971; Srivastava, 1975, 1987; van Konijnenburg van Cittert, 2002).

The rich and diverse pollen and spore content of the established associations reflects the different types of terrestrial vegetation. The first type is represented by ancient Pinaceae, Podocarpaceae, Cheirolepidiaceae, Araucariaceae, and Taxodiaceae, with contributions from Cycadophyta and *Ephedripites*. The second type (fern association) includes Gleicheniaceae, Schizaeaceae, Lycophyta, and Dicksonioideae/Cyatheaceae. Bryophytes play a major role.

If we consider Hauterivian and Barremian vegetation in total, we observe similarity in their systematic composition with the differences being reduced to the proportions of major plant groups. The dominance of Cheirolepidiaceae, as well as the large amounts of other gymnosperm pollen, is often associated with marine basin proximity. Other gymnosperms typically grow on elevated platforms and their slopes. According to the model proposed by Abbink et al. (2004), the bisaccate pollen of these plants can be assigned to the Upland SEG (Sporomorph Eco Group) ecological group.

Distribution analysis of Cheirolepidiaceae, which are thermophilic, subtropical plants, and of their *Classopollis* pollen shows that they were able to colonize a wide variety of habitats and grew in arid conditions, in more humid coastal-marine regions, and also away from them. It is notable that many *Classopollis* findings are accompanied by noticeable amounts of *Araucariacites* and *Callialasporites*, representing Araucariaceae which grew close to the coastline (Vakhrameev, 1988; Abbink et al., 2004). According to these authors, Cheirolepidiaceae and Araucariaceae are predominantly associated with coastal regions, so this allows the assignment of their pollen to the coastal habitat ecological group—Coastal SEG (Abbink et al., 2004).

Members of Taxodiaceae, such as *Perinopollenites*, appear to have colonized lowland plains and are associated with the Lowland SEG ecological group. *Cerebropollenites* pollen, closely related to Taxodiaceae, is presumably associated with the same group. Plants that produce such pollen (*Sciadopitys*) preferred moist and temperate habitats close to large water bodies (Sauer and Mchedlishvili, 1966).

The Polypodiopsida association is represented by the predominant Schizaeaceae and Gleicheniaceae, which are thermophilic subtropical plants. The Gleicheniaceae were seen as inhabitants of stagnant marshes and forest swamps located along the shores of seas and lakes (Bolkhovitina, 1968). However, according to other authors, including Van Konijnenburg-van Cittert (2002), they grew in various conditions. They were an important component of savannas and prairies in the subtropics. According to this author, Schizaeaceae inhabited banks of rivers, shallow lakes, and swamps or forests in the form of undergrowth. The hygrophilous property of Schizaeaceae is indicated by *Klukia*, which was supposedly a semiaquatic plant (Krassilov, 1972).

Representatives of Dicksonioideae/Cyatheaceae and lycophytes are moisture- and heat-loving plants growing in lowland plains or along river banks, so their spores are associated with Lowland and River SEGs (Abbink et al., 2004). Bryophyte spores are also associated with these ecological groups.

Miospore affiliation to certain ecological groups and the transformation of the vegetation during the transition from the coniferous community of the Hauterivian to the predominantly fern association of the Barremian prompt discussion of paleogeographic conditions. The dynamics of the changes in the established associations suggests a possible successive shallowing of the marine basin and the formation of a shallow shelf. As the sea level decreased, the exposed areas of land and shallow coast were mainly colonized by hygrophilous plants. The dinocyst diversity in microphytoplankton decreased and *Tasmanites* appeared. A change in climate, characterized by an increase in humidity and decrease in temperature, is indicated by the predominance of hygrophilous ferns, especially Schizaeaceae; the presence of lycophytes; the frequent appearance of Taxodiaceae (*Cerebropollenites* pollen) and Sphagnopsida (*Cingutriletes clavus*), which were almost entirely absent in the Hauterivian; and the significant decrease in thermophilic Cheirolepidiaceae and certain other conifers. These changes were already emerging in the Hauterivian, when Cheirolepidiaceae were still predominant but were significantly fewer than in the Valanginian and Berriasian, when they were prevalent in a number of Caucasus regions. The trend of increasing humidity and decreasing temperature continued in the Aptian. On the basis of Aimaki section data (Aleksandrova et al., 2010), Cheirolepidiaceae pollen (*Classopollis* spp.) is found as individual specimens or is entirely absent from the Aptian palynological assemblage, whereas Gleicheniaceae ferns and Sphagnopsida are prevalent, accompanied by an increase in Taxodiaceae pollen (*Cerebropollenites*).

To summarize, it should be noted that, regardless of the reliability with which pollen and spores can be associated with particular plants, a rich, diverse, hygrophilous subtropical vegetation can be inferred in the Middle Neocomian of Central Dagestan–eastern Caucasus, which was part of the European Province of the Euro-Sinian paleofloristic region (Vakhrameev, 1988).

## CONCLUSIONS

A rich palynological flora is established in the Hauterivian and Barremian deposits of Central Dagestan. Comparison of identified palynological assemblages with assemblages of other regions of the Caucasus reveals a high degree of similarity and indicates the growth of the associated plants in humid, subtropical conditions. A noticeable transformation of the vegetation, reconstructed on the basis of the taxonomic and quantitative miospore content, occurred during the Hauterivian–Barremian transition and was characterized by the replacement of the coniferous association with an association of ferns. The dominance of hygrophilous ferns in the Barremian, accompanied by lycophytes, as well as by representatives of Taxodiaceae and Sphagnopsida (which were nearly absent in the Hauterivian), and the significant decrease in thermophilic Cheirolepidiaceae and other conifers, also suggests a change in climate characterized by increased humidity and decrease in temperature. It is established that the appearance of angiosperm pollen in the studied deposits corresponds to the transitional interval between the Hauterivian and Barremian.

*Reviewers N.K. Lebedeva and M.E. Bylinskaya*

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