

ACTA UNIVERSITATIS SZEGEDIENSIS

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# ACTA BIOLOGICA

NOVA SERIES

TOMUS XXV

FASCICULI 1—2

SZEGED (HUNGARIA)  
1979

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Adjuvantibus

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Szerkeszti

**LIPTÁK PÁL**

A szerkesztő bizottság tagjai

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## WIRKUNG DER LUFTVERUNREINIGUNG AUF DIE VERARMUNG DER FLECHTENVEGETATION DER STADT SZEGED UND IHRER UMGEBUNG<sup>1</sup>

L. GALLÉ senior

(Eingegangen am 30. Juni 1978)

### Auszug

Die Luft der Stadt Szeged ist — aufgrund des Benehmens der Flechten als Bioindikatoren — viel reiner als die Luft anderer Städte. Die Schwefeldioxydverunreinigung der Luft zeigt die natürliche saisonmäßige Schwankung und überschreitet den erlaubten Grenzwert (0,15 mg/m<sup>3</sup>) nur in den Wintermonaten.

Zur Verarmung der Flechtenvegetation trägt auch die beschädigende Wirkung des Kohlenmonoxyds, der Bleiverunreinigung, des sich ablagernder Staubs, Rauchs und Russes bedeutend bei.

Epiphytische Flechten können in der Markung der Innenstadt nicht mehr gefunden werden. Die ersten Thalli der epiphytischen und epixylien Flechtenarten erscheinen ungefähr 4 km weit vom Stadtzentrum.

Die auf eine alkalische Unterlage angesiedelten epilithischen Flechtenarten dringen tief in die sogenannt „epiphytische Flechtenwüste“ hinein und assoziieren sich in den *Caloplacetum murorum*, *Lecanoretum albomarginatae* und *Caloplacetum citrinae* Zönosen.

### Einleitung

Die epiphytische Flechtenvegetation verarmt schnell um die industriellen Anlagen und Großstädte. Es wurde nachgewiesen, daß die Verunreinigung saurerer Reaktion, besonders der Schwefeldioxydgehalt der Luft bestimmend für die Verarmung der Flechtenvegetation ist. Es verschwinden zahlreiche Arten innerhalb des das Stadtzentrum und die industriellen verunreinigenden Herde umgebenden, bestimmbaren Umkreises. Diese Feststellung wird auch durch die in der Weltliteratur erscheinenden zahlreichen Mitteilungen unterstützt. Es wird aus ihren Untersuchungen klar, daß die Flechten — als Bioindikatoren — sehr empfindliche Test-Pflanzen und zusammen mit den Moosen die ersten Opfer der Luftverunreinigung sind.

### Kurze Geschichte der heimatlichen Forschung

Mit der auf die Flechten ausgeübten Wirkung der Luftverunreinigung der Städte hat sich — zahlreichen ausländischen Verfassern vorangehend — in diesem Land zuerst L. FELFÖLDY (1942) beschäftigt, der die auf die epiphytische Flechtenvegetation ausgeübte Wirkung der Stadtluft von Debrecen geprüft hat. Seine Pionierabhandlung wurde von den semipopularischen Publikationen von A. BOROS—

<sup>1</sup> Mit der Unterstützung des Ausschusses der Ungarischen Akademie der Wissenschaften in Szeged verfertigte Abhandlung.





### Hauptfaktoren der Luftverunreinigung

Mit der intensiven Industrialisierung und Urbanisierung haben sich die luftverunreinigenden Stoffe in den letzten Jahrzehnten sehr vermehrt. Die Feuerungstätigkeit der Industriewerke, des Verkehrs, die Einrichtungen und der Kleinhaushalte bringt ung. 20 verschiedene Stoffe festen und gasförmigen Aggregatzustandes in die Luft. Die Menge des Kohlendioxyds, Kohlenmonoxyds, Schwefeldioxyds, Schwefelwasserstoffs, Chlors, Fluors, der Schwermetalle (Quecksilbers und Bleis), der Stickstoffoxyde, der verschiedenen Kohlenwasserstoffe (z. B. 3,4-Benzpyren), des Staubs, Rauchs und Russes vermehrt sich mehr und mehr.

Die auf die Pflanzen ausgeübte Wirkung der die Atmosphäre verunreinigenden Verbindungen ist wohl bekannt. Es fallen in der Umgebung der die Luft verunreinigenden Herde selbst für die Unsachverständigen die welkenden Bäume dünner Kronen, die siechenden krautartigen Pflanzen auf. Aber die Schädigung, die von den weniger auffälligen Mitgliedern der Pflanzenwelt, den Flechten erlitten wird, wird nur von den Fachleuten wahrgenommen.

Die Forscher haben in kurzer Zeit herausgefunden, daß der Luftverunreinigung zufolge zuerst die Flechten Schaden erleiden, die wegen des Aufbaus ihrer Körper überhaupt nicht oder nur in sehr geringem Maße instande sind, sich gegen die in den Flechtenthallus eindringenden, die Photosynthese hindernden oder sie völlig blockierenden Gase giftiger Wirkung zu verteidigen.

Während in einer gesunder Atmosphäre, in Wäldern, in den Arboreten und Friedhöfen reiner Luft oder den Wegen kleineren Verkehrs entlang, an den Baumstämmen immer Flechtenthalli gefunden werden, ist an den Baumrinden der rauchigen Industrieanlagen und der dicht bewohnten Großstädte keine Spur von diesen zu finden (epiphytische Flechtenwüste).

Um festzustellen, welche diejenigen verunreinigenden Verbindungen seien, die die Beschädigung der epiphytischen Flechten in so großem Maße herbeiführen, wurden in Europa und den Großstädten der Welt in Plang emäß aufgestellten Beobachtungsstellen genaue Messungen ausgeführt. Es geschahen auf den Gebieten von Holland, dem Vereinigtem Königreich, den Vereinigten Staaten, Kanada, Frankreich, der Bundesrepublik Deutschland, Österreich, der Estnischen Sozialistischen Republik ebenso Messungen solcher Richtung, wie bei uns in Budapest, bzw. in unserer Stadt Szeged.

Es wurde aus den Messungen klar, daß aus den schon erwähnten 20 verunreinigenden Stoffen die größte Schädigung die Stoffe saurerer Reaktion und das Schwefeldioxyd verursachen. Die letztere Verbindung gasförmigen Aggregatzustandes vereinigt sich mit dem Niederschlagwasser und mit dem in den hygroskopischen Thalluskörper der Flechten absorbierten Wasser in eine Verbindung ebenfalls saurerer Reaktion schwefelige Säure ( $H_2SO_3$ ) und übt in dieser Form ihre beschädigende Wirkung aus. Außer dem Schwefeldioxyd haben auch das Kohlenmonoxyd, die als Verbrennungsprodukte der Explosionsmotoren in die Luft geratenden Bleiverbindungen, das 3,4-Benzpyren und der sich ablagernde Staub eine bedeutende Rolle.

Das Hauptgewicht wurde auch in Verhältnis von Szeged auf das Messen dieser Verunreinigungsstoffe gelegt. Die Messungen wurden von den Mitarbeitern der Station des Gesundheits- und Seuchenbekämpfungsdienstes und des Medizinisch-biologischen Instituts der Medizinischen Universität ausgeführt.



Ihre Hauptergebnisse sind die Folgenden: Kohlenmonoxyd (CO).

Das in die Luft geratende Kohlenmonoxyd stammt in erster Reihe von den Auspuffgasen der Explosionsmotoren, in kleinerem Maß von der unrichtigen Inbetriebhaltung der Haushaltsheizvorrichtungen. Die Mitarbeiter des Medizinbiologischen Instituts haben in den Jahren 1974–1975 den Kohlendioxydgehalt der Luft täglich dreimal, am Morgen zwischen 7 und 8, am Mittag zwischen 13 und 14 und am Abend zwischen 16 und 17 Uhren gemessen. Ihre Beobachtungsstellen waren bei der Kreuzung der verkehrsreichen Kossuth Lajos-Straße und der Pariser Ringstraße, an den vier Ecken der Kreuzung der Straßen. Ihre Messungen wurden mit Drägers Gasprüfer ausgeführt. Die erste Messungsperiode fiel zwischen 18 und 21 November, die zweite zwischen 26 und 28 November, die dritte zwischen 23 und 25 März und schließlich die vierte zwischen 13 und 16 Juli. Die Messungen sind also im Frühling, im Sommer und in den spätherbstlichen Monaten geschehen. Bei den Beobachtungsstellen war der durchschnittliche Fahrzeugverkehr ungefähr 1000 Einheiten pro Stunde.

Der Kohlenmonoxydgehalt der Luft war in der ersten Messungsperiode 25–38 mg/m<sup>3</sup>, in der zweiten Periode 10–19 mg/m<sup>3</sup>, in den dritten und vierten Perioden 6–19 mg/m<sup>3</sup>.

Es ist natürlich, daß entlang erwähnten Fahrstraßen die epiphytischen Flechten und auf den Dachziegeln die epilithischen Flechtenarten vollkommen ausgerottet wurden. Schwefeldioxyd (SO<sub>2</sub>).

Von den gasartigen Schmutzstoffen ist zur Kontrolle der Luftreinheit das Schwefeldioxyd das geeignetste und kann auch als ein Indikator benützt werden, weil seine Bildung nur vom Schwefelgehalt der benutzten Brennstoffe abhängt und weil seine Lebensdauer in der Luft von ihrer Feuchtigkeitsgrad abhängig mehrere Stunden und auch einige Tage lang sein kann.

Es wird von auf dicht bewohnten Gebieten gemessenen Angaben erwiesen, daß das Übergehen zur Gasheizung eine bedeutende Änderung in Schwefeldioxydgehalt der Luft hervorbringen kann. Dies ist die Lage auch auf dem Széchenyi Platz, wo der in 1967 gemessene auf 21,4 mg S/100 h bezügliche Gesamtschwefelwert in 1971 auf 5 mg S/100 h, d. h. tief unter den zulässigen Grenzwert gesunken ist. Dann konnte wiederholt ein langsamer Aufstieg beobachtet werden, so war z. B. in 1975 der Gesamtwert 7,4 mg S/100 h.

Aus diesen Werten gerechnet, war die durchschnittliche Schwefeldioxydkonzentration von Szeged in 1975 und 1976 0,05 mg/m<sup>3</sup>, im Unterschied zu dem für die Luft der geschützten Städte zulässigen 0,15 mg/m<sup>3</sup> Wert. Dieser Wert wechselte sich bei den herausgehobenen Meßpunkten (Széchenyi Platz, Wiener Ringstraße) zwischen 0,03 und 0,08 mg/m<sup>3</sup>, während in Újszeged ein Schwefeldioxydgehalt von 0,01–0,03 mg/m<sup>3</sup> beobachtet werden konnte.

Es ist wohl zu merken, daß die Menge des Schwefeldioxyds und des Gesamtschwefels in den niederschlagsreicheren Spätherbst-, Winter- und Frühlingsmonaten, als auch die Heizung erhöhteren Grades ist, höher als in den Sommermonaten ist.

Die Schwefeldioxydverunreinigung der Luft unserer Stadt ist also niedrig, sie ist hinter der Schwefeldioxydbelastung der Städte mit großen industriellen Anlagen weit rückgeblieben. Die Gründe davon sind unter anderen die Folgenden:

- a) Es gibt in unserer Stadt keine Schwefeldioxydquelle industriellen Charakters.
- b) Die bessere Durchlüftung der Stadt wird durch breite Straßen und Plätze gesichert.



c) Die Wohnungen und Einrichtungen gehen mehr und mehr von der Kohlen- und Ölheizung auf die Gasheizung über.

Es gestaltete sich dennoch auch in Szeged die sog. „epiphytische Flechtenwüste“, was zeigt, daß die Flechten selbst diese, für die menschlichen und tierischen Organismen weniger schädliche Schwefeldioxydquantität nicht ertragen können. 3,4-Benzopyren ( $C_{20}H_{12}$ )

In Verbindung mit der Luftverunreinigung ist die Ausmerksamkeit der Forscher von dem polyzyklischen Kohlenwasserstoffen auf das 3,4-Benzopyren gerichtet, das beinahe in der Luft allerstädtischen Siedlungen zu finden ist. Die Verunreinigung der Atmosphäre durch 3,4-Benzopyren wurde teils aufgrund der Schneemuster, teils der auf das Straßenpflaster angeladenen Staubmuster geprüft und mit einer modifizierten schichtchromatographischen System bestimmt.

Die Muster wurden von elf verschiedenen Stellen ausgenommen und in den Sommermonaten in gleicher Weise gesammelt.

Die konzentrierteste Verunreinigung wurde in der Umgebung des Autobusbahnhofes gefunden, und zwar im Winter in einer Quantität von  $4,2 \mu\text{g}/1 \text{ gr}$  Staub, im Sommer von  $3,85 \mu\text{g}/1 \text{ gr}$  Staub. Um den Personenbahnhof im Indóház Platz und auf dem Weg E/5 wurde eine dem  $2 \mu\text{g}/1 \text{ gr}$  entsprechende Konzentration gefunden. Auf dem Dom-Platz, in den äußeren Sektoren der Radialstraßen und in der Nähe der industriellen Betriebe wurde, hauptsächlich in der Winterperiode, der 3,4-Benzopyregehalt des Staubs ungefähr  $1 \mu\text{g}/1 \text{ gr}$  zu sein gefunden. Im Volkspark in Újszeged und auf dem Gebiet des Bezirks Tarjánváros wurde, bei der Gelegenheit von Wintermessungen, ein noch niedrigerer Konzentrationswert unter  $0,5 \mu\text{g}/1 \text{ gr}$  erhalten.

Der Ruß mit einem 3,4-Benzopyregehalt setzt sich von den Rauchfängen unmittelbar auf die Dachziegel an und bildet einen dunklen, teerartigen Überzug. Auf dem Gebiet der Innenstadt sind demzufolge auch die epilithischen Flechtenarten von den Dachziegeln verschwunden. Auf den Radialstraßen aber, schreitend aus dem Stadtzentrum hinaus, und in den Vororten auf den Dächern der kleineren, niedrigeren Häuser, selbst innerhalb des Runddammes, können den Verunreinigungen widerstandsfähigere epilithische Flechtenarten, so wie *Squamaria albomarginata*, *Caloplaca (Blast.) teicholyta*, *Lecanora albescens*, *L. dispersa*, *Verrucaria nigrescens* gefunden werden. Zu diesen assoziieren sich auf den Hausdächern außerhalb des Runddammes auch *Physcia vainioi* und *Lecidea fuscoatra* f. *regularis*.

### Bleiverunreinigung

Der zunehmende Kraftfahrzeugverkehr bringt außer dem Kohlenmonoxyd auch eine bedeutende Menge von Stickstoffgasen und Bleioxyd in die Luft. Dieser letztere Schmutzstoff entsteht durch die Oxydation des mit dem Benzin gemischten Bleitetraäthyl ( $Pb/C_2H_5/4$ ). An der Bleiverunreinigung leiden nicht nur die Kryptogampflanzen, sondern auch die Phanerogampflanzen entwickelterer Konstitution. Bei Laubfall häuft sich auch in den Blättern der Bäume und in dem vermahlten Rhytidom eine bedeutende Menge der Bleiverbindungen auf, die weder die Kryptogampflanzen noch die Blütenpflanzen aus ihren Organismen eliminieren können.

In Szeged wurden betreffs der Bleiverunreinigung der Luft bisher noch keine Messungen ausgeführt, es ist aber offenbar, daß dem zunehmenden Kraftwagenverkehr zufolge die Bleiverunreinigung der Luft in der Stadt bald schon zu einem bedeutenden Faktor wird. Im Medizinbiologischen Institut (KISZELY et al., 1977)

wurde die als Berufsbeschädigung auftretende Bleibelastung des menschlichen Organismus geprüft und es wurde festgestellt, daß die Bleibelastung der kontrollierten Werktätigen nur kleinen Maßes ist. Die Verhütung und Ablenkung stellen die Sani-tätsorgane noch vor keine größere Aufgaben.

Ein Übertritt zur Benützung des bleifreien Benzins würde die gegenwärtige Lage sehr verbessern.

Der Schutz der landwirtschaftlich utlilisierten Gebiete, hauptsächlich der Obstgärten könnte durch eine entlang den verkehrsreichen Wegen, von diesen 5 m weit gelegte lebende Hecke praktisch gelöst werden.

### Der abgelagerte Staub

Die epiphytischen Flechten ertragen die Staubigkeit schwer. Aber auch die empfindlicheren epilithischen Flechtenarten werden beschädigt.

Messungen des sich absetzenden Staubes wurden sowohl vom Medizinisch-Biologischen Institut als auch von der Station des Gesundheits- und Seuchenbekämpfungsdienstes seit Jahren ausgeführt. Es wurde aus ihren Messungen bekannt, daß die Lage der Staubverunreinigung in unserer Stadt bei weitem nicht so günstig ist, als z. B. im Falle des Schwefeldioxyds. Im Stadtzentrum, in Széchenyi Platz, in 1966, war das Maß der Staubigkeit  $5,0 \text{ gr/m}^3$ . Dies erhöhte sich in 1975 auf den Durchschnittswert  $20,1 \text{ gr/m}^3$ . In 1976 folgte eine kleinere Abnahme auf  $17,9 \text{ gr/m}^3$  Wert.

Der höhere Wert in 1975 kann damit erklärt werden, daß auf dem Platz Auto-bushaltestellen, Kraftwagenparkplätze angelegt wurden und auf dem Platz und in der Umgebung Gebäudeabriß- und Überholungsarbeiten begonnen.

Die Staubbelastung von Újszeged ist ein wenig besser. Sie war in 1975  $15,7 \text{ gr/m}^3$ , in 1976  $16,5 \text{ gr/m}^3$ . Aber auch diese Werte überholen die für die geschützte Stadtluft zulässige  $12,5 \text{ gr/m}^3$  Konzentration.

### Verarmung der Flechtenvegetation

Die in dem vorigen Abschnitt dargelegte Verunreinigungslage ist erst in den letzten Jahrzehnten eingetreten. Diese Feststellung wird durch die auf dem Gebiet der Stadt seit den 1920-er Jahren, also 50 Jahre lang, beobachteten Veränderungen der Flechtenvegetation, namentlich durch die stufenweise eintretende qualitative Schädigung der Flechtenvegetation und ihrer quantitativen Verhältnisse unterstützt.

Ich habe die Gestaltung der Anzahl der Flechtenarten auf dem Gebiet der Stadt von den 1920-er Jahren ab aufgrund der Publikationen der in der Einleitung schon erwähnten Verfasser und meiner eigenen Beobachtungen in einer Tabelle zusammengefaßt. In der Tabelle habe ich die auf das am rechten Ufer der Tisza liegende, dicht eingebaute, urbanisierte Gebiet und die auf den, auch den Stadtpark enthaltenden, Stadtteil Újszeged (der heute noch größtenteils einen Gartenstadtscharakter hat) bezüglichen Angaben getrennt dargestellt. Daß Mas der zu den einzelnen Perioden ins Verhältnis gestellten Abnahme wurde in prozentualen Werten gegeben.



Tabelle 1. Gestaltung der Anzahl der Flechtenarten zwischen den 1920-er und 1980-er Jahren

Fundort  Zeitpunkt des Vorkommens	Szeged				Újszeged			
	Anzahl der							
	epigae	epilith	epi- phy- ton	epixyl	epigae	epilith	epi- phy- ton	epixyl
	Flechtenarten							
1920-1940	5	37	5	6	5	14	25	13
1940-1970	3	24	2	5	3	10	14	7
Maß der Abnahme im Verhältnis zur vorigen Periode	40%	35,1%	60%	16,7%	40%	28,6%	44%	46,2%
1970-1980	1	22	0	5	2	8	11	6
Maß der Abnahme im Verhältnis zur ersten Periode	80%	40,5%	100%	16,7%	60%	42,9%	56%	53,8%

Die Tabelle — aufgrund der im ersten Abschnitt besprochenen Meßergebnisse — veranschaulicht wohl die selektierende und schädigende Wirkung der luftverunreinigenden Stoffe. Diese Schädigung ist besonders in Hinsicht der epiphytischen Flechtenarten auffallend, die von den innerhalb des Runddammes befindlichen Gebieten von Szeged vollkommen fehlen. Die stufenweise Abnahme kann aber auch bei den epigäischen, epilithischen und epixylen Flechtenarten beobachtet werden.

Diese auch in prozentuellem Wert gut ausdrückbaren Änderungen lassen sich natürlich nicht mit der schädigenden oder vernichtenden Wirkung eines oder anderes herausgegriffenen Faktors erklären, sondern sie sind als eine komplexe Wirkung aller bekannten Faktoren aufzufassen.

Die allerersten Opfer der Luft- und Umweltverunreinigung sind, wie schon erwähnt, die Flechten. Diese zeigen in unseren Tagen selbst in der verhältnismäßig reineren Luft des Gebietes von Újszeged eine 56%-ige Abnahme, im Verhältnis zu den 1920-er Jahren. Die Gründe davon sind bei der Theißbrücke und entlang den verkehrsreichen Straßen in der beträchtlichen Immittierung des Kohlenmonoxyds und Bleioxyde zu suchen. Es können aber bei diesem auch die Veralterung der Baumstämme im Volkspark und die mit der Zusammenneigung der Laubkrone gesteigerte Überschattung der Stämme und in den kleinen Obstgärten die Kratzung der Borke, bzw. die beharrliche Anwendung der Spritzmittel mitspielen. Es wäre eine einzige dieser Faktoren genug, um die epiphytische Flechtenvegetation zu vermindern. Ihre komplexe Wirkung aber hat die volle Vernichtung zur Folge.

So sind von den Linden der an der Volksgarten-Allee liegenden Seite des Volksparks die Thalli der *Lecanora carpinea*, *Physcia aipolia* und *Ph. stellaris*, von den

Pappelstämmen in der Umgebung des Spielplatzes die *Xanthoria parietina* und von den Stämmen der Obstbäume die Mitglieder *Physcietum ascendens* Zönose verschwunden.

Es konnten im Friedhof von Újszeged am Ende der 1920-er Jahre selbst noch auch die Thalli *Evernia prunastri* und *Physcia stellaris* gefunden werden. Sie sind aber bis zum Ende der 1960-er Jahre schon verschwunden. Der Grund dieser Erscheinung ist daß der Friedhof zwischen der Landstraße Szeged—Makó und der Eisenbahnlinie Újszeged—Battonya liegt. Die vernichtende Wirkung wurde durch die schon erwähnten Gase und den Staub von der Landstraße und durch den von der Eisenbahnlinie ausströmenden Rauch und Ruß zusammen ausgeübt.

Im einleitenden Teil habe ich schon darauf verwiesen, daß die sog. Oasen der städtischen „Flechtenwüste“ die Friedhöfe sind. Die epiphytischen Flechtenarten fehlten von den innerhalb des Runddammes liegenden Friedhöfen schon in den 1960-er Jahren ebenso, wie aus dem außerhalb des Runddammes, 2–2,5 km vom Stadtzentrum liegenden Innerstädtischen Friedhof. In 1976 aber wurde der Buda-pest—Szeged Kraftwagenverkehr von der Seite der Innerstädtischen Friedhofs mit der Errichtung der Izabelle—Brücke auf die Landstraße zurückgelenkt. Infolgedessen vermindert die auf 1/10 verminderte Immission die Niederlassung und Entwicklung der mehr widerstandsfähigen epiphytischen Arten nicht mehr. Es kann damit erklärt werden, daß die anspruchslosen Krustenflechtenarten der *Lecanoretum carpineae* (*Lecanora carpinea*, *Lecidea elaeochroma*, *L. glomerulosa* und *Physcia tenella*) bis zum Frühling 1978 an dem überirdischen Teil der Lindenbaumstämme des innerstädtischen Röm. Katholischen Friedhöfe, sowie die jungen Thalli der *Physcia tenella* in südlichen Exposition an den *Tilia* Stämmen in dem Reformierten Friedhof erschienen.

Die Anzahl der auf den bearbeiteten Hölzern lebenden, epixylen Flechtenarten ist auch bemerklich kleiner geworden. Dieses Phänomen kann an der Szeged—Seite (Rechtseite der Tisza) mit der Abreißung der Bretterplanken und mit dem Bau der Umfriedungmauern, bzw. mit der Abbrechung der Schindeldächer erklärt werden (anthropogene Wirkung). Dieselbe ist die Ursache der 53,8%-igen Verminderung in den Zahlen der Arten und Individuen auch auf dem Gebiete von Újszeged. Während aber an der Újszegediner Seite um die vom Stadtzentrum weiter liegenden Grundstücken einige mit Flechten bedeckte Bretterplanken, mit *Parmelia sulcata*, *Hypogymnia physodes*, *Lecanora allophana*, *Candelariella vitellina* Arten noch immer zu finden sind, kommt an der Szegediner Seite nurmehr auf den Brettern der in den Friedhöfen gelegten Hartholzbänken die *Lecanoretum albomarginatae* Zönose mit den *Squamaria albomarginata* f. *lignicola*, *Candelariella vitellina*, *Lecanora allophana*, *L. hageni*, *Physcia tenella* und selten mit den *Xanthoria parietina* Arten.

Es sei hier erwähnt, daß von einer der Bretterplanken der Újszegediner Felsökikötösor Straße am Tiszaufer die *Pseudevernia furfuracea* und *Usnea hirta* und von einer der Bretterplanken der Föfasor Straße die in 1929 von hier beschriebene *Pseudevernia furfuracea* f. *rosulata* SZAT. et GALLÉ (locus classicus), deren Typus-exemplare im hiesigen Herbarium bewahrt werden, heute schon fehlen.

Die Verminderung der Artenzahl der epilithischen Flechtenarten überholt heute schon 40% auf dem Gebiet sowohl von Szeged als auch von Újszeged. Die steinbewohnenden (epilithischen) Flechtenarten sind aber weniger empfindlich auf die die Luft verunreinigenden Schmutzstoffe. Der Grund davon ist teils, daß ihre Lager, bzw. ihre Apothezien eng an die Oberfläche des Gesteins oder den für Unterlage



dienenden Dachziegel haften und ihrer waagerechten oder — auf den Hausdächern — gelinde abfälligen Lage zufolge ein größerer Schutz für sie durch die Winterschneedecke eben in der Periode gesichert wird, als die Verunreinigung durch das Schwefeldioxyd größten Maßes ist. Es ist also verständlich, daß die epilithischen Flechtenarten in die „Flechtenwüste“ der Stadt tief hineindringen.

Die in der Tabelle 2. befindlichen Flechtenzönosen und ihre Fundorte:

1. *Verrucarietum nigrescentis* (KAISER) GALLÉ — Auf der Ziegelbedeckung der nach Norden liegenden Böschung des Runddammabschnittes bei der Petöfi-Siedlung.
2. *Verrucarietum nigrescentis* (KAISER) GALLÉ — Auf dem waagerechten Grabdecke eines der Grabdenkmäler des Innerstädtischen Friedhofs.
3. *Caloplacetum murorum* (DU RIETZ) KAISER — Auf dem Ziegelpflaster der nach Nord-Westen liegenden Böschung des Runddammes bei der Stadtteil Rókus.
4. *Caloplacetum murorum* (DU RIETZ) KAISER — Auf dem waagerechten Grabdecke eines der aus Beton gemachten Grabdenkmäler des Innerstädtischen Friedhofs.
5. *Caloplacetum murorum* (DU RIETZ) KAISER — Auf der nach Nordosten liegenden, aus Beton gemachten Oberfläche eines der Grabdenkmäler des Rókus-Friedhofs.
6. *Caloplacetum murorum* (DU RIETZ) KAISER — Auf der waagerechten Grabdecke eines der aus Beton gemachten Grabdenkmäler des Dugonics-Friedhofs der Oberstadt.
7. *Caloplacetum citrinae* (GALLÉ) BESCHEL — Auf der Kalkmörteldecke der Gartenmauer des Altersheimes in der Petöfi-Siedlung.
8. *Caloplacetum citrinae* (GALLÉ) BESCHEL — In Újszeged, auf dem Kalkmörteldecke der nach Nordwesten liegenden Gartenmauer eines der Grundstücke der Felsökikötösor Straße.
9. *Lecanoretum albomarginatae* (KAISER) GALLÉ — Auf der aus einem waagerechten Beton gemachten Grabdecke eines der Grabdenkmäler des Innerstädtischen Friedhofs.
10. *Lecanoretum albomarginatae* (KAISER) GALLÉ — Auf der aus einem ähnlichen Stoff gemachten Grabdecke ähnlicher Lage des Unterstädtischen Friedhofs.
11. *Lecanoretum albomarginatae* (KAISER) GALLÉ — Auf dem aus Schiefer gemachten, nach Norden liegenden Dache der Werkhalle der Seilerei im äußeren Abschnitt der Tolbuchin Radialstraße.
12. Auf dem mit Ziegeln bedeckten, nach Süden liegenden Dachteil des Gärtnerhauses, Bajai Straße 8.

In die Tabelle 2 wurden die auf dem Gebiet der Stadt in den 1960-er Jahren beobachteten epilithischen Flechtenarten aufgenommen. Die Fundstellen, Exposition, Unterlagen, der prozentuale Wert der in den bezeichneten Zeitpunkten beobachteten Deckung sind gegeben. Die aufgezählten Arten gehören zu den *Verrucarietum nigrescentis*, *Caloplacetum murorum*, *Caloplacetum citrinae* und *Lecanoretum albomarginatae* Zönosen. Zur Unterlage dienten die Ziegelbedeckung des Runddammes, der Kalkmörtelüberzug der Gebäude, der Ziegelmauern, die Dachziegel, die aus Beton bzw. Dolomitsplitt gemachten Grabdecken und Grabdenkmäler.

Die Flechtenvegetation des zu Hochwasserschutz zwecken dienenden Runddammes habe ich in zwei Aufsätzen (Gallé, 1939 und 1973) schon bekanntgemacht. Ich habe auch eine sich mit der Flechtenvegetation der Friedhöfe beschäftigende Ab-





handlung (GALLÉ, 1970) publiziert. Ich bespreche diese Fundorte deshalb nur tangentiell.

Ich habe die Flechtenvegetation des Runddammes im April 1978 neulich kontrolliert. Das Verderben der Flechtenvegetation ist im nördlichen Abschnitt bei dem Bezirk Tarján város das Höchstgradige, wo sich die Wirkung der Urbanisation von nahe und unmittelbar durchsetzt. In diesem Abschnitt können die am Ende der 1930-er Jahre noch so auffallenden, ung. ein Quadratmeter großen, gelben Ziegeloberflächen, deren Farbe durch die in einem großen Deckungsgrad ( $D=4-5$ ) erscheinenden *Caloplaca* (Gasp.) *murorum*, *Cal.* (Gasp.) *decipiens*, *C. citrina* und *Candelariella aurella* Thalli geliefert wurde, nicht mehr gefunden werden. Die aufgezählten Flechtenarten bestehen auch heute irgendwo, aber sie kommen unter den grauen *Lecanora albescens*, *Caloplaca* (Blast.) *teicholyta* und *Squamaria albomarginata* Thalli nur in einer verschwindend kleiner Quantität ( $(D=+-1)$ ) vor. Die Flechtenvegetation des Rókus-Abschnittes ist auch in ähnlicher Weise verdorben. Der originelle Zustand wurde am besten von dem Abschnitt westlicher Exposition der Tolbuchin Straße bewahrt.

Die epilithische Flechtenvegetation der Friedhöfe hat sich im Vergleich zu den 1960-er Jahren qualitativ kaum geändert. Nach einer eifrigen Forschung waren alle die publizierten Flechtenarten (GALLÉ, 1970) zu finden. Der Unterschied ist in den quantitativen Verhältnissen. Die einzelnen Zönosen erschienen, wie dies auch aus den Tabellen zu sehen ist, dem in den 1960-er Jahren beobachteten 30—70-prozentigen Deckungsgrad gegenüber, in 1978 nurmehr mit 10—40-prozentiger Deckung. Die Zunahme der einzelnen Thalli such hat ein langsames Tempo. Die Thallusränder sind noch intakt genug, aber z. B. bei der *Squamaria albomarginata* erscheinen zahlreiche in der Mitte verderbende Thalli (thallus centrifugus). Die photosynthetische Rate der einzelnen Arten auch vermindert sich, was durch die zahlreichen beschädigten gonidia gezeigt wird.

Die Lage der epilithischen Flechtenvegetation innerhalb unserer Stadt wird von den auf den Ziegel-, bzw. Schieferdächern der Häuser lebenden Flechten wohl abgespiegelt. Ich habe diese zehn Jahre lang, zwischen 1968 und 1978 untersucht. Ich habe meine Beobachtungen im Stadtzentrum begonnen und stufenweise nach außen fortschreitend, in den Vororten beendet.

Den Ziegelstoff des Dachwerks der hohen Häuser der Innenstadt habe ich verhältnismäßig leicht erreicht: ich habe den zerstörten Ziegelstoff der demolierten Häuser geprüft. Den Dächern der vorstädtischen niedriger Gebäude habe ich mit Hilfe einer Leiter genähert. So habe ich einen verhältnismäßig sehr guten Vergleichungsstoff erhalten.

Aufgrund der Prüfung von mehr als ein tausend Dachziegeln sind meine Ergebnisse die Folgenden.

Die Flechtenvegetation der Ziegeldächer der hohen Häuser der Innenstadt von Szeged wurde völlig vernichtet als das Ergebnis der Rauchbeschädigung. Auf den Ziegeln, die mit einem dunklen teerartigen Stoff gleichmäßig bedeckt sind, können keine Flechtenthalli mehr gefunden werden. Das 3,4-Benzpyren und die teerige Belegung des darin steckengebliebenen abgelagerten Staubs haben die Lebensbedingungen sowohl der Flechten als auch der Dachmoose vernichtet.

Vom Stadtzentrum nach Süden fortschreitend, auf den jüngstens noch nicht erneuerten Ziegeldächern der Privathäuser der sog. Unterstadt, ung. 2 Km weit vom Zentrum, beginnen die Mitglieder der *Verrucarietum nigrescentis* Flechten-

zönose: *Verrucaria nigrescens*, *Staurothele catalepta*, *Lecanora dispersa*, *L. albescens*, *Candelariella aurella* ( $D = + - 1$ ) zu erscheinen. Nach Westen, gleichfalls 2 Km weit, auf der nördlichen Neigung des Schieferdachs der Seilerei dringt die *Squamarium albomarginatae* Zönose in die epiphytische Flechtenwüste ein. Hier kommen außer den Charakterarten die *Lecanora albescens*, *L. dispersa*, *L. crenulata*, *L. hageni* v. *lithophila*, *Lecania erysibe*, *Caloplaca* (*Blast.*) *teicholyta*, *Candelariella aurella*, *Verrucaria nigrescens*, *Caloplaca* (*Gasp.*) *decepiens* Arten vor, annähernd in einer 20% Deckung ( $D = + - 3$ ).

Nach Süden weitergehend, außerhalb des Runddammes, ung. 1,5 Km weit davon, auf den Dachziegeln eines zu einem der äußersten Häuser der Ságvári-Siedlung gehörigen 50 Jahre alten Gartengebäudes, in westlicher Exposition, wurde Anfang September, um elf Uhr vormittags, bei 7 000 lux Lichtstärke, eine reichentwickelte *Caloplacetum murorum* Zönose mit den folgenden Arten gefunden: *Caloplaca* (*Gasp.*) *decepiens* ( $D = + - 2$ ), *Lecanora albescens* ( $+ - 1$ ), *L. dispersa* ( $+ - 1$ ), *L. crenulata* ( $+ - 1$ ), *Verrucaria nigrescens* ( $+ - 1$ ), *Staurothele catalepta* ( $+ - 1$ ), *Candelariella vitellina* f. *arcuata* (3-5), *Caloplaca* (*Blast.*) *teicholyta* (1-3), *Squamaria muralis* (1-2) und *Acarospora fuscata* ( $+ - 1$ ).

Ich habe in westlicher Richtung, ebenfalls außerhalb des Runddammes, dem Reformierten Friedhof gegenüber, ung. 3,5 Km weit vom Stadtzentrum, auf einem Ziegeldach südlicher Exposition eines Gärtnerhauses, im Spätapril, um 15 Uhr nachmittags, bei 8 000 lux Lichtstärke, eine auch, noch schöner als die Vorige, entwickelte *Squamarium albomarginatae* Zönose gefunden, die noch reicher entwickelt war als die von Schieferdach der Tolbuchin Radialstraße beschriebene Flechtengesellschaft. Die Flechtenläger waren wohlentwickelt, gesund, wachsend, fruchtbringend, der Deckungsgrad war ung. 20%. Hier, dem Fundort in der Tolbuchin Radialstraße gegenüber, kommen auch *Candelariella vitellina* ( $D = + - 1$ ), *Lecanora hageni lithophila* (+), *Physcia vainioi* (2-3) und *Lecidea fuscoatra* f. *tegularis* (1-2) Thalli vor. Ung 4 Km fern von Stadtzentrum leben also die steibewohnenden Flechten in einem Zustand ohne Schädigung. Die qualitative Zusammensetzung und die quantitativen Parameter der Gesellschaften entsprechen auch dem normalen Zustand.

Die Flechten zeigen, sich vom Stadtzentrum entfernend, schon selbst in dieser verhältnismäßig kleiner Entfernung, der Unterschied der Reinheit der Luft zwischen den Innen- und Außenbezirken.

Die Stufen der Poleotoleranz der epiphytischen Flechtenarten wurden in Hinsicht mehrerer Städte festgestellt. In Kenntnis der Umstände in Szeged, habe ich eine ähnliche Skala der epilithischen Arten zusammengestellt. Dies wird in der folgenden Aufstellung dargelegt:

Die Toxikotoleranz nimmt ab	↑	<i>Physcia vainioi</i> <i>Gasparrinia murorum</i> <i>(Caloplaca citrina)</i> <i>Candelariella aurella</i> <i>Lecanora albescens</i> <i>Lecanora dispersa</i> <i>Lecanora crenulata</i> <i>Verrucaria nigrescens</i> <i>Caloplaca (Blast.) teicholyta</i> <i>Squamaria albomarginata</i>	↓	Die Toxikotoleranz nimmt zu
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## POLYPHYLETIC ORIGIN OF ANGIOSPERMS IN THE LIGHT OF XYLOTOMY

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### Abstract

The author considers, contrary to Takhtajan's theory of monophyletic origin, that a polyphyletic origin of the Angiosperms is more probable, and wants to support his opinion by xylotomy of the homoxylous *Drymis*, comparing it with a *Juniperus* and a *Magnolia*. As *Drymis* has only tracheids with simple pits and is without vessels, while in the Magnoliales vessels occur, and as the tracheidic state is more primitive than the vessel-containing one, the homoxylous trees could therefore, not originate from Magnoliales.

It is not only today that the author asserts the polyphyletic origin of Angiosperms, he also did this sixty years ago.

### Introduction

According to the system of the prominent Soviet phylogeneticist, TAKHTAJAN, 32 families belong to the order Magnoliales, comprising 165 genera and approximately 700 species. Approximately 45,000 photomicrographs of sections from 16,000 samples of these trees were made by H. GOTTWALD of Hamburg, the Director of the Institute for Wood Research, in order to decide whether the development and relationship of Angiospermae could be ascertained on a xylotomic basis and whether the primitive type is represented by the *Magnoliales* with the other angiosperms — including *Monocotyledons* — descended from the that is to say whether these were the older, i.e. the more primitive angiosperms. H. GOTTWALD rendered an account of his work in a particular monograph (Plant. Syst. Evol. Suppl. pp. 111–121, 1977), delivered also at the International Symposium of Botanical Taxonomists. He has sent a reprint of this with a covering letter to the author. In this he writes: "Es geht hierbei um die von TAKHTAJAN wiederholte — aber nicht von den Systematikern geteilte Auffassung — dass alle lebenden höheren Pflanzen von den Magnoliales abzuleiten sind. Nach xylotomischen Merkmalen ist dies nicht vertretbar, da es außerhalb der *Magnoleales* noch primitivere Familien gibt, wie z. B. die *Hetoxicaeae*, *Dilleniaceae* u. a., die außerdem ein so differenziertes Strukturbild aufweisen, daß diese *unmöglich* (*italics added*: P. G.) aus den *Magnoliales* hervorgegangen sein können".

The author already took a completely similar point of view 60 years earlier (1918) and again in his recently (1955, 1964, 1971, 1979) published papers. (Cf. References). When the author received H. Gottwald's reprint, he took out his old sections and now wants to contribute to throwing new light upon this much discussed questions, adducing newer data, and thoughts among them same xylotomical ones. The direct origin of Angiosperms from Gymnosperms is considered as probable by



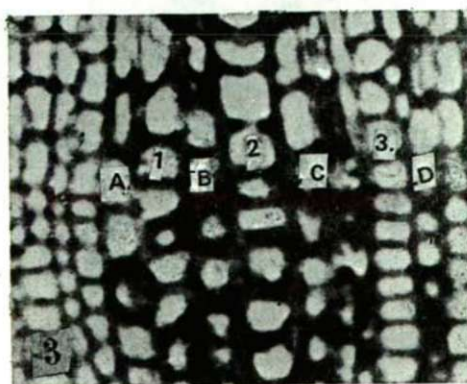
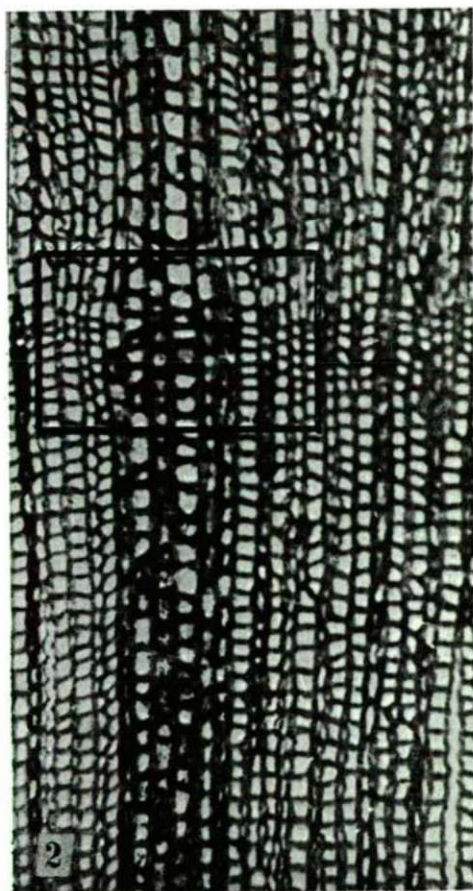
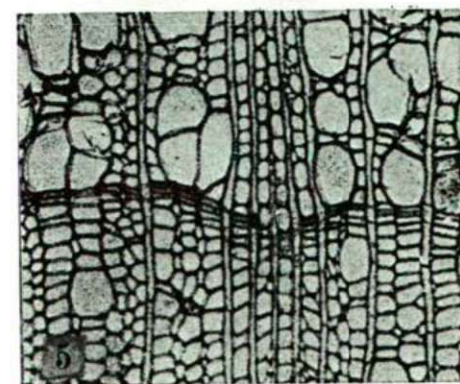
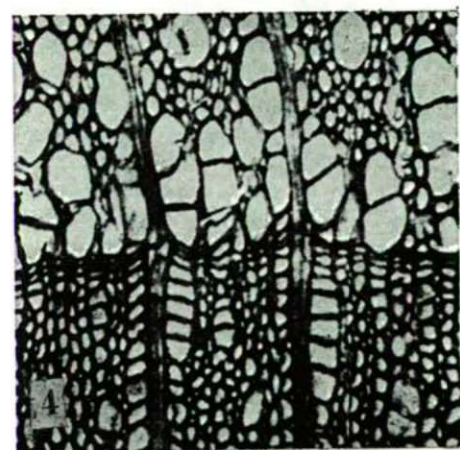
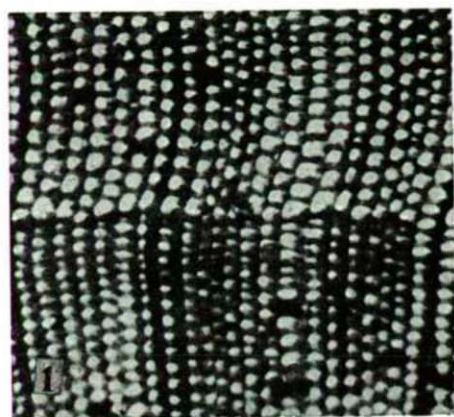
more than one phylogeneticist, e.g. by the Hungarian Soó, the Viennese EHRENDORFER, etc. because there are not known any so-called transitional forms, accepted by everybody, between the extant Angiosperms and Gymnosperms. But taking a closer look at the so-called homoxylic trees (*Drymis*, certain xybotomic characteristics of these will appear to be suitable for establishing likely phylogenetic connections in our opinion, such a xybotomic relationship is revealed Viennese EHRENDORFER, etc., because there are not known any so-called transitional forms, accepted by everybody between the extant Angiosperms and Gymnosperms. But taking a closer look at the so-called homoxylic trees (*Drymis*, *Tetracentron*, *Trochodendron*) from among the Angiosperms, certain xybotomic characteristics of these will appear to be suitable for establishing likely phylogenetic connections in our opinion, such a xybotomic relationship is revealed for instance by the tropical *Drymis winteri*, on the one hand with the Gymnosperms, more precisely the Conifers and on the other hand with the heteroxylic dicotyledonous *Magnolia acuminata*, and other *Angiosperms*. In order to be deliberate this question, we considered it desirable to compare with one another the xybotomies of a Conifer (*Juniperus macropoda*), a homoxylic tree (*Drymis winteri*) and a heteroxylic dicotyledon (*Magnolia acuminata*), reporting on the conclusion drawn from these.

However, in comparing the secondary xylem of homoxylic trees we have to think, in addition to the Conifers, of the Cycadaceae, also from among the Gymnosperms, and the Monocotyledons, more exactly the Arecaceae from the Angiosperms. These trees have, however, a quite different tissue structure. The Cycadaceae have, a very voluminous pith and a mono- or multilayer (monoxylic, polyxylic) xylem and pith ray. The palms, however, have scattered vascular bundles but without definite pith rays. The comparison of them, with homoxylic trees would, therefore, be known in advance to be useless and thus it cannot come into consideration in ascertaining the relationship. This seems, on the other hand, to confirm that among the present-day Angiosperms and the Gymnosperms several maintypes are living, or have lived, which are anatomically quite different and of different origin. They are, therefore, both of polyphyletic descent. The author wants to support the correctness of a comparison like this — separately from the genetic arguments in one (1979) of his latest papers — in the following, with some xybotomic arguments and photographs, on the basis of transverse, tangential and radial sections of trunks.

- Plate 1. Photograph 1. Cross-section of *Juniperus macropoda*, with annual-ring boundary and scanty parenchyma cells; no vessels. (x75).  
 Photograph 2. Cross-section of *Drymis winteri*. On the left, there is an aggregate pith ray; no vessels. (x70).  
 Photograph 3. Detail of photograph 2. Figures indicate the tracheids, lettersthe pith rays. (x130).  
 Photograph 4. *Magnolia acuminata*. Vessels and clusters of vessel occuring at the boundaries of annual rings. The ground substance is: xylem-fibres, wood parenchyma and tracheids. (x200).  
 Photograph 5. Aggregate pith ray of *Alnus glutinosa*, alongside it isolated or grouped vessels. (x150).



Plate 1





### Comparison of transverse sections

Plate 1. Photograph 1 illustrates the structure of a Conifer (*Juniperus macro-poda*) in transverse section. In the xylem, there are only tracheids and very scanty wood parenchymas. The tracheids in cross-section are angular or slightly rounded. As to their size, they are entirely homogeneous, there being small differences only at the boundary of annual rings. At the hardly observable annual-ring boundaries, the tracheids slightly flatten out. The pith rays are generally uniseriate. Multiseriate or aggregate pith rays — except in cases of Conifers with intercellular canals containing resin — do not occur in Conifers.

In the middle of the photograph and on the right side, in the "basic substance", 6 to 8 tracheid bundles seem to be separated a little, together with pith rays. Although this separation is not very distinct, yet the cross-sections of the smaller and larger tracheids make us think that this may possibly be the point of origin of aggregate pith rays. Aggregate pith rays first occur in certain types of the dicotyledonous Amentiflorae (*Alnus*, *Carpinus*, etc.) in which the shorter pith rays of breadth 1-3 are densely arranged, close to one another, and, consequently, there are between them no water conducting (tracheary) elements (Cf. Photograph 5a, x75).

Phot. 2. The structure of *Drymis winteri* in transverse section is generally very similar to that of Coniferae according to the significant observation that the xylem consists here, too, of thick-walled tracheids, rarely of wood fibres, with vessels (and perhaps in this species parenchyma cells, too) completely absent. The broad pith rays consist of short, square pith ray cells. The annual-ring boundary is indicated by slightly flattened tracheid series. On the left of the photograph stretches, a broader so-called aggregate pith ray. These are enclosed by so-called limiting cell series (perhaps primitive transverse tracheids??) which also verifies the heterogeneous structure of the pith ray. The inner pith-ray cells are rather square and much smaller than the tracheid series lying beside them. (Cf. also with Phot. 12) (x70).

Phot. 3 is an detail of phot. 2, in which the pith-ray cells and the tracheid series are seen, at a higher magnification (x130).

Phot. 4. The structure of the heteroxylic *Magnolia acuminata* in transverse section differs fundamentally from the two former tree types in as much as this tree already has vessels and the "basic substance" is filled with tracheids, wood parenchyma, and wood fibres. The vessels, which have large lumina are close to one another in the spring wood and at the boundary of annual rings they form a continuous wood. (tree with porous rings). The vessels in the field of annual rings are solitary or in pairs or groups, sometimes in pore-rays of 6 to 8 members. These three kinds of a new element distinct from former ones seem to make certain the verification of a more recent and higher stage of development (division of labour), i.e. greater perfection (x200).

Plate 2. Photograph 6. Tangential photograph of *Juniperus macro-poda*. The pith rays are uniseriate. No vessels. (x150).

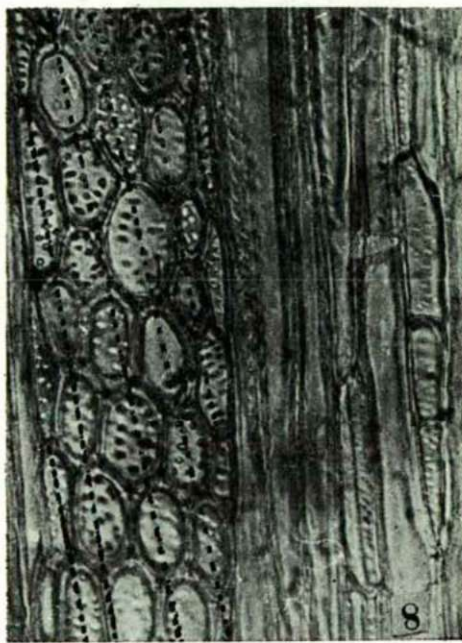
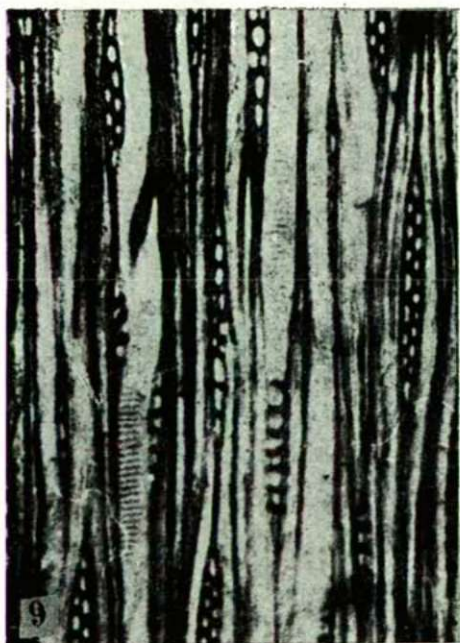
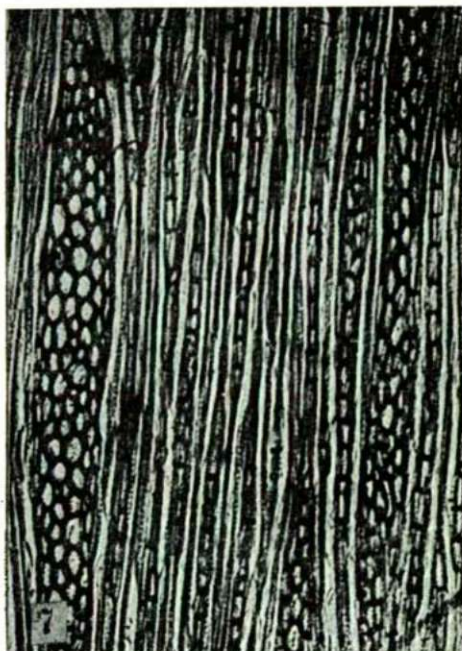
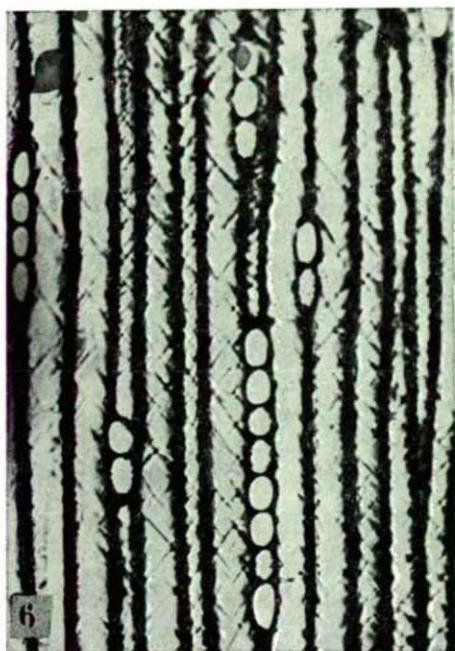
Photograph 7. Tangential photograph of *Drymis winteri*. On the right, pith. The pith rays of 1-3 layers. On the left, a broad pith ray. (x100).

Photograph 8. Single pith-ray cells, arranged in the broad pith ray of *Drymis winteri*, in longitudinal rows, in orthostichons and parastichons. These are indicated in the photograph by dotted black lines. (x300).

Photograph 9. Tangential section of *Magnolia acuminata*. In the vessels there is opposed, ladder-like thickening.



Plate 2



Phot. 5. illustrates the structure of the aggregate pith ray of *Alnus glutinosa*, in transverse section. This belongs to the series of dicotyledonous amentiferous plants (Amentiflorae). The single pith rays draw near to one another in the middle, between the tracheid series, their sum total reminds us of a quite broad pith ray (aggregate ray, gehäufter Markstrahl). This structure is very similar, even in its details, to the aggregate pith ray of *Drymis winteri*. A pith ray, like this, never occurs in the Magnoliae. Accordingly, this characteristic of *Drymis winteri* or *Alnus glutinosa* could not originate from any of the Magnoliales, which do not contain anything like this. This is a quite primitive characteristic, i.e. it is more ancient than the developed vascular state of the Magnoliales. BAILEY and NAST say of this that "in *Tetracentron*, which is placed among the Winteraceae, the primitive nature of the cambium and xylem excludes the possibility that it may once have developed vessels and lost this capacity only later." And elsewhere, they state that "taking into consideration all the evidence obtained from every organ of the plants, there is no convincing argument for deriving *Tetracentron* from Winteraceae, or, the other way round, for referring that these families are phylogenetically in a close relationship. It cannot be supposed, either, that other families, such as in the Ranales, could descend from these vesselless wood substance of Winteraceae with Gymnosperms, then its position should be with the secondary xylem of Pteridospermae and Bennettiales rather than with Coniferae and Cordaitales." As seen later on, we consider as more probable a relationship with the Coniferae and a connection with the dicotyledonous Amentiflorae; all the more so, as the *Drymises* have the most primitive carpels among the *Dicotyledons*.

It follows from these facts that the homoxylous trees, and thus *Drymis winteri*, are of more primitive origin. In the more advanced Magnoliales, and in several other dicotyledonous families true multiseriate pith rays are frequent and this leads us to conclude from the point of view of food conduction, too, that this is a more recent type of plant organisation. BAILEY's and JEFFREY's opinion was that the homoxyl trees, and thus *Drymis*, *Tetracentron*, and *Trochodendron* were "degenerate" vesselless trees. Such a degeneration in trees is surely not made by nature. (x150).

### Comparison of tangential structures

Phot. 6. As seen in tangential section in *Juniperus macropoda* the pith rays are uniseriate, and 2 to 10 cells tall. Alongside them there are longitudinal tracheids. There can also be observed, exceptionally pith rays two cell layers broad but never any of more cell layers. These can occur only with the origin of aggregate pith rays (Phot. 1). In the wood of *Conifers*, wood parenchyma cells also occur (x150).

Plate 3. Photograph 10. Ray structure of *Juniperus macropoda*. There are in the cross-fields 2 to 4 simple pits; in the tracheids are bordered pits. (x200).

Photograph 11. In the radial walls of *Juniperus macropoda* the bordered pits are arranged in single rows. (x150).

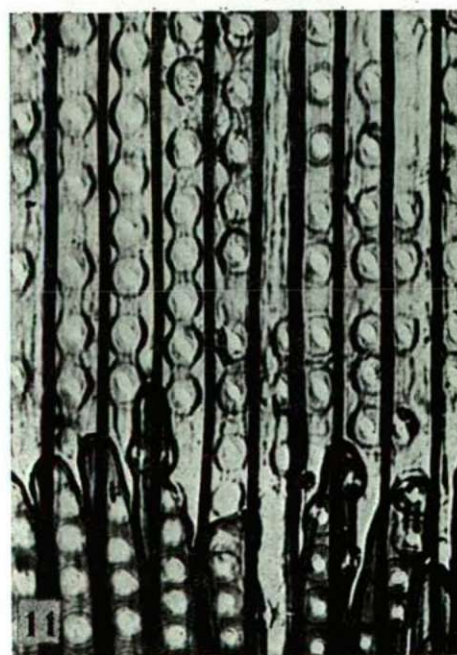
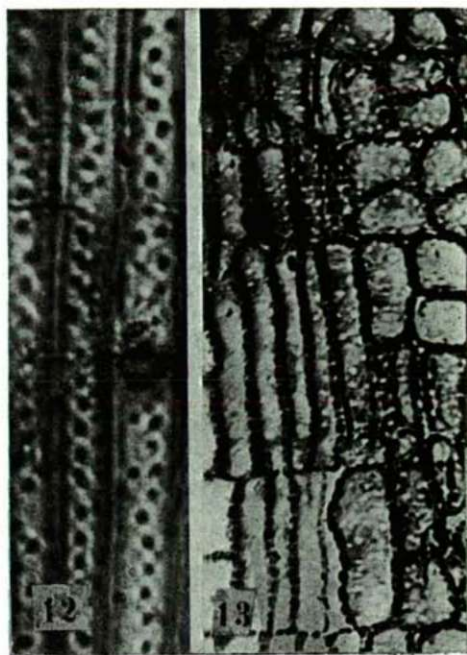
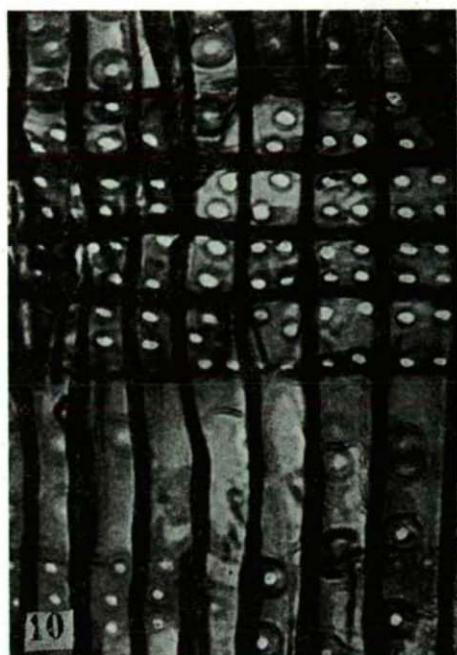
Photograph 12. Simple pits in 1—2 rows. The walls of three tracheids of *Drymis winteri*. (x150).

Photograph 13. Radial structure of the pith of *Drymis winteri*. The parenchyma cells are square-, rectangular or column-shaped, with dense simple pits in their walls. (x200).

Photograph 14. Ray structure of *Magnolia acuminata*. On the left, the vessels has opposed, ladder-like pits with simple apertures. The pith-ray cells are elongated rectangles; in the cross-fields there are several tiny simple pits. (x200).



Plate 3



Phot. 7. In the wood of the homoxyllic *Drymis winteri*, between the tracheids lie uniseriate pith rays and multiseriate (2-8 cells broad) aggregate and compound pith rays, sometimes 5 mm high. (According to METCALFE it has only "narrow" pith rays). From tangential sections it would be possible to think them uniseriate pith rays because there is no difference between them in transverse section; both of them can be regarded as a perpendicular cell chain. On the left of the photograph the pith rays, of 1 to 3 cell layers, are comparatively dense, 10-12 mm. If they are arranged terminally or round the vessel, then they are really parenchyma cells (x100).

Phot. 8. shows the internal structure of the aggregate pith rays. Observing better, in this pith ray the pith-ray cells and tracheids are aligned in regular longitudinal lines, essentially in single layers. At the endings of the single-cell rows there are corresponding similar, narrower border-cells, while the inner thick-walled pith cells — owing to the twisting of wood — follow one another in somewhat slanting, ortho- and parastichous lines. The inner ones are generally isodiametric; only those at the end of cell-rows seem to be more elongated and flatter, with several simple pits in their wall. This also shows that the aggregate pith rays are in fact composed of cell laminae, which agrees fully with the heterogeneous structure of pith rays (x300).

Phot. 9. shows the structure of *Magnolia accuminata*. The pith rays are 1-2 (-5) cell-layers broad and 10-15 cells high. In the "basic substance" between the vessels (which have wide lumina) xylem fibres, tracheids and parenchyma cells are distributed. The tangential walls of vessels are here and there covered with ladder like thickenings and oppositely arranged pits. (It may be that they got to the tangential side as a result of a cut or twisting (x150).

#### Comparison of the radial structures

Phot. 10 shows the radial structure of the pith ray and tracheids of *Juniperus macropoda*. In the quadratic cross fields of pith-ray cells there are 2 to 4 simple cupressoid pits. In the radial walls of tracheids, the bordered pits follow one another in one line and are distributed in a scattered manner. The "court" and circular aperture are distinct (x200).

Phot. 11. In the radial wall of the tracheids of *Juniperus macropoda*, the bordered pits are arranged in single rows. An arrangement like this occurs only in homoxylous trees and conifers (x200).

Phot. 12 is the radial structure of *Drymis winteri*. In the walls of the three longitudinal tracheids large, round, simple pits occur, alternating in single or double lines (Cf. also with photographs 15, 16, 19, (x150).

Phot. 13 is the pith-ray structure of *Drymis winteri*. The pith-ray cells are more or less isodiametric, the bordering cells are somewhat longer, sometimes elongated

Plate 4. Photograph 15. Tracheids by the ray of *Drymis winteri*. The pits are large, located in 1 or 2 rows. (Photograph 19 is the magnifying of phot. 15.)

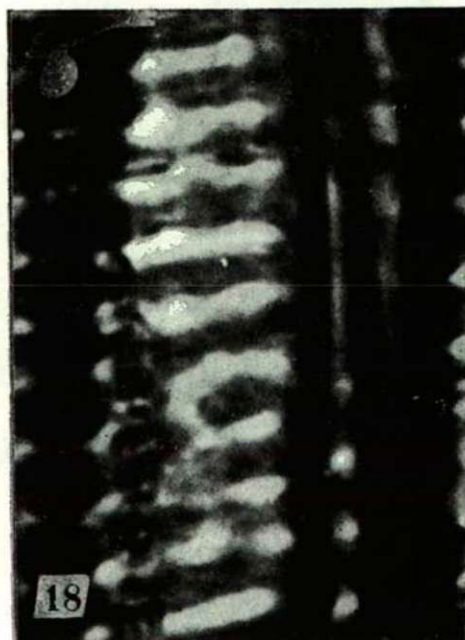
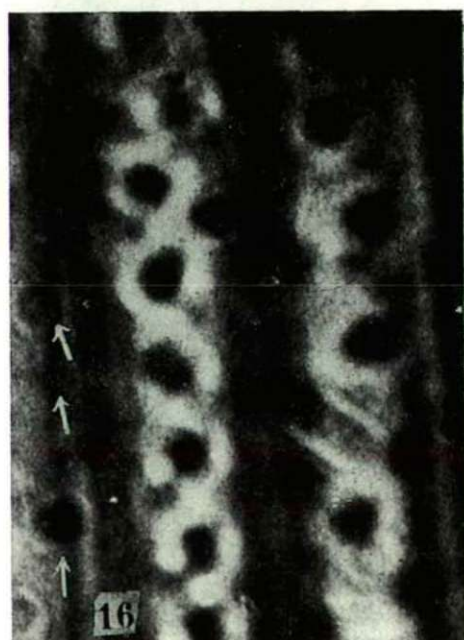
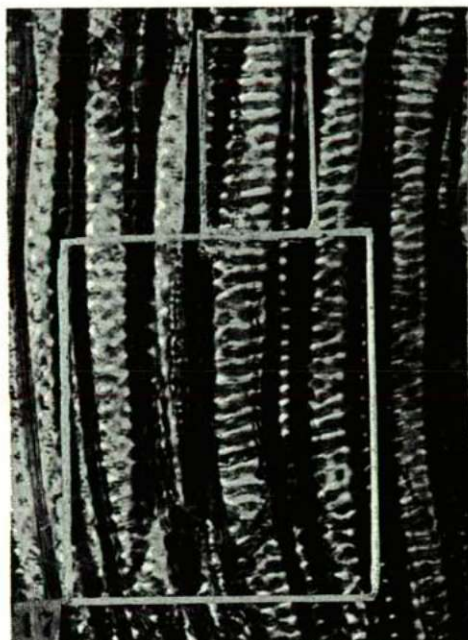
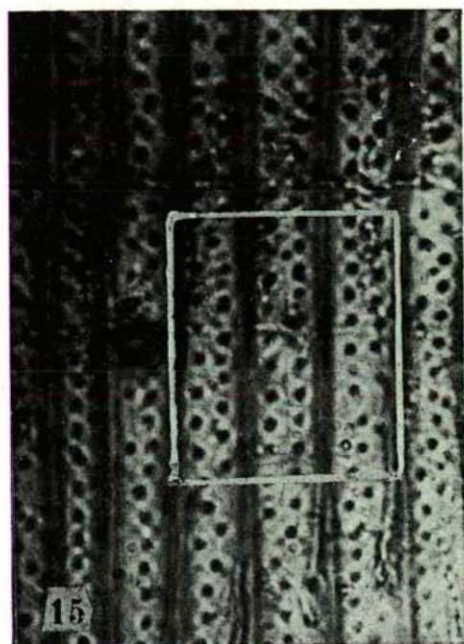
Photograph 16. In the tracheids, the simple pits are circular, without "court" and torus. (Cf. at the arrow.) (x300).

Photograph 17. Alternate pits, bordered and spiral thickening in the early wood of *Drymis winteri*. (Cf. with the framed square in Phot. 20.) (x150).

Photograph 18. Magnification of the rectangle towards the top of Phot. 17. The edges of the ladder-like thickening are not straight. The apertures came into being by the fusion of the apertures of simple pits. (x300).



Plate 4



tracheid-like, with single or double-rows of pits in their walls. The simple structure of the pits is similar to that in tracheids (x200).

Phot. 14 is the pith-ray structure of *Magnolia* in radial section. On the right is a simple perforation of a vessel, with long elongated, opposite ladder-like thickenings in its wall. This ladder-like thickening may have come about from the horizontal lengthening of a simple transverse bordered pit. The horizontally lying pith-ray cells — differently from the more primitive *Drymis* — are elongated in the radial direction, with several simple pits in the cross-fields. Between the vessels, which have large cavities, there are longitudinal wood elements (tracheids, xylem fibres and xylem parenchyma cells). This pith-ray structure is somewhat similar to the radial structure of *Drymis winteri*, but there are no vessels in the xylem of *Drymis*. This is a very important difference between the two tree types (x200).

Phot. 15. In the radial walls of the tracheids of *Drymis winteri*, are alternately arranged circular pit apertures in 1–2 rows, which seem to be simple pits, therefore they could even essentially be thick-walled parenchyma cells (they may have formed from such cells). The pits are not quite uniform, and not always regularly circular. They are larger than simple pits or (generally) than the pores of parenchyma cells (Cf. also with photograph 19 (x150)).

Phot. 16. The pits are regular or irregular circles. (Cf. at the arrows). Some of them are elliptical. Beside them the marks of "courts" cannot be observed; at most wall thickenings in the longitudinal elements (cf.: right side). In this respect this pittedness is also to be considered as a primitive characteristic. A structure like this has, not been known, up to this point at least not in the tracheids of Conifers. (x300).

Phot. 17. It seems to be another new phenomenon, that in the broader tracheids the alternating pits link up close together, two or three or four at a time. Consequently, the apertures of three or four pits almost meet one another, and in this way ladder-like thickenings come about (x150).

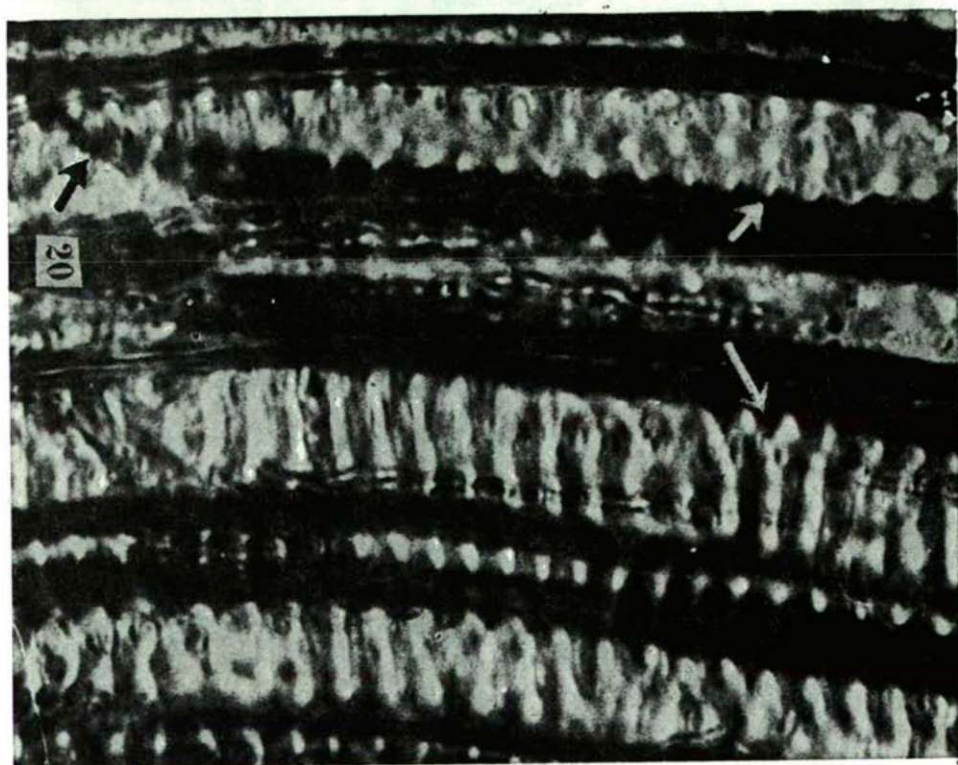
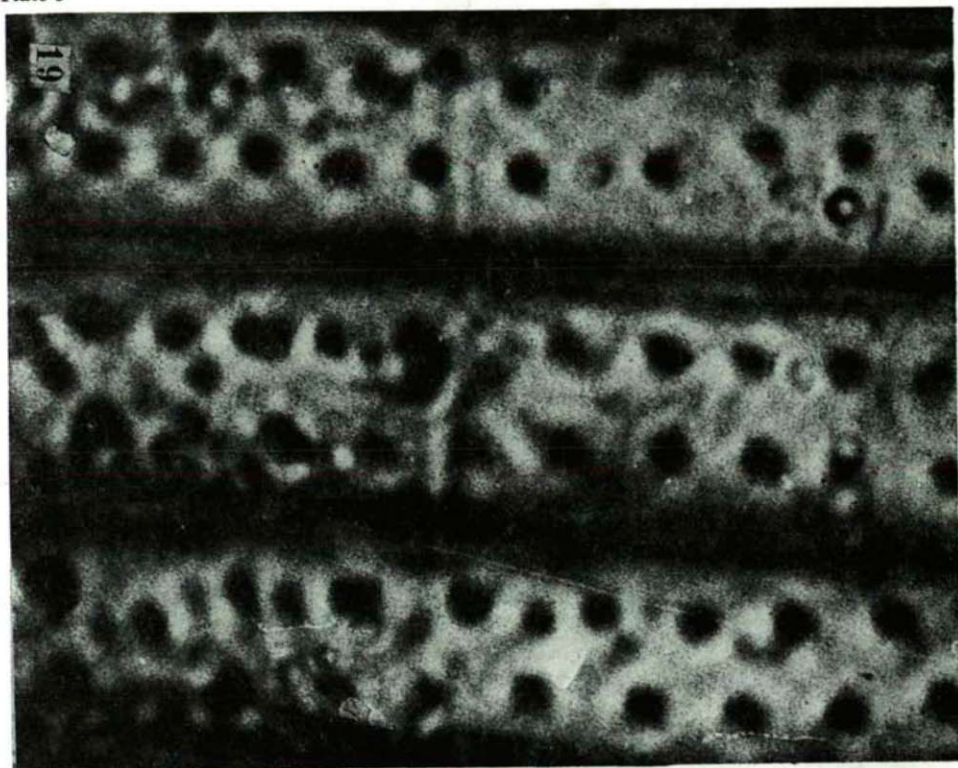
Phot. 18. This ladder-like thickening differs fundamentally from the ladder-like thickening of Magnoliales. While the rungs of the ladder and the apertures in Magnoliales come about from the lengthening of a single bordered pit — i.e. the border of the aperture is a horizontal straight line — in *Drymis winteri* the rungs of the ladders and the apertures come into being from the fusing of several alternating circular pores. Due to this, the two borders of the rungs are not straight lines but irregular ones (x300).

Phot. 19 is a detail of Photograph 15, at higher magnification. We see, in the radial walls of the three longitudinal tracheids, their simple pittedness. In these tracheids, not bordered but simple pits are present, arranged in pairs or alternately. Were they bordered pits, then the apertures and courts (+ –) would be regular circles or apertures of equal size. These apertures, however, are of different size and shape, so this structure points to simple pittedness without any torus. The pittedness of the pith-ray parenchyma is quite similar to that of tracheids, only that there the pits are much larger (Cf. also phot. 21). This is a very primitive peculiarity,

Plate 5. Photograph 19. Magnification of the framed square of Phot. 15. The large pits in the walls of tracheids are generally circular, elongated or angular. Around the apertures there are comparatively wide rings (x350).

Photograph 20. The framed square of phot. 17. Below, at the arrow, the contact two tracheids is to be seen at the upper left white arrow, in the tracheids are 2–3 alternating pits. At the arrow on the right, the apertures of pits are continued in a spiral (x350).





from which it is to be concluded that the tracheids essentially come from the parenchyma and that, therefore, their pittedness is similar, as well. In Magnoliales there is no such primitive feature. Hence homoxylous trees cannot originate from Magnoliales (x350).

In phot. 20 we can see one of the details of phot. 17, the formation of the ladder-like and spiral thickenings from the simple, and bordered pits, at a higher magnification. Here and there, a border to the pits also appears, and the aperture may even become rod-like. Pits like this can be observed in the xylem of *Drymis winteri*. At the black arrow, below, the ends of two tracheids appear. The white arrows show how the thickening of bordered pits turns into the spiral. This structure occurs particularly in the tracheids of the season (x350).

Finally, phot. 21 to 24 are presented to confirm that tracheid pitting and pith-ray structure similar to those in *Drymis winteri*, occur in early dicotyledonous woody plants as well, and that there is a probable relationship along this line. I have mentioned in my book "Occurrence of Tertiary trees in Hungary" that, for instance, in the tracheids and vessels of *Myristicoxylon hungaricum* GREGUSS and *M. bajnaense* GREGUSS, the same kinds of simple pits occur as in the living *Drymis* (Phot. 21, 22), and even the aggregate pith rays show a similar structure (phot. 24). It was possible to detect similarly large, round pits in another fossil broad-leaved tree, as well, which could not be determined more exactly (Phot. 2, 3). All this seems to support the view that it is better to suppose phylogenetic connection with *Drymis* and the more primitive dicotyledonous deciduous trees than with Bennettites or Pteridospermae, as postulated by BAILEY and JAMES (x200).

### Summary

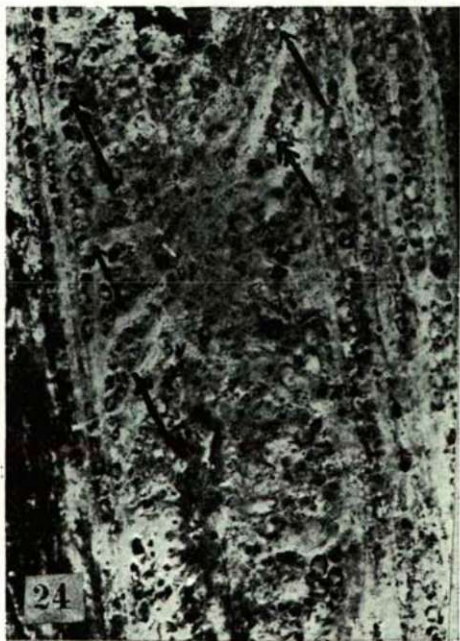
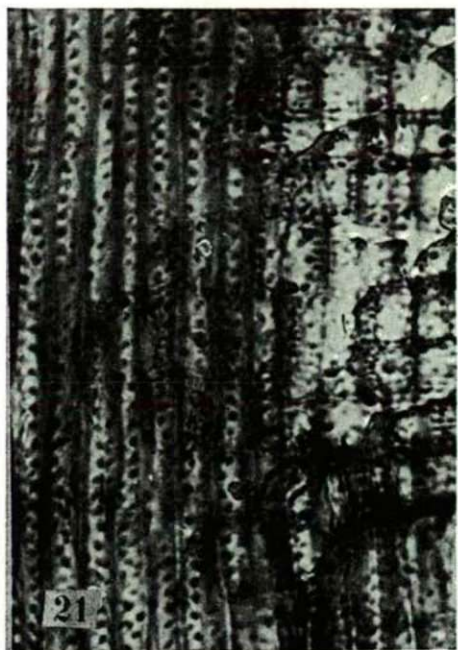
Vessels and perhaps parenchyma cells are missing or scanty in *Drymis winteri* while in *Magnolia acuminata*, apart from tracheids of her wood elements also occur: vessels (tracheae), wood parenchyma and wood fibres, these being characteristic of the most highly developed wood structure. Hence, from these considerations, the structure of the wood tissue of the vesselless *Drymis winteri* is to be considered as older, i.e. more primitive, than that of Magnoliales. For this reason, the *Drymises* could not have descended from Magnoliales.

The phenomenon that in the walls of tracheids instead of the normal bordered pits, large and simple pits are present, is to be regarded as another primitive feature and conclusiv proof. But in the walls of the tracheids of *Drymis winteri* the ladder-like thickening also originates in an essentially different way from those in Magnoliae. Another primitive feature in *Drymis* is the occurrence of aggregate pith

- Plate 6. Photograph 21. A radial detail of the wood of *Drymis winteri*. In the walls of tracheids, there are some comparatively large simple pits and also there are several simple pits in the walls of pith-ray cells (x100).  
 Photograph 22. In the wall of vessels of *Myristicoxylon hungaricum* large pits, similar to those in *Drymis*, occur in 1—2 lines (x200).  
 Photograph 23. In the walls of vessels of an unknown plant fossil from the Oligocene, large, simple pits are present, similar to those in *Drymis* (x100).  
 Photograph 24. Aggregate pith rays in *Myristicoxylon hungaricum* (Cf. at the arrows.) (x200).



Plate 6





rays. Such rays are absent from Magnoliales. This also supports the view that the origin of homoxyulous trees, among of Takhtajan's heteroxyulous vascular Magnoliales. Hence *Drymises* could not have originated from Magnoliales. Incidentally, about 45 species of *Drymises* are known and these occur mainly in the Far East and Australia.

It is also to be considered as primitive, and a conclusive proof, large simple pits are found. In the walls of the tracheids of *Drymis* the ladder-like thickening arises in a way which is essentially different from that in Magnoliales. A further primitive mark in *Drymis winteri* is the occurrence of aggregate pith rays. Rays like these are missing from Magnoliales. It is proved by this, too, that the origin of homoxyulous trees, and among them *Drymises*, may have been older than that of Takhtajan's heteroxyulous vascular Magnoliales. As already mentioned, "Drymises have, among all the Angiospermae, the most primitive carpel".

Takhtajan derives even the Monocotyledons from Magnoliales, i.e. he considers the Angiosperms essentially as monophyletic — and this is fundamentally at variance with our polyphyletic conception.

It is a fact that the opposers of polyphyletic origin present some arguments to support their statements. Thus, among others, they mention the double fertilization which takes place in Mono- and Dicotyledons by and large in a similar way. This objection can, however, be easily refuted. Within the Pteridophytes (Lycopsidea, Pteropsida, Sphenopsida) zoogamy takes place essentially in a similar way, which seems to verify a monophyletic origin though there are, in many respects, essential differences between them. The structure of the reproductive organs of Lycopodia, horsetails and ferns, archegonia and antheridia, is by and large similar. In the finer, essential details, however, there farreaching differences between them are to be seen. Thus, for example, the absence or presence of the suspensor, or the formation of the bi- or multi-ciliated spermatozoids, etc. Nevertheless, very few botanists may state that these descended from one another, or that Pteridophytes, such as *Calamites*, *Sigillaria* and *Lepidodendron* that lived side by side in the Devonian and the Carboniferous Period, originated one from the other: the descent of these was also polyphyletic. In this respect, why should the Angiosperms be the exception?

And if the supposition that Monocotyledons came from the dicotyledonous hermaphroditic Polycarpaceae, or from Magnoliales, is false, then the conclusions drawn from this are also erroneous. Therefore — in our opinion — the opinion cannot be defended that the hermaphroditic flower of Magnoliales is the more primitive flower, the more ancient (originating earlier) hence is also less advanced than the dioecious and monoecious Amentiflorae or the above-discussed *Drymis winteri*. According to such a conception, the flowers of the entomophilous orchids or those of apple-trees would be more imperfect than for instance the flowers of the anemophilous *Typha* or the poplar catkin, or the non-branching palm trunk would be more primitive and imperfect than the branching old oak-tree, or an oak imperfect than, for instance, a *Yucca* leaf or parallel venetaion, or that insect pollination would be less advanced than the pollination by wind, etc. How many contradictions occur, and how much impossibility, if we accept a monophyletic descent of Angiosperms, rather than our polyphyletic conception!

The author has wanted, with this xylotomic paper, to endorse against Takhtajan's conflicting position — H. Gottwald's statements, arrived at on the basis of

xylotomy, according to which it is impossible to derive the homoxyulous trees of primitive structure, as well as the monocotyledonous trees from Magnoliales. This is supported, apart from morphological, palaeontological and genetic arguments, by xylotomic data.

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## DISPERSED MATONIACEAE SPORES FROM THE HUNGARIAN LOWER AND MIDDLE CRETACEOUS SEDIMENTS

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### Abstract

The author studied spores of Matoniaceae affinity coming from Lower and Middle Cretaceous sediments of Hungary. 13 species were separated, among them are described five new species and four new combination. Seven laevigate, valvate species were classified among *Matonisporites* genus, one ornamented, valvate species into the *Trilobosporites*, four laevigate forms with uniformly thickened exine into *Phlebopterisporites* new genus and one ornamented species with uniformly thickened exine into *Phanerosorisporites* new genus. It may be supposed that the acme of the Matoniaceae fern family was in the Wealden and the Albian of the Cretaceous.

### Introduction

The Matoniaceae, one of the ancient fern families of Filicales, are, as a relict, inhabitants of a narrow ecological area of the Earth, the humid, hot tropical Indo-Malaysian Archipelago (Sumatra, Borneo), with a low number of species (2 genera, 3 species). The questions arise: when was the acme-stage of the Matoniaceae, and what were its ancient representatives and their spores like?

In the present paper, on the basis of studying the literature on mega- and microfossils, as well as of our own palynological researches, we should like to look for answers to these questions.

### Previous investigations

The "past" of the Matoniaceae is evidenced by data from several mega- and microfossils. Their first representatives were found in sediments from the Triassic, but there are available several data from the Jurassic and Cretaceous as well. It can be ascertained on the basis of megafossils that the fossil Matoniaceae species were generally ferns of large size, with long creeping rhizomes, siphonosteles; their leaves reached as much as 2 m long, the petiole forks into two lateral branches, which in turn branch again many times, resulting in a fan-shaped frond with pinnate branches radiating from the end of the petiole. Among the leaf remains, sterile and fertile leaves have been found. The sori were arranged in two rows and each sorus consists of from six to 13 sporangia, which covered by indusium. To date, the following fossil genera have been selected: *Phlebopteris* (*Laccopteris*) BRONGNIART 1828, *Matonidium* SCHENK 1871, *Selenocarpus* SCHENK 1866, *Matoniella* HIRM. et HOERH. 1936, *Piazopteris* LORCH 1967.

The morphologically more different *Weichselia* STIEHLER 1857 genus, of uncertain taxonomical place, is also counted here by some authors, on the sole basis of the matoniaceous structure of spores (ALVIN, 1968; DABER, 1968).

In situ spores have been obtained from the sporangia of several specimen:

a) Data have been published by several authors on spores from fossils of *Phlebopteris muensteri* (SCHENK) HIRM. et HOERH. 1936, found in the Rhaeto-Liassic of Greenland, France and Germany and in the Mid-Jurassic of the Soviet Union;

b) Spores of *Phlebopteris angustiloba* (PRESL) HIRM. et HOERH. 1936 have been also described from several places in Europe, from sediments of the Upper Triassic and Jurassic;

c) The species *Phlebopteris hirsuta* and *Phlebopteris indica* were described by SAHNI et SITHOLEY (1945); they published photographs of specimens in a very good state of preservation;

d) *Phlebopteris utensis* ARNOLD 1956 from the Upper Triassic in Arizona and *Phlebopteris galleyi* ARNOLD 1956 from the Upper Cretaceous in Kansas are also spore-bearing megafossils.

e) The in situ spores of *Selenocarpus munsterianus* (PRESL) SCHENK and *Matonidium goepperti* (ETT.) SCHENK were obtained by HIRMER et HOERHAMMER (1936).

It was established by Couper (1958) that many forms among the Mesozoic dispersed spores are very similar to in situ spores of the fossil species of Matoniaceae. He created the formgenus *Matonisorites* with two species: *Matonisorites phlebopteroides* and *Matonisorites equiexinus*. At same time, on the basis of analysing morphologically the recent and fossil matoniaceous spores, he established two types of in situ spores:

1. "phlebopteroides" — type: the exine is smooth, thick, strongly thickened at the corners. To be classified here are: *Phlebopteris hirsuta*, *Phlebopteris indica*, *Phlebopteris muensteri*.

2. "equiexinus" — type: the exine is smooth, very thick, but uniformly thickened. The species to be classified here are: the recent *Matonia pectinata*, as well as the fossil *Phlebopteris angustiloba*, *Selenocarpus munsterianus*, *Matonidium goepperti*.

The *Matonisorites* formgenus, created by COUPER, included botanically related but — on the basis of the morphological system customary in palynology — heterogeneous forms. First DETTMANN (1963) tried to abolish this contradiction by emending the *Matonisorites* to leave it for the spores with smooth or nearly smooth walls but with strongly thickened corners (valvate), and transferring the *Matonisorites equiexinus* to the *Dictyophyllidites* genus, created also by COUPER (1958) for taking in the smooth-walled spores with cheiroleptiaceous character. The taxonomic position of *Matonisorites equiexinus* is not resolved at present. DÖRING (1965) places it into the large genus *Leiotriletes* which is suitable for taking in almost any smooth spores. POCKOCK (1970), asserting the invalidity of *Matonisorites*, mentions it as falling into the genus *Harrisipora*, created by himself. SUKH DEV (1961) sets up the formgenus *Boseisporites*, the type species of which, *Boseisporites praeclarus* has a valvate wall-thickening, similar to *Matonisorites phlebopteroides*, but is described as having an infragranulate surface. DETTMANN (1963) considers *Boseisporites* as a junior synonym of *Matonisorites*, and its "laevigate, infragranulate" surface as a corroded smooth surface. SINGH et al. (1964) and BHARADWAY et KUMAR (1971) emended the *Boseisporites* in a rather contradictory way. But, in our opinion, together with the other genera created for triangular, valvate spores (*Lametratriletes* SINGH et



KUMAR 1970, *Venusteaesporites* SINGH et KUMAR 1970, *Callispora* (DEV. 1961) BHARADWAY et KUMAR 1971), they demonstrate the raising of differences at species level to the rank of genus. The above mentioned formgenera can be drawn into the *Matoniasporites* (COUPER) DETTMANN 1963. DÖRING (1965) draws the valvate spore-forms of smooth and richly ornamented surfaces together in the genus *Trilobosporites*: *Trilobosporites* (*Trilobosporites*) subformgenus for the smooth, valvate spores, *Trilobosporites* (*Tuberosisporites*) subformgenus for the ornamented, valvate spores. This grouping, on a strictly morphological basis, which is clumsy because of the use of subgenera, draws the attention, from the botanical point of view, to two facts: 1. In the Wealden flora of Western Europe the presence of matoniaceous spores is not rare; the ascribing of the four valvate, smooth spore-forms, described by DÖRING from the Wealden of Germany, to the Matoniaceae is therefore not excluded; 2. The structure of several valvate spore-forms, classified in *Trilobosporites* (with the exception of the ornamenting elements) is very similar to that of the smooth, valvate forms. Thus, although ornamented valvate in situ spores, have not been found, as yet from megafossils; nevertheless, there may have existed some ancient Matoniaceae species that produced the spores of this type.

From the sediments of the Lower Cretaceous of Hungary, Matoniaceae-type spores were first described by DEÁK (1964), from the clayey-marl sediments of the Bakony, then thought to be of the Upper-Aptian but actually of the Middle-Albian. She described three new species: *Matoniasporites major* DEÁK 1964, *Matoniasporites simplex* DEÁK 1964, *Matoniasporites minor* DEÁK 1964.

On the basis of the spores of the species of recent *Matonia* and *Phanerosorus* and of the in situ spores of the fossil species of Matoniaceae, we should compare the following morphological characters in considering the placing of Lower and Middle Cretaceous dispersed spores in the Matoniaceae:

1. thickness of the spore-wall,
2. ornamentation,
3. presence of the torus, accompanying the laesura.

#### 1. Thickness of the spore-wall:

the thick exine is uniformly characteristic of the recent and fossil matoniaceous spores. The exine can be of two kinds:

- a) valvate exine: stronger thickening occurring at the corners,
- b) uniformly thickened exine.

The thickness of the exine is to be regarded as the most important character!

#### 2. Ornamentation:

- a) The decisive majority of the valvate and nonvalvate spores is of smooth exine (laevigate, unornamented).
- b) The exine is almost smooth (scabrate, punctate, microrugulate). A finely ornamented surface occurs mainly in recent species. ERDTMAN (1957) reports on spores of microrugulate surface from *Phanerosorus*. ERDTMAN et SORSA (1971) described "blunt spinulose to granulum-like processes" in *Matonia pectinata*.
- c) It can be supposed that valvate forms of verrucate ornamentation occur among the fossil forms.

## 3. Presence or absence of the torus:

- a) In recent and fossil spores the torus can sometimes be also ornamented;  
 b) The torus may also be absent. Its presence or absence may also be the function of the state of preservation! In spores of comparatively thinner wall (possibly "abortiv spores") it can be found more rarely.

In our opinion, apart from the *Matonisorites*, which serves to take in the valvate, laevigate spores, it is necessary to set up two new genera:

1. one to take in the matoniaceous forms of smooth, uniformly thick exine, sometimes having a torus instead of *Dictyophyllidites* (COUPER) DETTMAN (1963), which is very heterogeneous both from the morphological and botanical points of views;

2. another to take in the spores of uniformly thick exine but of slightly ornamented surface, a genus which suggest similarity with the recent species of *Matonia* and *Phanerosorus*.

We propose *Phlebopterisporites* nov. genus for the former forms and *Phanerosporites* nov. genus for the latter.

## Taxonomic part

Anteturma: Sporites H. POT. 1893

Turma: Trilites (REINSCH) DETT. 1963

Suprasubturma: Acavatriletes DETT. 1963

Subturma: *Zonotriletes* WALTZ 1933

Infraturma: *Auriculati* (SCHOPF) DETT. 1963

Genus: *MATONISPORITES* (COUPER 1958) DETTMANN 1963

Type species: *Matonisorites phlebopteroides* COUPER 1958.

Further species to be placed here are as follows:

1. *Matonisorites conspicuus* (BOLCH. 1953) DETT. 1963
2. *Matonisorites* (al. *Dicksonia*) *paragaudius* (BOLCH. 1953) n. comb.
3. *Matonisorites* (al. *Triquitrites*) *rotalis* (WEYL. et KR. 1953) n. comb.
4. *Matonisorites crassiangulatus* (BALME 1957) DETT. 1963
5. *Matonisorites praeclarus* (DEV. 1961) DETT. 1963
6. *Matonisorites cooksonii* DETT. 1963
7. *Matonisorites* (al. *Toroisporis*) *planitorosus* (DÖR. 1964) n. comb.
8. *Matonisorites major* DEÁK 1964
9. *Matonisorites simplex* DEÁK 1964
10. *Matonisorites minor* DEÁK 1964
11. *Matonisorites* (al. *Trilobosporites*) *weylandi* (DÖR. 1965) n. comb.
12. *Matonisorites* (al. *Trilobosporites*) *aornatus* (DÖR. 1965) n. comb.
13. *Matonisorites* (al. *Trilobosporites*) *crassiangularis* (DÖR. 1965) n. comb.
14. *Matonisorites* (al. *Trilobosporites*) *tenuiparietalis* (DÖR. 1965) n. comb.
15. *Matonisorites suemegensis* n. fsp.

*Matonisorites weylandi* (DÖRING 1965) n. comb.

Pl. 1., figs. 1, 2

1965 *Trilobosporites* (*Trilobosporites*) *weylandi* n. fsp.

DÖRING, p. 53, Pl. 19. figs. 4, 5. Westmecklenburg (GDR). Wealden A.



1963 *Matonisorites phlebopteroides* COUPER 1958

BRENNER, p. 55, Pl. 12., fig. 1. Maryland (USA) Potomac Group, Albian.

Remarks: This form — on the basis of its larger size (70–90  $\mu$ ), its strongly thickened valvae (10–15  $\mu$ ), as well as the absence of a torus accompanying the laesura — can be clearly isolated from the Jurassic form *Matonisorites phlebopteroides* COUPER. Several specimens were examined we have never found any very thick tori like that to be seen in the holotype of the latter species. The spore described by BRENNER (1963) quite agrees with the Albian forms of Hungary.

Occurrence: It occurs in the Barremian—Albian deposits of the Bakony and Gerecse in Hungary. In the Sümeg Formation it is rare, in the Vértessomló Formation most frequent, while in some samples of the Tés Formation (Mid-Albian) it is abundant spore form.

*Matonisorites simplex* DEÁK 1964

Pl. 1., fig. 4

1964 *Matonisorites simplex* n. sp.

DEÁK, p. 100, Pl. 2, figs. 12–13. Zirc (Mts Bakony), "Munieria" marl. Mid-Albian (non Upper Aptian).

Remarks: The size range of this type is given by DEÁK (1964) as up to 50  $\mu$ . We have generally found specimens between the limits 35–40  $\mu$ , mostly with straight outer sides and pointed valvae.

Occurrence: It has so far been found only in the clayey-marl sediments in the Tés Formation of Mts Bakony. (Mid-Albian).

*Matonisorites major* DEÁK 1964

Pl. 1., figs. 3, 5

1964 *Matonisorites major* n. sp.

DEÁK, p. 99, Pl. 1, figs. 1–4. Eplény (Mts Bakony), "Munieria marl" Mid-Albian (non Upper Aptian)

Remarks: this form is very similar to *Triquitrites rotalis* WEYL. et KRIEG. 1953, and *Dicksonia paragaudia* BOLCHOVITINA 1953, but the defective description of these two forms does not convince us of their identity with *Matonisorites major* DEÁK 1964.

Occurrence: It appears in larger numbers in the aleurolit of Lower Albian (Mts Gerecse, Vértessomló Formation); in the clayey-marl sediments of the Tés Formation is dominant. It is the most frequent matoniaceous species of the Hungarian Lower and Middle Cretaceous.

*Matonisorites minor* DEÁK 1964

Pl. 1., fig. 6

1964 *Matonisorites minor* n.sp.

DEÁK, p. 99–100, Pl. 1, figs. 5, 6. Eplény (Mts Bakony), "Munieria" marl, Middle Albian (non Upper Aptian).

Remarks: It differs from the other species in its smaller size and thick, strongly rounded corners.

Occurrence: This form is a rare species from Lower and Middle Albian rocks of Hungary.



*Matonisorites cf. minor* DEÁK 1964

Pl. 1., fig. 8

Remarks: In the illustrated specimen, a ring of 21  $\mu$  lumen, 2  $\mu$  thick wall can be seen well on the distal surface of the spore.

*Matonisorites suemegensis* n. fsp.

Pl. 1., fig. 9.

Holotype: Pl. 1., fig. 9. Preparation Süt—17, 320 m/1. P: 27/91.5.

Locus typicus: Sümeg (Mts Bakony), Borehole Süt—17. 320,2 m.

Stratum typicum: Sümeg Formation, aleurolit. Upper Barremian.

Diagnosis: trilete, triangular miospores, with concave outer and inner sides and pointed corners. Laesura is simple, straight, r-1. The exine is smooth. At the corners 10–14  $\mu$  long, 7–9  $\mu$  wide valvae are to be found.

Size: 43–55  $\mu$ .

Comparison: *Matonisorites suemegensis* n. fsp. differs from the other *Matonisorites* species in its strongly concave sides and very strongly elongated valvae at the corners, which are long in comparison to the size of the spores.

Occurrence: To date it has only been found occasionally in the Barremian and Lower Aptian layers of Sümeg Formation.

*Matonisorites planitorosus* (DÖRING 1964) n. comb.

Pl. 2., fig. 10

1964 *Toroisporis* (*Crassianguლისporis*) *planitorosus* n. fsp.

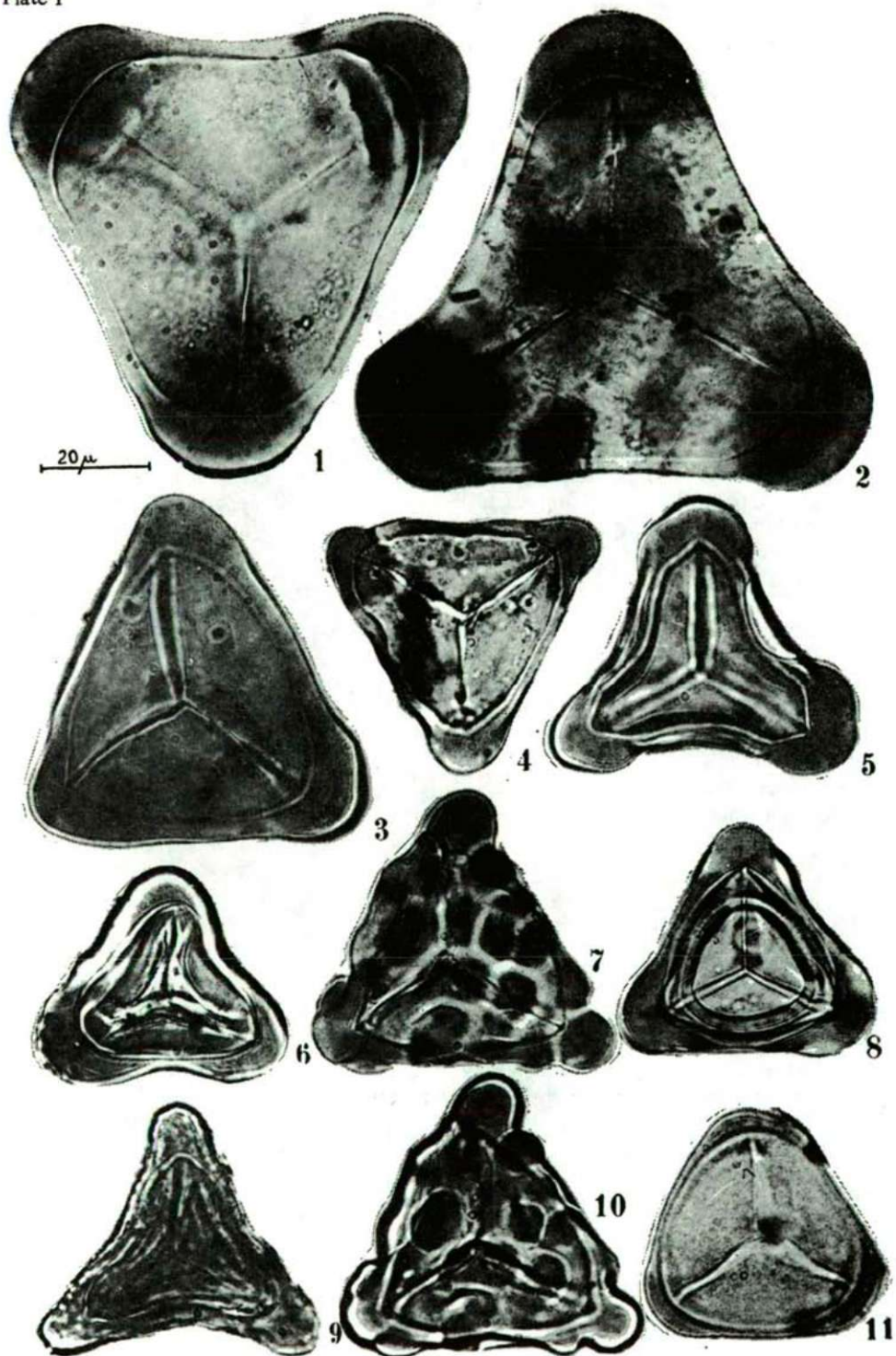
DÖRING, p. 1102, Pl. 3, figs. 7–9.

Remarks: This form is described by SRIVASTAVA (1972) as a synonym of *Matonisorites phlebopteroides*. He has observed great differences among the spores described by him as *M. phlebopteroides*, in the size of the spores and the length of valvae. Similarly, he has also found specimens with slightly thickened cor-

## PLATE I

- 1 *Matonisorites weylandi* (DÖR. 1965) n. comb.  
Súr-1, 556,7 m/1. P: 41, 2/102,2. Tés Formation, Middle Albian.
- 2 *Matonisorites weylandi* (DÖR. 1965) n. comb.  
Süttő-3 (Mts Gerecse), 82/2. P: 33,2/98. Vértessomló Fm, Lower Albian.
- 3 *Matonisorites major* DEÁK 1964.  
Környe-24, 242/2. P: 41,5/105. Vértessomló Fm., Lower Albian.
- 4 *Matonisorites simplex* DEÁK 1964.  
Súr-1, 520 m/3. P: 32,5/107,2. Tés Fm., Middle Albian.
- 5 *Matonisorites major* DEÁK 1964.  
Olaszfa, Ot-84, 106 m/1. 45/108,2. Tés Fm., Middle Albian.
- 6 *Matonisorites minor* DEÁK 1964.  
Oroszlány, O-1891, 533 m/1. P: 31,2/107. Tés Form., Middle Albian.
- 8 *Matonisorites cf. minor*  
Súr-1, 556,7/1. P: 35,4/99,2. Tés Fm., Middle Albian.
- 9 *Matonisorites suemegensis* n. fsp. Holotypus.  
Süt-17, 320,2/1. P: 27/91,5. Sümeg Formation, Upper Barremian.
- 11 *Matonisorites* sp.  
Hárskút, Hk-4, 126,3/3. P: 29,1/106. Pénzeskút Fm., Lower Cenomanian.
- 7, 10 *Trilobosporites góczáni* n. fsp. Holotypus.  
Súr-1, 533,6/1. P: 31,9/96. Tés Fm., Middle Albian.

x1000





ners, similar to *Matonisporites planitorosus* (DÖRING) n. comb., in the assemblages of the Maestricht age.

Occurrence: It is a spore that often occurs in the Hungarian Lower Cretaceous (Barremian or older ages).

*Matonisporites* sp.

Pl. 1., fig. 11

Remarks: This form shows a great similarity to the species published by SRIVASTAVA (1972, Pl. 21, figs. 3–10) under the name *M. phlebopteroides*. In Hungary, it was found in the young — Lower Cenomanian — sediments of Mid-Cretaceous. Thus, it is nearer in age to the spores published from the Edmonton Formation than to *M. phlebopteroides*, which was already absent from the younger sediments of the Cretaceous.

Genus: PHLEBOPTERISPORITES nov. gen.

Diagnosis: trilete miospores, rounded, or rounded-triangular amb, with convex or straight sides. The laesura is straight, long, running generally as far as the inner spore-wall. It is accompanied by a torus or a thickened laesurate margin. The exine is smooth, and thick, on both the proximal and distal surfaces, its thickness being 1/4 to 1/7 of the spore-radius.

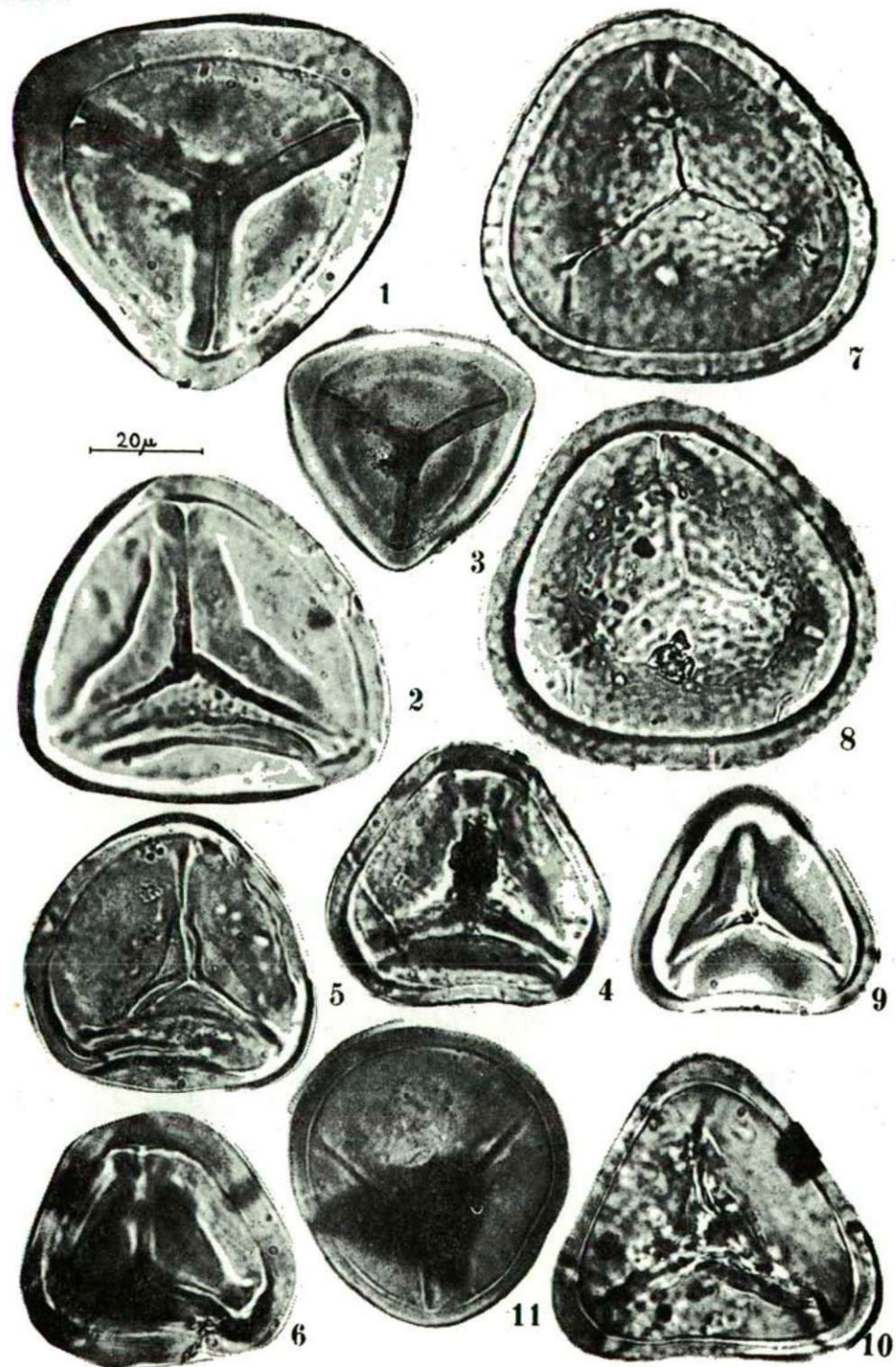
Differential diagnosis: *Phlebopterisporites* n.gen. differs from the other laevigate spore-genus in its thick exine, generally convex sides, as well as in the presence of the torus, which often accompanies the laesura. The exine of *Leiotriletes*, *Todisporites*, *Dictyophyllidites*, *Toroisporis*, *Harrisipora* is generally thinner; in the first two there is no torus. In the genus *Deltoidospora* MINER, there are also species of thicker exine to be found but the shape of these is deltoid and they have no torus.

Remarks: This genus contains the spores of matoniaceous affinity, with smooth exine and uniformly thickened wall. It is a tendency to put the laevigate spores together in large genera (*Deltoidospora*, *Leiotriletes*, *Dictyophyllidites*), with

PLATE 2

- 1, 3 *Phlebopterisporites hungaricus* n. fsp. Holotypus.  
Súr-1, 498,6 m/2. P: 36/104. Tés Fm., Middle Albian.
- 2 *Phlebopterisporites hárskutensis* n. fsp. Holotypus.  
Hárskút, Hk-4, 404/1. P: 42,5/106,5. Pézseskút Fm., Lower Cenomanian.
- 5 *Phlebopterisporites hárskutensis* n. fsp.  
Csehbánya, Cseh-5, 225,5 m/2. P: 44/113,9. Tés Fm., Middle Albian.
- 4 *Phlebopterisporites* cf. *equixinus* (COUPER) n. comb.  
Csehbánya, Cseh-5, 262 m/3. P: 41,3/106,1. Tés Fm., Middle Albian.
- 6 *Phlebopterisporites equixinus* (COUPER 1958) n. comb.  
Tatabánya, Ta-1363, 124/1. P: 45/92,3. Vértessomló Fm., L-Albian.
- 9 *Phlebopterisporites equixinus* (COUPER 1958) n. comb.  
Sümeg, Süt-17, 297 m/1. P: 37/103. Sümeg Fm., Upper Barremian.
- 7, 8 *Phanerosporites surensis* n. fsp. Holotypus.  
Csehbánya, Cseh-5, 262/3. P: 46,5/94,3. Tés Fm., Middle Albian.
- 10 *Matonisporites planitorosus* (DÖR, 1965) n. comb.  
Tés, Tt-27, 46,0 m/2. P: 38,5/116,4. Tés Fm., Middle Albian.
- 11 *Phlebopterisporites globosus* (KIMYAI 1966) n. comb.  
Ta-1363, 369,2/1. P: 45/110,7. Vértessomló Fm., Lower Albian.

(Fig. 3 = x600, the others = x1000.)





which it is not practicable to work in the course of further research on botanical connections. Under such circumstances the probable botanical affinity may also grow blurred. DETTMANN (1963) to remove the heterogeneity of *Matonisorites*, transferred *M. equixinus* COUPER 1958 into the genus *Dictyophyllidites*: in the course of emending the genus, she considered the presence of a thickened laesurate margin as a primary diagnostic character. In this way, the thick-walled "equixinus" and the thin-walled *Dictyophyllidites harrisii* (of affinity with the Cheiropleuriaceae) got into one genus.

Type species: *Phlebopterisporites hungaricus* n. fsp.

Other species:

1. *Phlebopterisporites harskutensis* n.fsp.
2. *Phlebopterisporites equixinus* (COUPER 1958) n. comb.
3. *Phlebopterisporites globosus* (KIMYAI 1966) n. comb.

*Phlebopterisporites hungaricus* n. fsp.

Pl. 2., figs. 1, 3.

Holotype: Pl. 2., figs. 1, 3. Preparation: Súr-1, 498/2. P: 36/104.

Locus typicus: Súr (Mts Bakony), Borehole Súr-1, 498.6 m.

Stratum typicum: Tés Formation, clayey-marl, Middle Albian.

Diagnosis: trilete miospores, amb triangular, with convex sides, rounded corners. Laesura is straight, slightly open, reaching as far as the inner border of the spore-wall. The laesura is accompanied by a 2–4  $\mu$  wide torus. The proximal and distal surfaces are smooth, the exine is uniformly thickened, very thick: 7–10  $\mu$ , 1/4–1/5 of the spore-radius.

Spore size: 60–72  $\mu$ .

Differential diagnosis: *Phlebopterisporites hungaricus* n. fsp. differs from the other smooth, trilete, spores with uniformly thickened exine, by its extremely thick spore-wall and the presence of torus.

Occurrence: From clayey-marl, marl sediments of Tés and Pénzeskút Formation in Mts Bakony (Middle- and Upper Albian).

*Phlebopterisporites harskutensis* n.fsp.

Pl. 2., figs. 2, 5.

Holotype: Pl. 2., figs. 2. Prep.: Hk-4, 404/1. P: 42.5/106.5.

Locus typicus: Hárskút (Mts Bakony), Borehole Hk-4, 234.3 m.

Stratum typicum: Pénzeskút Formation, "turrillites marl", Lower Cenomanian.

Diagnosis: trilete miospores, amb subcircular, with convex sides and slightly rounded corners. Laesura is straight, long,  $r=1$ ; the laesura bordered by 2–6  $\mu$  wide torus. The proximal and distal surfaces are smooth, the distal part is strongly convex. Exine is thick, about 1/7 of the spore-radius, its thickness being 4–5  $\mu$ . Spore size: 53–70  $\mu$ .

Differential diagnosis: *Phlebopterisporites harskutensis* n. fsp. differs from the other smooth trilete forms of subcircular shape in its comparatively thick exine and the frequent occurrence of a torus.

Occurrence: It is common form in the sediments of Tés and Pénzeskút Formation of Mts Bakony.

*Phlebopterisporites equiexinus* (COUPER 1958) n. comb.  
Pl. 2., figs. 4, 6, 9.

- 1958 *Matonisorites equiexinus* n. sp.  
COUPER, p. 140, Pl. 1, figs. 13, 14
- 1963 *Dictyophyllidites equiexinus* (COUPER 1958) n. comb.  
DETMANN, p. 27.
- 1965 *Leiotriletes equiexinus* (COUPER 1958) n. comb.  
DÖRING, p. 20, Pl. 5, figs. 4-6.
- 1970 *Harrisipora equiexina* (COUPER 1958) n. comb.  
POCOCK, p. 38-39, Pl. 6, fig. 15.

Remarks: Different authors placed this formspecies of COUPER into more than one genus, due to the fact that COUPER, in creating the genus *Matonisorites*, classified it the same genus as the morphologically different, valvate "*phlebopteroides*".

DÖRING (1965) sees heterogeneity even in the two pictures of *M. equiexinus*, published by COUPER, and considers them as two different formspecies. The exine of one of the illustrated specimens is, in fact, somewhat thinner. In order to describe the species exactly, it would be necessary to re-examine the holotype and the forms similar to it.

Occurrence: It is frequent in the Neocomian and Albian sediments in Hungary, as a species of matoniaceous character.

*Phlebopterisporites globosus* (KIMYAI 1966) n. comb.  
Pl. 2., fig. 11.

- 1966 *Matonisorites globosus* n. sp.  
KIMYAI, p. 467, Pl. 1., fig. 9.

Description: trilete spores, amb circular, with convex sides. The laesura is simple, long, reaching to the inner surface of the spore-wall. Both the proximal and distal surfaces are smooth, the exine is 3-5  $\mu$  thick. Spore size: 45-52  $\mu$ .

Remarks: KIMYAI (1966) described a species of somewhat thinner walls, of matoniaceous character. In the specimens examined by us, the laesura often branched in the vicinity of the exine. A similar form was published by GRAY et GROOT (1966) under the name *Matonisorites equiexinus*, and by HEDLUND (1966) under the name *Matonisorites impensus* n. sp. The latter proposes an affinity of the latter species with the Lygodiaceae fern family.

Occurrence: This form is generally a species of the Lower Albian or older sediments of Hungary.

Genus: PHANEROSORISPORITES nov. genus

Diagnosis: trilete miospores, amb triangular or subcircular, with straight or convex sides, strongly rounded corners. Laesura is long, frequently bordered by a torus.

The proximal and distal surfaces are ornamented. The ornamenting element are: punctae, granulae, microrugulae. The exine is thick, 1/7-1/8 of the spores radius.



Differential diagnosis: The *Phanerosporites* n.gen. differs from *Phlebopterisporites* n. gen. in its ornamented surface, and from the genera *Punctatisporites*, *Granulatisporites*, *Rugulatisporites* in its thick exine and the frequent occurrence of a torus, from other genera by ornamented surface in its thick exine, torus and subcircular outline.

Type species: *Phanerosporites surensis* n. fsp.

Other species:

1. *Phanerosporites* (al. *Matonia*) *pectinataeformis* (BOLCH. 1953) n. comb.
2. *Phanerosporites* (al. *Dictyophyllidites*) *pectinataeformis* (DETTMANN 1963) n. comb.
3. *Phanerosporites* (al. *Dictyophyllidites*) *adiaphoros* (PHILLIPS et FELIX 1971) n. comb.
4. *Phanerosporites* (al. *Dictyophyllidites*) sp. (PHILLIPS et FELIX 1971) n. comb.

*Phanerosporites surensis* n. fsp.

Pl. 2., figs. 7, 8.

Holotype: Pl. 2., figs. 7, 8. Prep.: Cseh-5, 262/3. P: 46.5/94.3.

Locus typicus: Csehbánya (Mts Bakony), Borehole Cseh-5, 262.5 m.

Stratum typicum: Tés Formation, clayey-marl, Middle Albian.

Diagnosis: trilete miospores, amb circular-subcircular, with convex sides and rounded corners. Laesura is simple, straight, reaching to 3/4 of the radius, sometimes branching at the end. The both proximal and distal surfaces are ornamented by microrugulate sculptur-elements. The rugulae are about  $0.5\mu$  long, running irregularly, uniformly distributed on both surfaces. Exine is  $4-5\mu$  thick, it 1/7 of the spore-radius.

Spore size:  $58-70\mu$ .

Differential diagnosis: The *Phanerosporites surensis* n. fsp. is similar to some species, described under the name of *Cyathidites punctatus* or *Concavissimisporites punctatus* (BRENNER, 1963, Pl. 14, fig. 6) but it always has thicker exine and never has concave sides.

Occurrence: Primarily in the Middle Albian sediments of the Tés Formation, in the area of Csehbánya, Súr, Oroszlány.

Genus: TRILOBOSPORITES PANT 1954 ex POT. 1956

Type species: *Trilobosporites hannonicus* (DEL. et SPR. 1955) POT. 1956.

Remarks: *Trilobosporites* contains the trilete, valvate forms with ornamented exine.

VENKATACHALA et AL. (1968) assigned the non-valvate forms placed till then in *Trilobosporites*, to *Impardecispora* VENKAT. et al. 1968 genus. In this way the number of species belonging to the genus *Trilobosporites*, decreased. The more known species belonging here are: *Trilobosporites hannonicus* (DEL. et SPR. 1955) POT. 1956, *Tr. bernissartensis* (DEL. et SPR. 1955) POT. 1956, *Tr. rarigranulatus* DÖRING 1965, *Tr. lantzae* DEÁK et COMBAZ 1967.

These forms show a great similarity to the species of *Matonisporites* which are also valvate but laevigate. Although, according to the literature these spores are of a connection with the *Lygodiaceae*, in our opinion the relationship with the *Matoniaceae* is not excluded.

*Trilobosporites goczani* n. fsp.

Pl. 1., figs. 7, 10.

Derivatio nominis: In honour of the Hungarian palynologist, DR. FERENC GÓCZÁN.

Holotype: Pl. 1., figs. 7, 10. Prep.: Súr-1, 533/1. P: 31.9/96.

Locus typicus: Súr (Mts Bakony). Borehole Súr-1, 233.6 m.

Stratum typicum: Tés Formation, clayey-marl. Middle Albian.

Diagnosis: trilete miospores, amb triangular, with straight or slightly convex sides, protruding valvate corners. Laesura is straight,  $r=1$ . The proximal surface is smooth or punctate; 6-9 large, semicircular verrucae are to be found in an irregular arrangement on the distal surface. The verrucae are generally 4-5  $\mu$  high, 7-11  $\mu$  wide. At the corners, 10-12  $\mu$  long, 10-14  $\mu$  wide valvae can be found. The interradial thickening is 2-4  $\mu$ .

Spore size: 50-60  $\mu$ .

Differential diagnosis: This new *Trilobosporites* species differs from the other species belonging to this genus, in the large verrucae and the button-like projecting valvae.

Occurrence: It mostly occurs in the Lower Albian sediments of Mts Gerecse (Vértessomló Formation), but the specimens in the best state of preservation were found in the clayey-marl rocks of the Tés Formation.

### Conclusions

The recent representatives of Matoniaceae live on a narrow ecological range in the Indo-Malaysian regio, in the very rainy, lagoon-like areas of the tropical rain zone. It is to be supposed that their ancient ancestors, primarily in the Jurassic and Cretaceous, developed under similar ecological conditions. Megafossils, and more importantly, dispersed spores, that demonstrate the presence of spore formation by of Matoniaceae, were found in the largest numbers from the Wealden and Albian of the Cretaceous. Coal-deposits arose from remains of the marshy forests in the neighbourhood of the brackish waters and shoals of the Wealden.

*Weichselia*, probably of the Matoniaceae genus, is recorded by BATTEN (1974), in the course of the reconstruction of the Wealden deltaic flora in England, as a plant of riversides and coastal sand-banks. In Hungary, the spores of Matoniaceae were found in the best state of preservation, largest numbers and in variety of shape from the samples of the Tés Formation, which is attributed to sandy, fresh-water sedimentation. It was mentioned in our earlier work (JUHÁSZ, 1977) that the acme-stage of the Schizaeales (which are related to the Matoniaceae and mostly live today under similar ecological conditions) may have been in the Lower and Middle Cretaceous. Our proposition can also be extended to the Matoniaceae of which two acme centres may be stated as probable: one of these in Wealden in Western Europe, the other in the time of the Middle-Upper Albian in Hungary.

The latter one is proved by the palynological results summarized in our present paper, recording the occurrence of the following species in the Hungarian Lower and Middle Cretaceous: *Matonisporites weylandi* (DÖR., 1965) n. comb., *Matonisporites major* DEÁK 1964, *Matonisporites simplex* DEÁK 1964, *Matonisporites sueme-*



*gensis* n. fsp., *Matonisorites minor* DEÁK 1964, *Matonisorites planitorosus* (DÖR. 1965) n. comb., *Matonisorites* fsp., *Phlebopterisporites hungaricus* n. gen. et n. fsp., *Phlebopterisporites harskutensis* n. fsp., *Phlebopterisporites equixinus* (COUPER 1958) n. comb., *Phlebopterisporites globosus* (KIMYAI 1966) n. comb., *Phanerosorites surensis* n. gen. et n. fsp., and *Trilobosporites goczani* n. fsp.

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## INVESTIGATION OF SOME SPORE GENERA FROM THE LOWER AND MIDDLE CRETACEOUS IN TRANSDANUBIA

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### Abstract

The author has investigated the foveate, foveoreticulate, foveorugulate and raretuberculate spores occurring in the spore-pollen complexes of the Lower and Middle Cretaceous rocks in Transdanubia (Hungary), and separated some species to *Ischyosporites*, *Klukisporites*, *Foveasporis* and *Acritosporites* genera. He created a new formgenus, *Fueloepisporites*, with five new species. From among these, the species of *Klukisporites*, *Ischyosporites* and *Fueloepisporites* are primarily suitable for characterizing the sediments older than the Albian; *Acritosporites* and *Foveasporis* are frequent in the Albian-Cenomanian sediments.

The examined spore-types are in most probably botanical relationship with the Lygodiaceae and Klukiaceae families.

### Introduction

The sedimentary rocks of the Lower and Middle Cretaceous can be found in the western part of Hungary, in the Transdanubian Central Mountains and Villány Mountains. Several geological formations have already been described by HAAS et al (1977).

In the course of studying the spore-pollen complexes of these formations, some spore-types that are interesting morphologically, and from the point of view of nomenclature and botany, as well, were found. We should like to deal with these in our paper in greater detail.

### Previous works

From among the Jurassic—Cretaceous spores, a number of formgenera have arisen for taking in the foveate-foveoreticulate spores. BALME (1957) created the genus *Ischyosporites* for taking in the trilete forms with foveoreticulate ornamentation on the distal face of spore, and which are valvate but with smooth or punctate proximal surface. COUPER (1958) placed the proximally smooth to granulate but distally foveoreticulate, non-valvate forms into the genus *Klukisporites*. KRUTZSCH (1959b) proposed the formgenus *Foveasporis* for taking in the forms that are both proximally and distally foveate-foveoreticulate. As in several cases of Mesozoic spores, problems of nomenclature have arisen here too.

DÖRING (1965), SCHULZ (1967), TRALAU (1968) and GUY (1971) think that the valvate or non-valvate character of spores is not sufficient for separating two genera, and giving priority to the *Ischyosporites* BALME 1957, they consider *Klukisporites* as a junior synonym of the former genus. GUY (1971) goes even further in restric-



tion, placing the majority of the species classified in these two genera into a single species, *Ischyosporites variegatus* (COUPER 1958) SCHULZ 1967.

DETMANN (1963) proposed that both genera are valid, and separated them on the basis of the presence or lack of equatorial wall-thickening (valvae). SINGH (1971) and SRIVASTAVA (1975) agree with Dettmann's conception and we also accept this. The proximally foveate spores may be classified into the emended genus *Foveasporis* (W. KR.), while we have not found any genus for taking in the spores that are foveorugulate sculpture on their proximal and distal surface. For these, we suggest, therefore, the introduction of the new formgenus *Fueloepisporites*.

An interesting group of spores is a rare tuberculate formgroup, described by different authors in different genera, although the genus *Acritosporites*, created by OBONIZKAJA (1964), is very suitable for taking in these spores, which come mostly from the Upper Cretaceous.

### Systematic part

Genus: ISCHYOSPORITES BALME 1957

Type species: *Ischyosporites crateris* BALME 1957

*Ischyosporites estherae* DEÁK 1964

Pl. 1., figs. 1, 2.

1964 *Ischyosporites estherae* n.sp.

DEÁK, p. 103–104, Pl. 5, figs. 36, 37, and Pl. 6, figs. 41–44.

Remarks: *Ischyosporites estherae* DEÁK is a large-sized (67–90  $\mu$ ) thick-walled spore, the distal surface of which is generally foveoreticulate, the lumina have a diameter of 6–12  $\mu$  and are hexagonal or polygonal, rarely roundish. The exine is valvate at the corners, the ornamenting elements in part pass through to the proximal surface, the contact area of which is smooth.

Occurrence: It can be found in the Middle Albian coaly-clay sediments of the Tés Formation, generally together with similarly thick-walled *Plicatella trichacantha* MALJ., and *Matonisporites* species. We may suppose that its mother plant lived in a vegetation close to a riverside or in a marsh.

*Ischyosporites baconicus* n.fsp.

Pl. 1., figs. 3, 4.

Holotype: Pl. 1., figs. 3, 4. Prep.: Ot-84, 11/1. P: 39.7/95.

Locus typicus: Olaszfalu, Mts Bakony, Borehole Ot-84, 110 m.

Stratum typicum: Tés Formation, clayey-coal. Middle Albian.

Diagnosis: trilete, triangular miospores, with convex or straight sides, rounded corners. Laesura is straight,  $r=4/5$ . The distal surface is strongly convex, with foveoreticulate ornamentation. Muri are of various thicknesses (2–7  $\mu$ ). The lumina similarly vary in size and shape. They may be roundish-polygonal or elongated, wide canal-like. In this species they are 2–5  $\mu$  wide, 4–5  $\mu$  long. The ornamenting elements bring about thickening at the equatorial corners (valvae), in part passing through to the proximal surface, as far as the end of the laesura. Along the inter-radial sides, thin ridges may similarly extend over the proximal part, the contact area of which is always smooth.

Spore size: 51–65  $\mu$ .

Differential diagnosis: The new species differs from *Ischyosporites estherae* DEÁK in its smaller size, thinner (1.5–3  $\mu$ ) exine, and irregular foveoreticulate to reticulate distal ornamentation. It may form a transition between *Ischyosporites* and *Cicatricosisporites*.

Occurrence: In the sediments of the Tés Formation, mainly in some coaly-clayey strata in borehole Tt-27, and Ot-84.

Genus: *KLUKISPORITES* COUPER 1958

Type species: *Klukisporites variegatus* COUPER 1958

*Klukisporites foveolatus* POCOCK 1964

Pl. 1., figs. 5, 6.

Remarks: The holotype described by POCOCK (1964) is of 36–42  $\mu$  in size, the proximal surface of the spore is smooth, at the distal surface the foveolae are 2.5–5  $\mu$  in diameter, circular. The spore examined by us is 40  $\mu$  in size, the diameter of the lumina is 3–5  $\mu$ .

Occurrence: In Hungary, in the marl of the Pénezskút Formation (Upper Albian — Lower Cenomanian). In Canada: Upper Mannville (Pocock, 1964), Loon River Formation (SINGH, 1971).

*Klukisporites scaberis* (COOKS. et DETT. 1958) DETT. 1963

Pl. 1., figs. 7, 8.

1958 *Ischyosporites scaberis* sp.nov.

COOKSON et DETTMANN, p. 104, Pl. 15, figs. 7, 9.

1963 *Klukisporites scaberis* (COOKS. et DETT. 1958) n.comb.

DETTMANN, p. 48, Pl. 8, figs. 1–7. Otway Basin, Australia, Albian.

Occurrence: Hungary: in aleurolitic sediments of Vértessomló Formation (Lower Albian).

*Klukisporites lacunus* FILATOFF 1975

Pl. 1., figs. 9, 10.

1975 *Klukisporites lacunus* n.sp.

FILATOFF, p. 69–70, Pl. 15, fig. 9, and Pl. 16, figs. 1, 2.

Remarks: The holotype of this species is 44  $\mu$  in size, its lumina are 4–10  $\mu$ , 25–40 of them are to be found on the distal surface of the spore. The size of the species examined by us is 42–56  $\mu$ , diameter of the lumina is 5–9  $\mu$ , 22–28 of them can be found on the distal surface. The proximal surface is smooth.

Occurrence: In the sediments of the Sümeg Formation (Barremian-Aptian), and Vértessomló Formation (Lower Albian).

*Klukisporites tuberosus* (DÖRING 1965) n.comb.

Pl. 2., figs. 1, 2.

1965 *Ischyosporites tuberosus* n.sp.

DÖRING, p. 43, Pl. 16, figs. 4–6. Westmecklenburg (GDR), Wealden A.

Occurrence: In Hungary, it generally occurs in the Neocomian sediments of the Mts Gerecse and the Barremian rocks of the Mts Bakony.



## Genus: FOVEASPORIS (W. KR. 1959b) emend.

Type species: *Foveasporis fovearis* W. KR. 1959b.

Emended diagnosis: trilete miospores, with circular amb. The exine sculpture is foveate on both the proximal and distal surfaces. On both surfaces the lumina of the foveae may be of various sizes. Their shape is generally regular, of circular outline. These lumina are often large but they are not arranged in rows. Muri are strong, massive. The laesura is simple, often short,  $r=1/3-1/4$ .

Remarks: KRUTZSCH (1959b, p. 162) mentions in the genusdiagnosis — probably due to a misprint — “azonomonolete microspores”. He does not mention the ornamentation of the proximal surface, although this is the important character for separating *Foveasporis* from the genera *Ischyosporites* and *Klukisporites*, also of non-foveate proximal surface. In his latter work, KRUTZSCH (1963, p. 14) separates three genera from each other, but then with both the other genera he emphasizes the irregularity of the lumina, which is not a fundamental diagnostic character either for the genus diagnosis of these or in the description of the species in these genera.

Cretaceous forms to be classified in the genus:

1. *Foveasporis agathoecus* (R. POT. 1934) W. KR. 1959b.
2. *Foveasporis* (al. *Foveotriletes*) *budejovicensis* (PACLT. 1961) n.comb.
3. *Foveasporis crassixinous* (BRENNER 1963) DÖRING 1966

*Foveasporis agathoecus* (R. POT. 1934) W. KR. 1959b  
Pl. 1., figs. 11, 12.

1934b *Sporites agathoecus* n.sp.

R. POTONIÉ, p. 43, Pl. 1, fig. 25. Geiseltal, lower part of Upper Cretaceous.

1959b *Foveasporis agathoecus* (R. POT. 1934) n.comb.

KRUTZSCH, p. 165, Pl. 30, figs. 334-335. Geiseltal, Turonian.

Remarks: This spore of circular outline and medium size (45-60  $\mu$ ) has a 3-5  $\mu$  thick exine and, on both sides, with large foveas (3-12  $\mu$  in diameter).

Occurrence: It is a spore-type of the Upper Cretaceous. In Hungary, it was first found in the upper section of the Pénzeskút Formation (Lower Cenomanian).

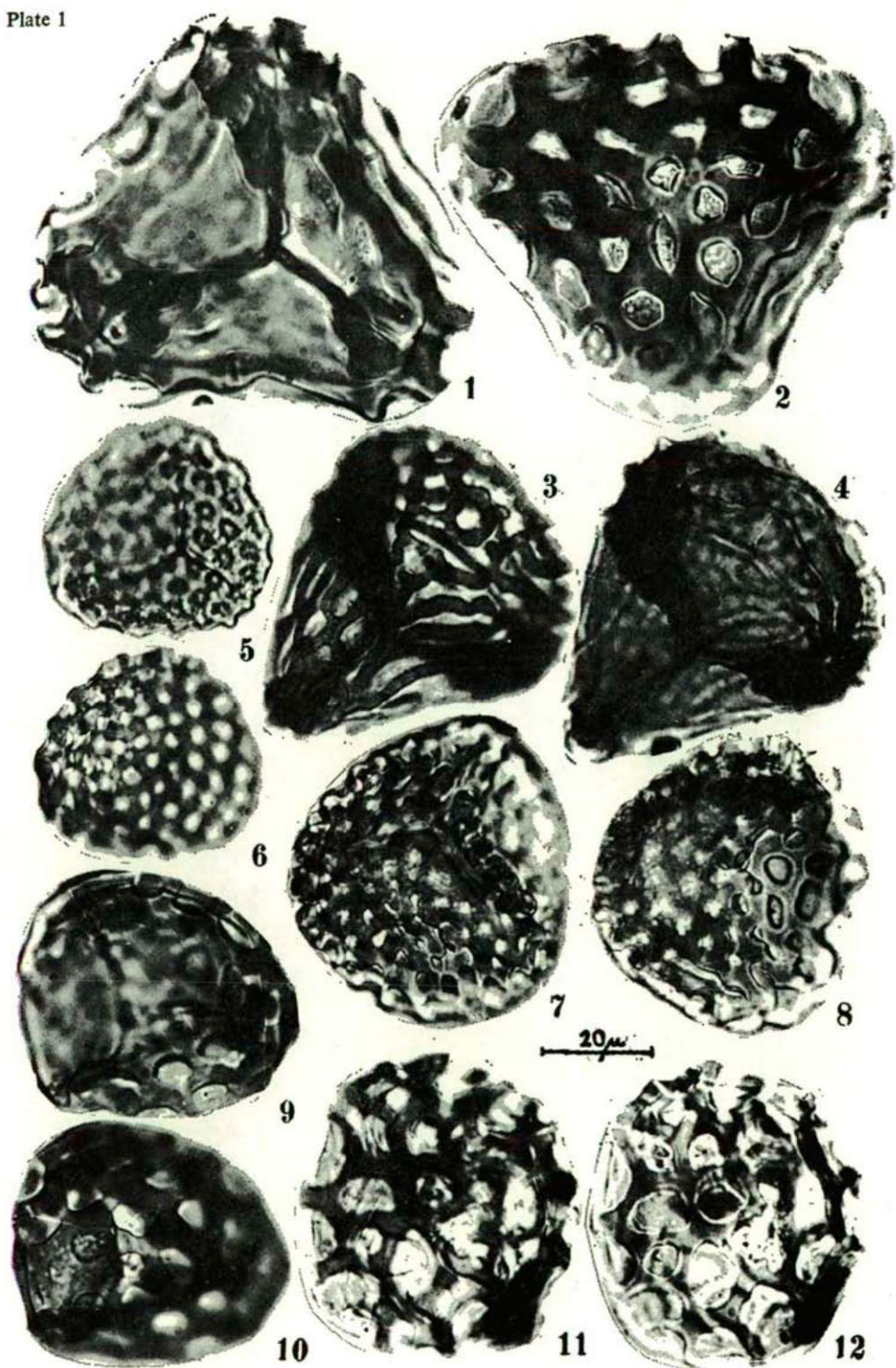
## Genus: FUELOEPISPORITES nov.gen.

Type species: *Fueloepisporites hungaricus* n.fsp.

Derivatio nominis: In honour of the Hungarian geologist, DR. JÓZSEF FÜLÖP.

## PLATE 1

- 1, 2 *Ischyosporites estherae* DEÁK 1964.  
Súr (Bakony Mts), Bore Súr-1, Prep. 556/3. P: 42/98,3. Middle Albian.
- 3, 4 *Ischyosporites baconicus* n. sp.  
Olaszfa (Bakony Mts), Bore Ot-84, Prep. 11/1. P: 39,7/95. M-Albian.
- 5, 6 *Klukisporites foveolatus* POCOCK 1964.  
Olaszfa (Bakony Mts), Bore Pe-31, 307/8. P: 35/100,2. L-Cenomanian.
- 7, 8 *Klukisporites scaberis* (COOK. et DETT. 1958) DETTMANN 1963.  
Tatabánya Basin, Bore Ta-1364, 300/1. P: 31/98. Lower Albian
- 9, 10 *Klukisporites lacunus* FILATOFF 1975.  
Bikol (Gerecse Mts), Bore Süttő-3, 30/3. P: 33/112. Lower Albian.
- 11, 12 *Foveasporis agathoecus* (R. POT. 1934b) W. KR. 1959b.  
Olaszfa (Bakony Mts), Bore Pe-31, 351/1. P: 29/98. L-Cenomanian.





Diagnosis: trilete miospores, with subtriangular or circular amb, convex (rarely straight) sides. Laesura is simple, generally long. Exine is generally thick (sometimes cingulum-like). Both the proximal and distal surfaces are ornamented, sunken into the exine, of irregular shape, sometimes with anastomosing, longer or shorter, smaller or wider foveae-foveolae, mostly forming foveorugulate surfaces.

Differential diagnosis: *Fueloepisorites* nov.gen. is distinguished from the genera *Klukisporites* and *Ischyosporites* by the fact that its distal surface is not foveoreticulate and its proximal surface is foveate — foveorugulate, never being smooth. The foveae of *Foveosporites* W. KR. are regular, circular, they do not anastomose. *Foveosporites* BALME 1957, of affinity with the *Lycopodiaceae*, has thinner exine, smaller size, more regular foveolae. In the new genus, the anastomosis of foveae-foveolae may sometimes bring about a canal, thus it may be similar to the genus *Bikolisporites* (al. *Corrugatisporites*) JUHÁSZ 1972, in which the proximal surface is of corrugate ornamentation. The latter genus has, however, much thinner exine and has no foveolae. Transitional forms, however, can be observed toward this genus.

Further species to be ranged into the genus:

1. *Fueloepisorites* (al. *Trilites*) *asolidus* (W. KR. 1959b) n.comb.
2. *Fueloepisorites* (al. *Ischyosporites*) *foveasolidus* (W. KR. 1967) n.comb.
3. *Fueloepisorites* *crassus* n.fsp.
4. *Fueloepisorites* *vokanyensis* n.fsp.
5. *Fueloepisorites* *minor* n.fsp.
6. *Fueloepisorites* *rotundus* n.fsp.

*Fueloepisorites hungaricus* n.fsp.

Pl. 2., figs. 3, 4.

Holotype: Pl. 2., figs. 3, 4. Prep.: Pgy-4, 69/1. P: 34/95.2.

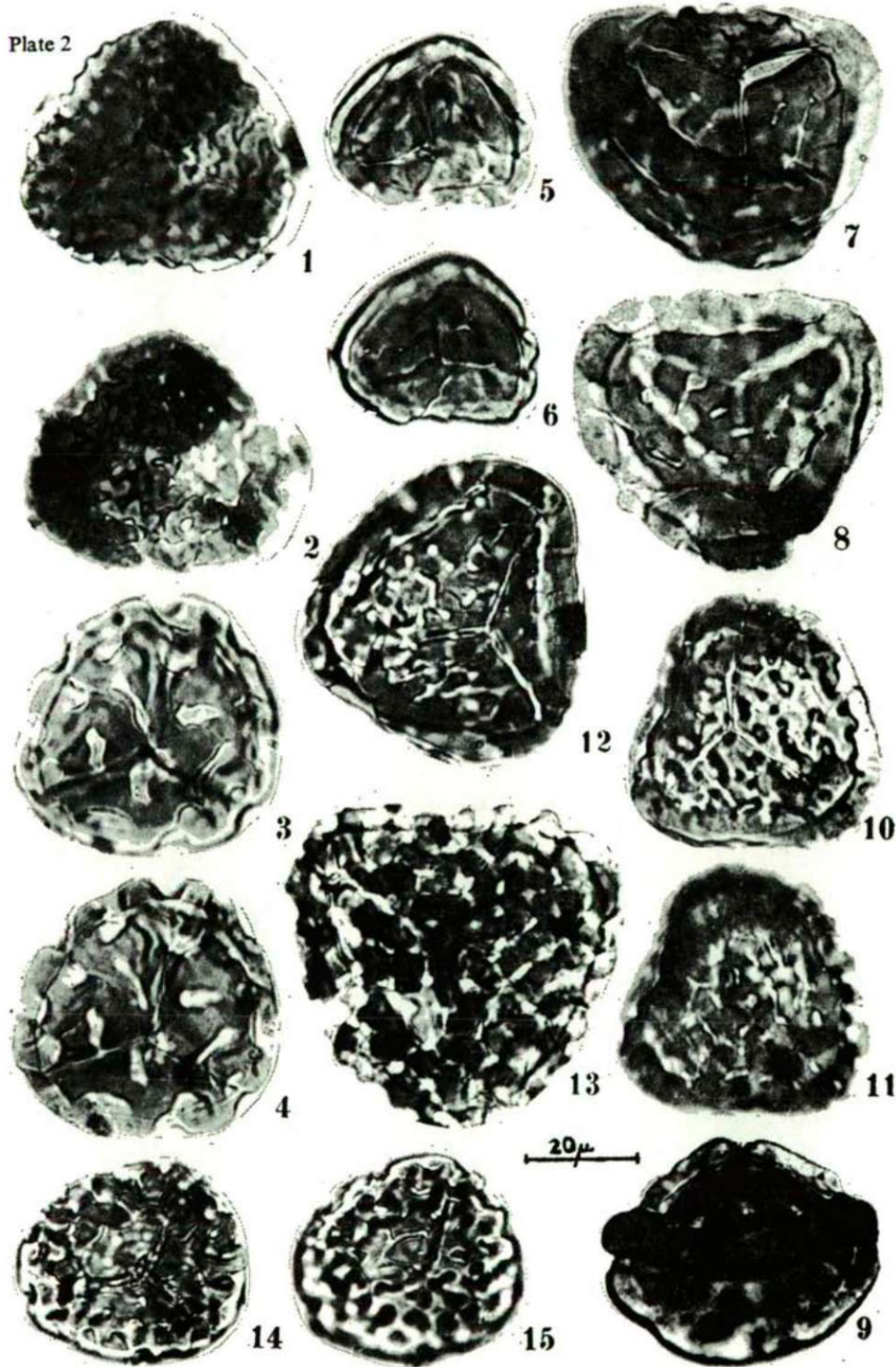
Locus typicus: Pénzesgyőr (Mts Bakony) Bore Pgy-4, 69.5 m.

Stratum typicum: Pénzeskút Formation, marl. Upper Albian.

## PLATE 2

- 1, 2 *Klukisporites tuberosus* (DÖRING 1965) n. comb.  
Bikol (Gerecse Mts), Bore Süttő-3, 104/2. P: 37,5/108,2. L-Albian.
- 3, 4 *Fueloepisorites hungaricus* n. sp.  
Pénzesgyőr (Bakony Mts), Bore Pgy-4, 69,5/1. P: 34/95,2. U-Albian.
- 5, 6 *Fueloepisorites minor* n. sp.  
Tatabánya Basin, Bore Ta-1329, 480,5/1. P: 32,2/100,3. Neocomian.
- 7, 8 *Fueloepisorites crassus* n. sp.  
Tatabánya Basin, Bore Ta-1358; 369,5/2. P: 33,6/106. Lower Albian
- 9 *Fueloepisorites crassus* n. sp.  
Tatabánya Basin, Bore Ta-1495; 360/1. P: 40,8/105,8. Lower Albian.
- 10, 11 *Fueloepisorites vokanyensis* n. sp.  
Tatabánya Basin, Bore Ta-1495; 378/1. P: 45,4/110. Lower Albian.
- 12 *Fueloepisorites vokanyensis* n. sp.  
Vokány (Villány Mts), Bore Vo-4, 67/2. P: 38/94. Albian.
- 13 *Fueloepisorites* cf. *foveasolidus* (W. KR. 1967) n. comb.  
Oroszlány (Bakony Mts), Bore O-1891; 545/1. P: 37/106,7. M-Albian.
- 14, 15 *Fueloepisorites rotundus* n. sp.  
Sümeg (Bakony Mts), Bore Süt-17; 320/2. P: 46,5/95,2. U-Barremian.

Plate 2





Diagnosis: trilete miospores, with circular amb, convex sides. Laesura is thin, straight,  $r=1$ . Both at the proximal and distal surfaces, sunk into the exine, irregularly running, generally longitudinal foveae can be found. The foveae are 6–11  $\mu$  long, 3–4  $\mu$  wide, and 2–3  $\mu$  deep, anastomosing rarely. The exine is 5  $\mu$  thick, becoming only 1–1.5  $\mu$  thick at foveae.

Spore size: 46  $\mu$ .

Differential diagnosis: *Fueloepisorites hungaricus* n.fsp. differs from the foveate-foveoreticulate species in having its foveae sunk into the whole surface of the spore, formed "pond-like" and having an irregular shape, and in its thick exine, circular outline.

Occurrence: It first occurred in the lower part of the Pénzeskút Formation. We have not found it in older rocks.

*Fueloepisorites minor* n.fsp.

Pl. 2., figs. 5, 6.

Holotype: Pl. 2., figs. 5, 6. Prep.: Ta-1329, 480/5. P: 32.2/100.3.

Locus typicus: Tatabánya Basin, Borehole Ta-1329, 480.5 m.

Stratum typicum: Neocomian sandstone.

Diagnosis: trilete miospores, with rounded amb, convex sides. Laesura is simple, straight,  $r=1$ . Exine is 2.5–3  $\mu$  thick. Both at the proximal and distal surfaces, there are narrow, long foveorugulate canals, sunk into the exine. Their length can be 3–6  $\mu$ ; sometimes they "meet".

Spore size: 32–38  $\mu$ .

Differential diagnosis: *Fueloepisorites minor* n.fsp. differs from the other species classified in this genus, in its small size and its narrow, canal-like foveorugulae.

Occurrence: it is mainly to be found in the Neocomian sediments of the deep bores in the environs of Tatabánya.

*Fueloepisorites crassus* n.fsp.

Pl. 2., figs. 7–9.

Holotype: Pl. 2., figs. 7, 8. Prep.: Ta-1358, 369/2. P: 33.6/106.

Locus typicus: Tatabánya Basin, Borehole Ta-1358, 369.5 m.

Stratum typicum: lower part of Vértessomló Formation, Lower Albian.

Diagnosis: trilete miospores, with subcircular amb, convex sides and strongly rounded corners. Laesura is straight,  $r=3/4$ . Exine is smooth, 5–6  $\mu$  thick, widened out cingulum-like. Sunk into its surface are narrow foveorugulae which are rarely roundish, generally of irregular shape, and by anastomosing may even form a convolute-corrugate-like surface on the proximal side. The distal surface is strongly convex, the foveae, found sunk into its surface, are roundish, elongated, sometimes anastomosing.

Spore size: 45–60  $\mu$ .

Differential diagnosis: *Fueloepisorites crassus* n.fsp. differs from the other species arranged into this genus in its very thick exine and its corrugate-like proximal surface. *Bikolisporites toratus* (WEYLAND et GREIFELD) JUHÁSZ is somewhat similar to the described species but it has much thinner exine and on its proximal and distal sides the surface is corrugate in a regular fashion.

Occurrence: In Hungary, in the aleurolithic sediments of Vértessomló Formation and Sümeg Formation. (Barremian to Lower Albian).

*Fueloepisporites vokanyensis* n.fsp.

Pl. 2., figs. 10-12.

Holotype: Pl. 2., figs. 10-12. Prep.: Ta-1495, 378/1. P: 45.41 I.O.

Locus typicus: Tatabánya Basin, Borehole Ta-1495, 378 /m

Stratum typicum: Vértessomló Formation, grey marl, Lower Albian.

Diagnosis: trilete miospores, with triangular-subtriangular amb, straight or convex sides, strongly rounded corners. Laesura is simple, straight,  $r=3/4$ . Exine is 3-4  $\mu$  thick. Both the proximal and distal surfaces are ornamented with irregularly running, mostly elongated, narrow foveolae of varied shape, anastomosing only rarely and uniformly ornamenting the whole surface of the spore.

Spore size: 42-68  $\mu$ .

Differential diagnosis: *Fueloepisporites vokanyensis* n.fsp. differs from *F. crassus* n.fsp. in its triangular shape thinner exine, uniformly foveorugulate surface. *Fueloepisporites asolidus* (W. KR. 1959b) n.comb. is of smaller size, its ornamenting elements form a positive foveorugulate surface. The foveolae of *Fueloepisporites foveasolidus* (W. KR. 1959b) n.comb. are wider and form larger cavities.

Occurrence: This form generally occurs in the Lower- (more rarely in the Middle-) Albian sediments in Hungary (Gerecse and Villány Mts) but in the Tés Formation (Bakony Mts) it has not yet been found.

*Fueloepisporites rotundus* n.fsp.

Pl. 2., figs. 14, 15.

Holotype: Pl. 2., figs. 14, 15. Prep.: Süt-17, 320/2. P: 46.5/95.2.

Locus typicus: Sümeg (Bakony Mts); Bore Süt-17, 320.2 m.

Stratum typicum: Sümeg Formation, clayey marl, Upper Barremian.

Diagnosis: trilete miospores, with circular amb, rounded sides. Laesura is short,  $r=1/2$ . Exine is 2  $\mu$  thick, The proximal and distal surfaces are rugulate. Between rugulae roundish or long, narrow foveolae run and sometimes anastomose. Spore size: 35-42  $\mu$ .

Differential diagnosis: This form is intermediate between *Fueloepisporites minor* n.fsp. and *F. vokanyensis* n.fsp. It differs from these two other forms, however, in its characteristic rotund shape and short laesura.

Occurrence: In the Barremian-Aptian stages of the Lower Cretaceous it is a fairly frequent species in Hungary; in the Lower Albian rocks it occur rarely.

*Fueloepisporites* cf. *foveasolidus*

Pl. 2., fig. 13.

Occurrence: This foveorugulate form of comparatively large size is a rare species occurring in the Sümeg- and Vértessomló Formations.

Genus: ACRTOSPORITES (OBONIZKAJA 1964) emend.

Emended diagnosis: trilete spores, with triangular or subcircular amb and generally convex, rarely straight sides. Laesura is straight and often bordered by generally long, sometimes thick torus or protruding kytom. On the proximal sur-



face of the spore circular or elliptical depressions (lacunae) may occur, caused by the thinning of the exine; on the distal surface one (rarely two) lacuna can be also found. In these lacunae. On the proximal side, one or two spherical tubercula can occur; on the distal side one (sometimes this is absent). The further parts of the exine are either smooth or with verrucate-rugulate ornamentation.

Type species: *Acritosporites aralensis* OBONIZKAJA 1964

Further species classified in this genus:

1. *Acritosporites sibiricus* (BOLCH. 1961) OBONIZ. 1964
2. *Acritosporites excavatus* (BRENNER 1963) n.comb.
3. *Acritosporites* (al. *Chomotriletes*) *triangularis* (DEÁK 1965) n.comb.
4. *Acritosporites* (al. *Chomotriletes*) *oculatus* (DEÁK 1965) n.comb.
5. *Acritosporites kyrtomus* n.fsp.
6. *Acritosporites transdanubicus* n.fsp.
7. *Acritosporites rasellus* (ALEKS. 1962) n.comb.

*Acritosporites kyrtomus* n.fsp.

Pl. 3., figs. 1, 2.

Holotype: Pl. 3., figs. 1, 2. Prep.: Pe-31, 215/1. P: 42.8/107.2.

Locus typicus: Olaszfalu (Bakony Mts), Bore Pe-31, 125 m.

Stratum typicum: Pénzeskút Formation, marl, Lower Cenomanian.

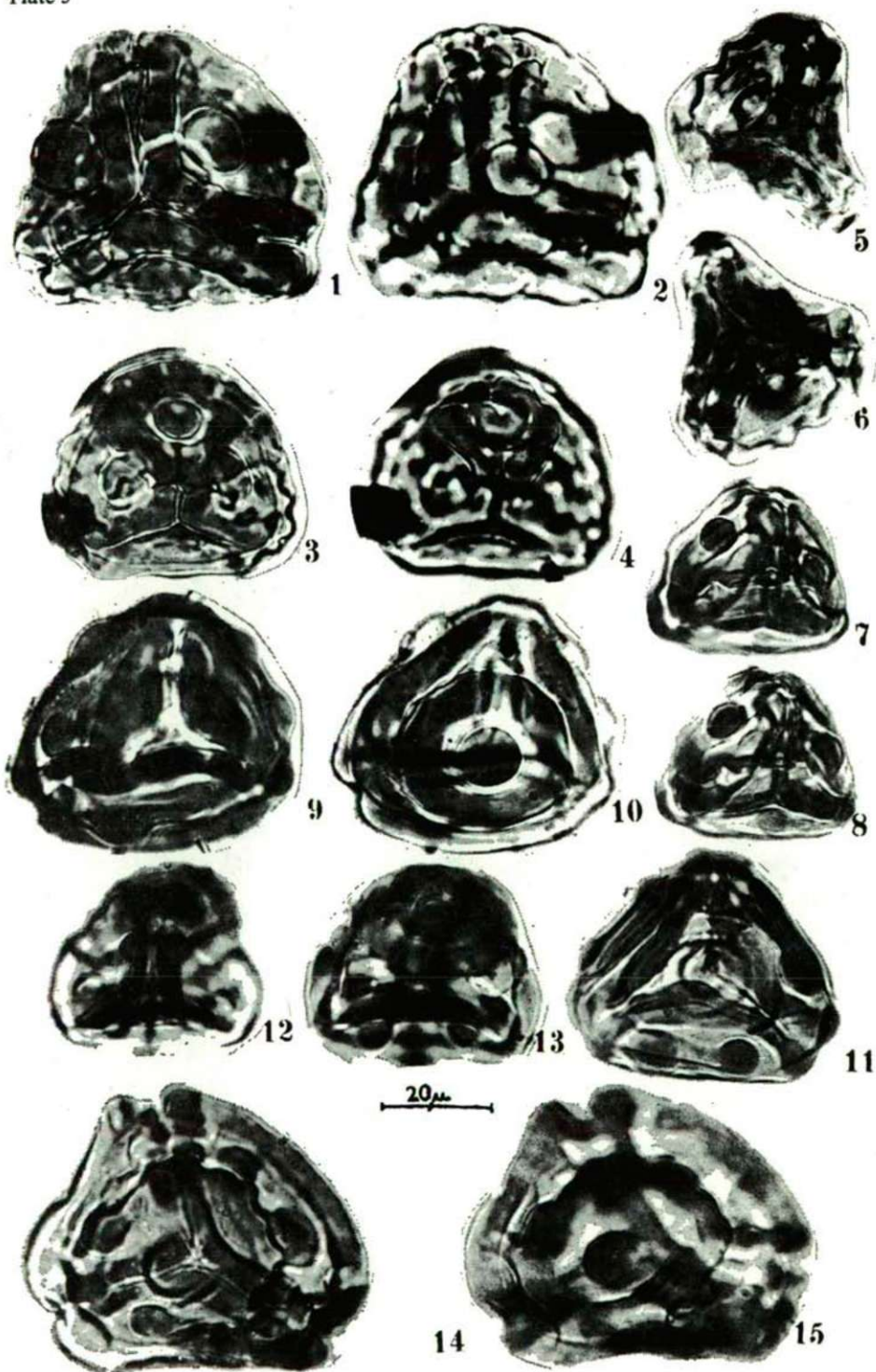
Diagnosis: trilete miospores with triangular-subcircular amb, convex sides, and rounded corners. Laesura is long, straight,  $r=1$ , bordered on the two sides by a thick, 4–7  $\mu$  wide and 2–4  $\mu$  high kyrtom. On the proximal surface there are three lacunae, in each of which one spherical tuberculum of 8–11  $\mu$  diameter is located. On the distal surface there is one central lacuna, with a tuberculum of 11–13  $\mu$  size in the middle. Exine is 3–5  $\mu$  thick; in the further parts of both surfaces it is smooth. Spore size: 60–68  $\mu$ .

Differential diagnosis: The new species differs from *Acritosporites sibiricus* in having not seven but only four tubercula and a protruding well developed kyrtom. *Acritosporites triangularis* has no tuberculum on the proximal side, while *Acritosporites oculatus* has two tubercula on the distal surface.

Occurrence: In the upper part of Pénzeskút Formation (Lower Cenomanian).

### PLATE 3

- 1, 2 *Acritosporites kyrtomus* n. sp.  
Olaszfalu (Bakony Mts). Bore Pe-31; 215/1. P: 42,8/107,2. L-Cenomanian
- 3, 4 *Acritosporites transdanubicus* n. sp.  
Olaszfalu (Bakony Mts) Bore Pe-31; 351/4. P: 29/105. L-Cenomanian.
- 7, 8 *Acritosporites transdanubicus* n. sp. Holotype.  
Olaszfalu (Bakony Mts), Bore Ot-83; 30/1. P: 40,9/102. M-Albian.
- 5, 6 *Acritosporites* cf. *triangularis* (DEÁK 1965) n. comb.  
Urkút (Bakony Mts), Bore U-4, 44,4/5. P: 29/99. Middle Albian.
- 9, 10 *Acritosporites sibiricus* (BOLCH. 1961) OBONIZ. 1964.  
Zirc (Bakony Mts) Bore Zt-61; 69,5/1. P: 35,8/98,3. M-Albian.
- 11 *Acritosporites sibiricus* (BOLCH. 1961) OBONIZ. 1964.  
Oroszlány, (Bakony Mts) O-1891; 521/2. P: 45,5/103,5. M-Albian.
- 12, 13 *Acritosporites sibiricus* (BOLCH.) OBONIZ. f. *minor* n. f.  
Tés (Bakony Mts). Tt-27; 39/1. P: 36,9/106. Middle Albian.
- 14, 15 *Acritosporites rasellus* (ALEKS. 1962) n. comb.  
Olaszfalu (Bakony Mts), Pe-31; 307/4, P: 41/108. Lower Cenomanian





*Acritosporites transdanubicus* n.fsp.

Pl. 3., figs. 3, 4 and 7, 8.

Holotype: Pl. 3., figs. 7, 8. Prep.: Ot-83, 30/1. P: 40.9/102.

Locus typicus: Oroszlány (Vértes Mts), Bore Ot-83, 30.0 m.

Stratum typicum: Tés Formation, clayey marl, Middle Albian.

Diagnosis: trilete miospores, with triangular amb, convex sides, and rounded corners. Laesura is simple and does not project from the surface of the spore. On the proximal surface three lacuna occur, in each of which is located one spherical tuberculum of 4–7  $\mu$  diameter. In the middle of the distal surface there is a lacuna, generally surrounded by a ring-like border, 2–3  $\mu$  thick. In this, centrally, a tuberculum 8–10  $\mu$  in size is located.

Spore size: 33–42  $\mu$ .

Differential diagnosis: *Acritosporites transdanubicus* n.fsp. similarly to *A. kyrtomus* n.fsp. has an exine ornamented only with four tubercula but it is of smaller size than that of the latter species, and with a thinner exine (2–2.5  $\mu$  thick) with no torus in it.

Occurrence: The genus *Acritosporites*, represented by this species, first appears in the upper level of the Vértessomló Formation and even in the Pénzeskút Formation several specimens occur. (Lower Albian to Lower Cenomanian).

*Acritosporites* cf. *triangularis* (DEÁK 1965) n.comb.

Pl. 3., figs. 5, 6.

1965 *Chomotriletes triangularis* BOLCH., DEÁK, p. 60, Pl. 3, figs. 1–4. (non *Chomotriletes triangularis* BOLCH. 1956).

Diagnosis: see DEÁK (1965, p. 60), as a description.

Remarks: DEÁK (1965) described a species that has lacunae on its proximal surface but tuberculum occur only in the distal lacuna. This species forms, therefore, a transition between the form *Acritosporites* (al. *Matonisporites*) *excavatus* described by BRENNER (1963), having only a distal lacuna, and the form *Acritosporites aralensis*, described by OBONIZKAJA (1964), having proximal and distal lacunae, as well as the species having tuberculum in lacunae (*A. sibiricus*, *A. transdanubicus*).

Occurrence: Tés Formation (Bakony—Vértes Mts).

*Acritosporites sibiricus* (BOLCH. 1961) OBONIZ. 1964

Pl. 3., figs. 9–11.

1961 *Lygodium sibiricum* n.sp., BOLCHOVITINA, p. 84, Pl. 27, fig. 4., Krasnoyarsk (USSR), Cenomanian—Turonian.1963 *Tauocusporites spackmanii* n.sp., BRENNER, p. 69–70, Pl. 22, figs. 2, 3. Potomac Group, II/B, Albian.1964 *Acritosporites sibiricus* (BOLCH. 1961) n.comb., OBONIZKAJA, p. 123–124, Pl. 10, fig. 5. Kizikum (USSR), Cenomanian—Turonian.1966 *Lygodium sibiricum* BOLCH., MARKOVA, p. 218, Pl. 2, fig. 24. West-Siberia (USSR), Cenomanian—Turonian.

Remarks: OBONIZKAJA (1964) recorded the sizes of ten specimens and obtained the following size-limits at this species: spore size = 47.9–80  $\mu$ ; length of laesura = 11.3–29.7  $\mu$ ; thickness of the exine = 3.1–5  $\mu$ ; diameter of distal lacuna = 25.5–33.2  $\mu$ ; diameter of distal tuberculum = 10.0–25.1  $\mu$ ; diameter of proximal

tubercula = 9.0–16.0  $\mu$ . On the basis of the sizes of the *Taurocusporites spackmanii* BRENNER 1963 and of presence of a torus and six proximal tubercula, it may be considered as a junior synonym of *A. sibiricus*. There are also six tubercula on the proximal surface of the torus-bearing form, described by DEÁK (1964) under the name *Chomotriletes oculatus*. On its distal surface, however, occur not one but two tubercula, in a lacuna surrounded by one ring.

Occurrence: *A. sibiricus* in its Siberian sites is a characteristic spore of the Cenomanian—Turonian. In the Albian of Potomac Group of USA and in the Albian sediments in Hungary it can also be found.

*Acritosporites sibiricus* (BOLCH.) OBONIZ. 1964

f. *minor* nov. f.

Pl. 3., figs. 12, 13.

Remarks: The new form of the former species is of 34–40  $\mu$  size, with 1–3  $\mu$  thick exine. It is a spore with torus, having seven tubercula.

Occurrence: this form firstly appeared in the upper part of the Tés Formation but frequently can be found only in Pénszeskút Formation.

*Acritosporites rasellus* (ALEKS. 1962) n.comb.

Pl. 3., figs. 14, 15.

1962 *Lygodium rasellum* n.sp. ALEKSANDROVA (in ALEKSANDROVA, BOEVA, and GRIGORJEVA, 1962).

1966 *Lygodium rasellum* ALEKS, MARKOVA, p. 218, Pl. 2, fig. 23 a, b.

Description: trilete spore, with subcircular amb and convex sides. Laesura is long,  $r=1$ , on both sides bordered by a thick torus, which forms a thickened part of the exine. In the proximal lacunae six, in the distal lacuna one tubercula can be found, their diameter being 12–14  $\mu$ . The distal lacuna has a diameter of approximately 26  $\mu$  and is surrounded by a 4–5  $\mu$  thick, protruding ring of irregular outline. The exine is 4–6  $\mu$  thick, on the distal surface the part between the ring and the equatorial edge are of verrucate ornamentation.

Remarks: This species is similar to the *A. kyrtomus* n.fsp. with four tubercula, but having verrucate ornamentation on the distal surfaces.

Occurrence: It is rare form of the sediments of Pénszeskút Formation (Lower Cenomanian).

### Conclusion

In the taxonomic part, 19 sporomorph types are described, among these one new genus and nine new species. This demonstrates the great richness in ornamented spores of the Lower and Middle Cretaceous in Hungary.

Foveate, foveoreticulate, foveorugulate and raretuberculate forms are described and illustrated photographically. Taking into consideration their stratigraphical distribution in the Transdanubian Cretaceous sediments examined by us, the following conclusions may be drawn from Table 1.:



Table 1. Stratigraphical distribution of the examined spores in the Transdanubian sediments

Sümege Formation		Vértes-Somló Fm.	Tés Fm.	Pénzeskút Fm.		Lithostratigraphic units
Barre-mian	Lower Aptian	Lower	Middle Albian	Upper	Lower Cenoma-nian	Chronostratigraphic units
						<i>Klukisporites tuberosus</i>
						<i>Fueloepisporites minor</i>
						<i>Fueloepisporites rotundus</i>
						<i>Klukisporites scaberis</i>
						<i>Klukisporites lacunus</i>
						<i>Fueloepisporites crassus</i>
						<i>Fueloepisporites vokanyensis</i>
						<i>Fueloepisporites cf. foveasolidus</i>
						<i>Acritosporites transdanubicus</i>
						<i>Ischyosporites baconicus</i>
						<i>Ichyosporites estherae</i>
						<i>Acritosporites cf. triangularis</i>
						<i>Acritosporites sibiricus f. minor</i>
						<i>Acritosporites sibiricus</i>
						<i>Fueloepisporites hungaricus</i>
						<i>Klukisporites foveolatus</i>
						<i>Foveasporis agathoecus</i>
						<i>Acritosporites rasellus</i>
						<i>Acritosporites kyrtomus</i>

1. The Middle-Albian sediments (Tés Formation) have a central place on the time-axis of the spores examined here. The of certain species comes to an end here while that of other species begins here. In respect of the spore-pollen complexes, this period may be regarded as the time of change of the flora.

2. The majority of the species of the genera *Klukisporites* and *Fueloepisporites*, are characteristic of the Lower Cretaceous, up to the Lower Albian stage, while the representatives of the genera *Foveasporis* and *Acritosporites* appear from the Middle Albian, occur in the younger sediments.

In an earlier paper (JUHÁSZ, 1977), studying the Lower and Middle Cretaceous spores, we established that the large number of species of the schizaeaceous spores reflects the situation that the mother plants of the spores of this types had their acme at that time. We have suggested dealing with the *Lygodium*-type spores at the level of the family Lygodiaceae within the order Scizaeales. On this basis, we would classify among the spores of lygodiaceous and klukiaceous affinity several representatives of *Concavissimisporites*, *Impardecispora*, *Trilobosporites*, *Trilites* and, in all probability, we may also place here the species of the genera *Klukisporites*, *Ischyosporites*, *Foveasporis*, *Fueloepisporites* and *Acritosporites*.

COUPER (1958) placed the first described species of *Klukisporites* into the "relationship circle" of the Schizaeales, on the basis of their great similarity to the in situ spores of *Klukia exilis* (PHILLIPS) RACIBORSKI and *Stachypteris picans* POMEL, plants of schizaeaceous nature. Their place in this order is rendered probable by the species described by BALME (1957) as well. KRUTZSCH (1959b) on the problem of *Foveasporis agathoecus*, has asserted the schizaeaceous nature too.

BOLCHOVITINA (1961) and MARKOVA (1966) put the *Acritosporites* species in the genus *Lygodium* because, by the thick exine and the ornamentation of these forms, affinity with the Lygodiaceae is suggested. The thick exine and ornamentation of the species placed in *Fueloepisporites* new genus are very close those of the recent *Lygodium* spores. We suppose, therefore, that the spores considered in the present paper show the greatest affinity with the tropical fern family the Lygodiaceae and Klukiaceae which have been lived the acme-stage in the Lower and Middle Cretaceous.

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**INTRASPECIFIC MORPHOLOGICAL VARIATIONS  
AT RECENT ANGIOSPERMATOPHYTA POLLEN GRAINS  
(Short communication)**

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**Abstract**

In this paper the taxonomical value of the morphological varieties of the recent Angiospermatophyta pollen grains is summarized. We have succeeded in establishing more than one type of varieties. The numerical variety of the germinal aperture at *Brevaxones* is frequent enough, at *Longaxones*, however, it is rare. A fundamental morphological variety occurred at the *Loranthus* species. The varieties of qualitative characteristics can be ascertained in the course and characteristic of the colpus, in case of *Longaxones*.

The intraspecific morphological variations have a great significance in the exact knowledge of sporomorphs. In this respect, the results connected with the trilete spores and the Gymnosperm pollen grains with bladders (KEDVES 1961; MARTIN 1961) are to be mentioned. In case of the Angiosperm pollen grains this problem is less investigated, as yet, there were only published a few data (VAN CAMPO 1961, 1973, 1976; STOCKMARR 1970; KÖNIGSSON 1971).

We have performed light-microscopical examinations on the pollen grains of a very large number of recent Angiosperms. In the course of these investigations, we took precious good care of the qualitative morphological variations. We came generally to the following conclusions.

1. The Angiosperm pollen grains are in respect of their qualitative traits comparatively permanent, some variety manifests itself primarily in size, resp. in the measurable characteristics.

2. In certain cases, there are obvious qualitative varieties, as well, but between these species no evolutionary connection can be established. The qualitative variation may appear in different branches of the development of the Angiosperms. It is probably an atavic phenomenon, a remainder of the obviously great variational disposition of the primitive ancestors.

As to the single variations, we have established the following types and set examples for these:

1. Numerical variation at certain characteristics, in particular cases the change in the number of germinalia. This question is most known primarily in case of the pollen grains of *Brevaxones*.

2. The variation of the fundamental morphology of the pollen.

3. The qualitative variation of a characteristic which is essential from the point of view of characterizing the pollen.



4. The lack of an essential characteristic of the pollen grain as a variation phenomenon.

1. The numerical variation of the germinal pore is frequent enough in case of *Brevaxones*. At *Longaxones* it is rare, particularly at the tricolporate pollen grains. We have observed the tetracolporate variation of a pollen grain of this type in case of *Cassia artemisioides* (Plate, 3, 4).

2. A fundamental morphological variation was observed in more than one *Loranthus* species. From among these, *L. platyphyllus* and *L. acaciae* are to be mentioned. For the pollen grains of this type in the genus some ancestral peculiarities may be established. Namely, their morphology, in polar aspect, is very similar to the *Complexiopolis* fgen. which represents one of the most ancient types of the *Brevaxones* pollen grains. This is interesting in itself, in case of the *Loranthus* species, following a special course in life, so much the more because — according to JARZEN and NORRIS (1975) — the genus *Macrosolen* (Loranthaceae) is similar to the species of *Aquilapollenites* (cf. ERDTMAN 1971). In this way, the two main types of the ancient Angiospermatophyte pollen grains (*Normapolles*, resp. *Aquilapollenites*) equally show some morphological similarity with Loranthaceae. In the cases investigated the triplan form is extremely frequent (Plate, 7, 8, 11, 12) which is similarly an ancient characteristic, a variation of the extreme concave ancient forms. The pollen grains of this type were originally described in the *Latipollis* fgen. by KRUTZSCH (1959). This taxonomy was later taken over by several authors. GÓCZÁN, GROOT, KRUTZSCH and PAČLTOVÁ (1967) recognized that the *Latipollis* type was a variation phenomenon and divided the here classified species into the genera, recognized in the polar aspect. In this respect we have so far not known a corresponding recent variation phenomenon. It is probable that in this case the point in question is convergence.

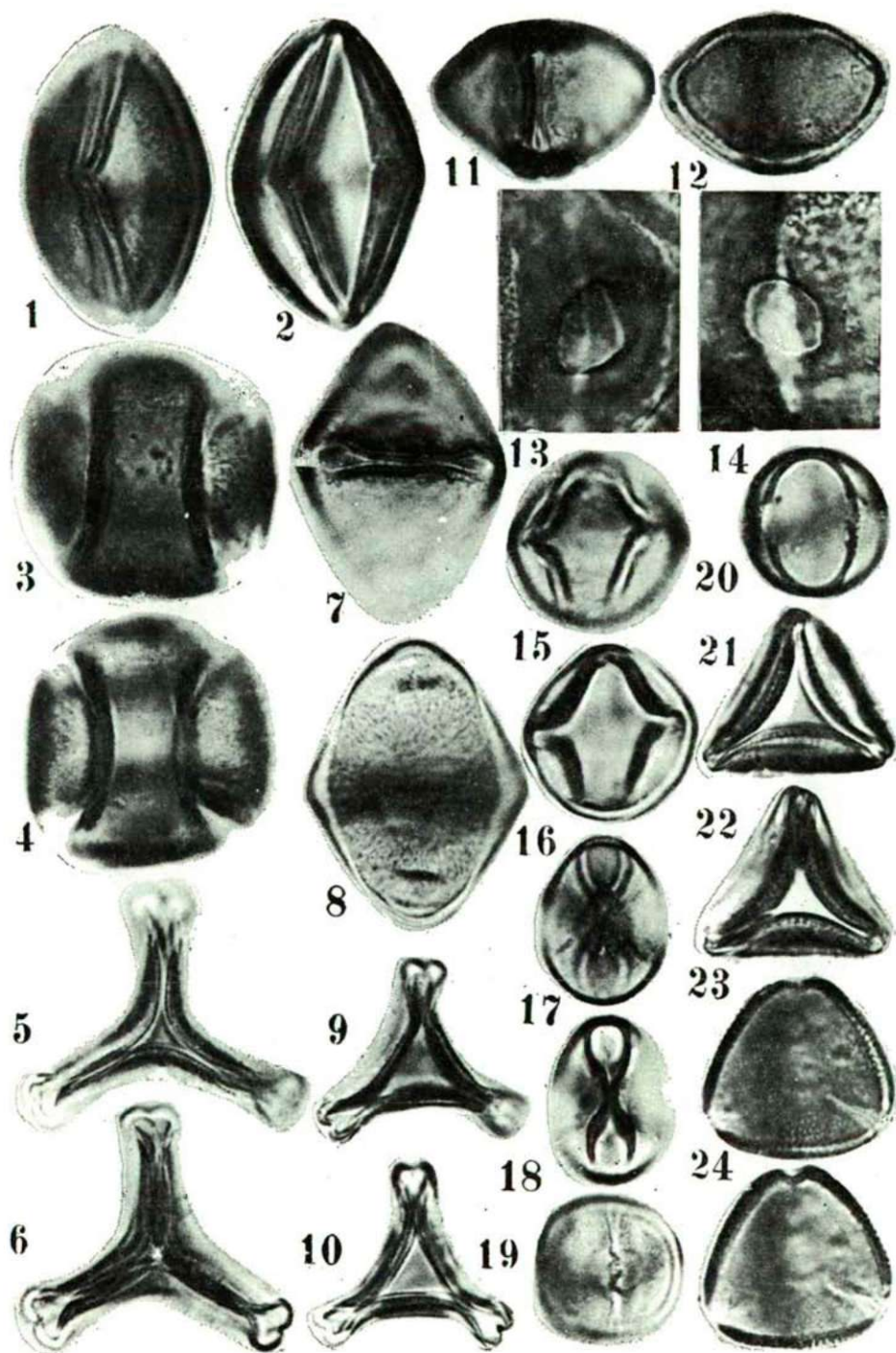
3. There are published here two data concerning the qualitative variation of a characteristic.

We have observed the numerical variation of the partly short colpi of the *Alangium platanifolium* (Plate, 13, 14). 3 colpi: 41 per cent, 4: 57 per cent, 5: 2 per cent. According to ERDTMAN's book (1952), this is characteristic of the single species of the genus. The exine of the species investigated is thick enough, particularly the nexine. This surrounds the endogerminalia with a characteristic caverna (Plate, 13). In some extreme cases this can be missing (Plate, 14).

#### PLATE EXPLANATION

- 1, 2 *Cassia artemisioides* GAUD. Tricolporate, typical pollen.
- 3, 4 *Cassia artemisioides* GAUD. Tetracolporate form, in polar view.
- 5, 6 *Loranthus platyphyllus* HOCHST. ex A. RICH., polar aspect, typical form.
- 7, 8 *Loranthus platyphyllus* HOCHST. ex A. RICH. Form of "Latipollis type".
- 9, 10 *Loranthus acaciae* ZUCC., typical form, in polar aspect.
- 11, 12 *Loranthus acaciae* ZUCC. Form of "Latipollis type".
- 13, 14 *Alangium platanifolium* HARMS. Details from the fine structure of colporus.
- 15, 16 *Clethra alnifolia* L.
- 17, 18 *Trichodesma africanum* (L.) R. BR. var. *abyssinicum* BRAND, typical form.
- 19, 20 *Trichodesma africanum* (L.) R. BR. var. *abyssinicum* BRAND, casually occurring form.
- 21, 22 *Comandra pallida* A. D. C., typical form.
- 23, 24 *Comandra pallida* A. D. C., casually occurring form

N: x1000





At the tricolporate pollen grains the course of the colpus may often be decisive even from the point of view of identification and it is a remarkable characteristic in any case. Such is, for instance, the pollen grains of the Cyrillaceae, Clethraceae, and Theaceae genera. We are publishing, for instance, the typical pollen of *Clethra alnifolia* (Plate, 15, 16) where the declination of colpi in the direction of the equator has proved to be a constant character. The contrary of this, the convergence of colpi, gives the characteristic of the *Trichodesma africanum* var. *abyssinicum* pollen (Plate, 17, 18). We have, however, observed at this species, if rather rarely, so-called colpi of regular course, as well (Plate, 19, 20). At fossil investigations the deviation like this is today already rather intergeneric than interspecific.

4. The pollen grain of *Comandra pallida* is very interesting, with certain peculiarities that are characteristic of the ancient *Brevaxones* (Plate, 21–24). The arcus-like formations of its typical forms, reaching from apex till apex, are characteristic. In case of a few specimens this characteristic is entirely missing (Plate, 23, 24). This morphological difference is followed in case of fossil forms by essential taxonomical consequences.

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## CHANGES INDUCED BY CHILLING IN THE ION UPTAKE, GROWTH AND ANATOMICAL STRUCTURE OF RICE ROOTS

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### Abstract

The after-effect of a brief cold treatment on the ion uptake, growth and the anatomical structure of thermophilic rice (*Oryza sativa* L.) and non-thermophilic wheat (*Triticum aestivum* L.) roots was investigated. It was established that in rice an unexpectedly large K-ion uptake occurred following the cold stress. In the case of wheat under similar experimental conditions neither the ion uptake nor growth showed any irregularity. The anomalous ion transport in thermophilic rice was considered a passive influx (or exchange), made possible by the change in permeability of cell membranes as a result of cold stress. The anatomical investigations confirmed that cold treatment resulted in the destruction of the root hairs and 4—5 cell layers of the primary cortex. The meristematic cells of the root apex were disorganized to such an extent after chilling that no root elongation could be detected. Vigorous side rooting from the pericycle, about 2—3 cms from the tips of roots (still in the root hairs zone) occurred 6—7 days after the chilling. Full regeneration of the roots followed on the 8—9th days after the brief cold treatment when the basiton type root was detected.

### Introduction

During our earlier ion uptake experiments it was established that the roots of thermophilic plants, such as rice, cucumber, sorghum, melon, etc. show an anomaly in K-ion uptake after a sudden change in temperature (ZSOLDOS, 1968). A considerably larger K-ion influx than expected was observed at 0 °C or near it. A close connection can be detected between the degree of anomalous influx and the length (age) of the root: the shorter (younger) the root, the more pronounced is the K-ion uptake anomaly (ZSOLDOS, 1975).

It was also established that the K-ion uptake anomaly belongs to determined root zones. In the case of rice, e.g., it occurred mainly in the one centimeter segment of the tip, while with the cucumber it was detected in the second 1 cm segment counted from the tips on account of the fairly long calyptra (ZSOLDOS—KARVALY, 1978).

Better understanding of the K-ion uptake anomaly was gained from examinations dealing with the K-content of root segments. At low temperature the K-content of the thermophilic rice roots decreased considerably as a result of the increased permeability of cell membranes, occurring mainly in the apical zone of the roots (ZSOLDOS—KARVALY, 1978).

Related to the important metabolic role of the K-ion, other symptoms occur after cold treatment, too. It is important to notice that under completely similar experimental conditions with non-thermophilic wheat, neither the ion uptake ano-



maly, nor the K-ion loss could be detected in the root tips. From this we supposed that there may be an important difference in the compositions of the cell walls and membranes of root cells of thermophilic and non-thermophilic plants.

It is well known that many plant species of tropical and subtropical origin are subject to chilling injury when exposed to temperatures below about 10 °C, but above the freezing point (LYONS, 1973; LEWIS—WORKMAN, 1964). Chilling injury is one limiting factor in crop production that has received increased attention. Although the importance of low temperature to the life of the plants has been known for a long time the problems relating to the effects of cold stress that are important for both practical and theoretical reasons, are still not clear.

Though most plants survive the cold stress, later (under normal temperature conditions) disturbances in metabolism and growth and consequently decrease in production can be expected. It follows that the examination of the so-called after effects must be considered very important, too.

Thus we here give an account of our investigations on the ion uptake, and on the growth structural changes in roots of rice and wheat seedlings exposed to cold stress.

### Materials and Methods

1. Growth of seedlings: Rice (*Oryza sativa* L. cv. *Dunghan Shali*) and winter wheat (*Triticum aestivum* L. cv. *Jubilejnaja*) seedlings, grown in  $5 \times 10^{-4}$  M  $\text{CaSO}_4$  solution, were used in our experiments. Surface sterilized seeds were rinsed in running tap-water for 6 hours (rice) and 3 hours (wheat) respectively, and then allowed to germinate on filter paper for 2 days (rice) and 1 day (wheat), respectively. The seedlings were grown in  $5 \times 10^{-4}$  M  $\text{CaSO}_4$  solution under standard conditions in a phytotron (CONVIRON, Cabinet Model EF7) at 25/30 °C day/night temperatures with 16-hour illumination of  $10^4$  lux and with 65% relative humidity.

2. Ion uptake experiments: The potassium uptake studies were carried out in a  $5 \times 10^{-4}$  M  $\text{K}^{86}\text{RbCl}$  solution. The roots of 6–8 day old plants were excised and immediately washed for 10 minutes in distilled water at room temperature. After a 30 minute chilling pretreatment at 0, 10 and 22 °C about 2 g of the root material was immersed in 500 ml of aerated uptake solution at room temperature. The pH of the uptake solution was adjusted to 6.3–6.4 by adding 0.1 N HCl, and was checked again after the absorption period. For technical reasons  $^{86}\text{Rb}$  was to monitor the  $\text{K}^+$  ion movement; the suitability of this method was carefully checked before the experiments were conducted. The uptake medium contained 15  $\mu\text{Ci}$   $^{86}\text{Rb}$  per litre in each case. Root samples were removed from the absorption solution at 10 minute intervals, rinsed three times in distilled water at 22 to 23 °C, and left to dry for thirty minutes on filter paper. The isotope contents of experimental material were measured with a scintillation counter as described earlier (ZSOLDOS—KARVALY, 1978).

3. Chilling treatment of intact plants: The seedlings were chilled for five hours at 0 °C on the sixth day after the start of germination, after which they were cultivated in Hoagland stock solution diluted thirty times and/or in tapwater. The growth of plants, the pH value of the water culture, etc. was systematically checked and photographed.

4. Root anatomical investigations: Preparation for light microscopy was carried out as follows. Specimens of the roots taken on the third and sixth days after the brief 5 hour chilling treatment, were fixed in 40% ethanol. Fixed tissue was dehydrated in a graded series of alcohol (40, 50, 70, 96 and 100% alcohol). For microtome sectioning a 2–3 cm root tip and that portion of the root tip where the side branching starts were then embedded in celloidine. Then 10–15  $\mu$  thick sections were prepared with a sliding microtome, stained with Erlich-type acidic haematoxyline, fixed in Canadian balsam, and used for light microscope and photograph investigations.

### Results and Discussion

1. Ion uptake investigations: Fig. 1 shows the  $K^+$ -ion uptake under normal ( $22^\circ C$ ) temperature conditions of rice roots, previously exposed to 30 minutes cold stress. The time curves clearly demonstrate that the  $K^+$  ion uptake as an after-effect of the cold injury differs from the normal: the lower the temperature of the water used for the precooling, the higher the  $K^+$ -ion uptake at  $22^\circ C$ . Because according to our earlier investigations the permeability of cell membranes considerably increases and a passive  $^{86}Rb-K^+$ -ion exchange (or leakage) occurs especially in the apical zone of root after  $0^\circ C$  chilling (ZSOLDOS—KARVALY, 1978), we can say that the ion influx (or exchange) described above is not connected to metabolism. This is justified by uptake experiments done with different root segments of thermophilic plants under cold stress (ZSOLDOS—KARVALY, 1978a).

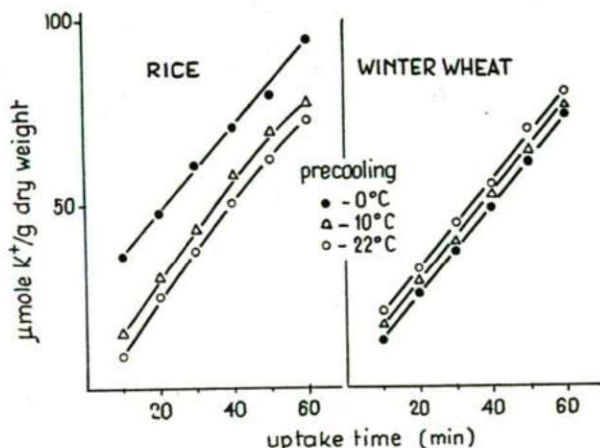


Fig. 1. The after-effect of precooling on the potassium uptake of rice and winter wheat roots. Uptake solution:  $5 \times 10^{-4}$  M  $K(^{86}Rb)Cl$ ; precooling time: 30 min.

Not only is it true that non-thermophilic plants, such as winter wheat, do not show any  $K^+$ -ion uptake anomaly under the same experimental conditions, it is true that after cold treatment unfavourable metabolic effects result in a moderately decreased ion uptake as may be seen in Fig. 2. Because the cold treatments were brief, it is obvious that in thermophilic plants under such conditions only the change in membrane permeability (damage) makes possible the  $K^+$  influx anomaly (or ion exchange) and the considerable  $K^+$ -ion leakage of the apical root-zone during the cold treatment, respectively (ZSOLDOS—KARVALY, 1978).

2. Growth experiments: Fig. 3 shows the growth of rice and winter wheat seedlings after 5 hours cold treatment. A growth disturbance in both rice roots and shoots can be detected as soon as two days after the relatively brief low temperature treatment. At the same time, under completely identical experimental conditions no damage was detected in non-thermophilic winter wheat.



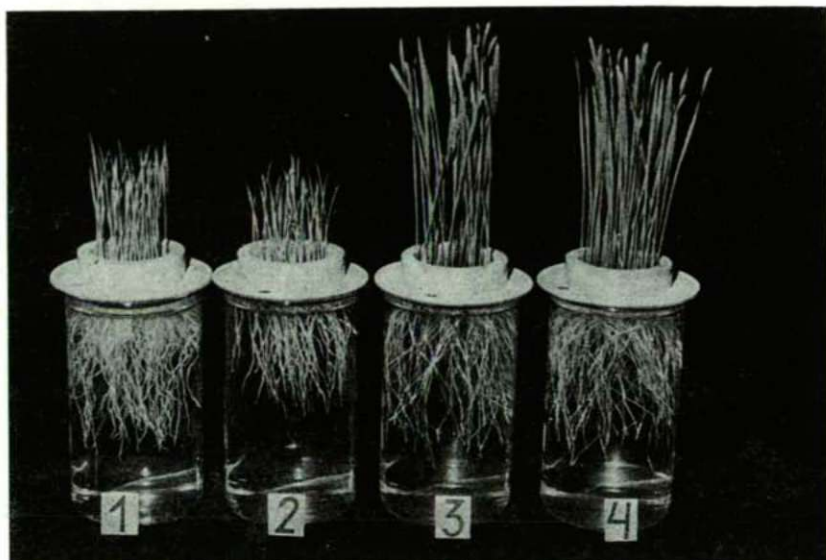
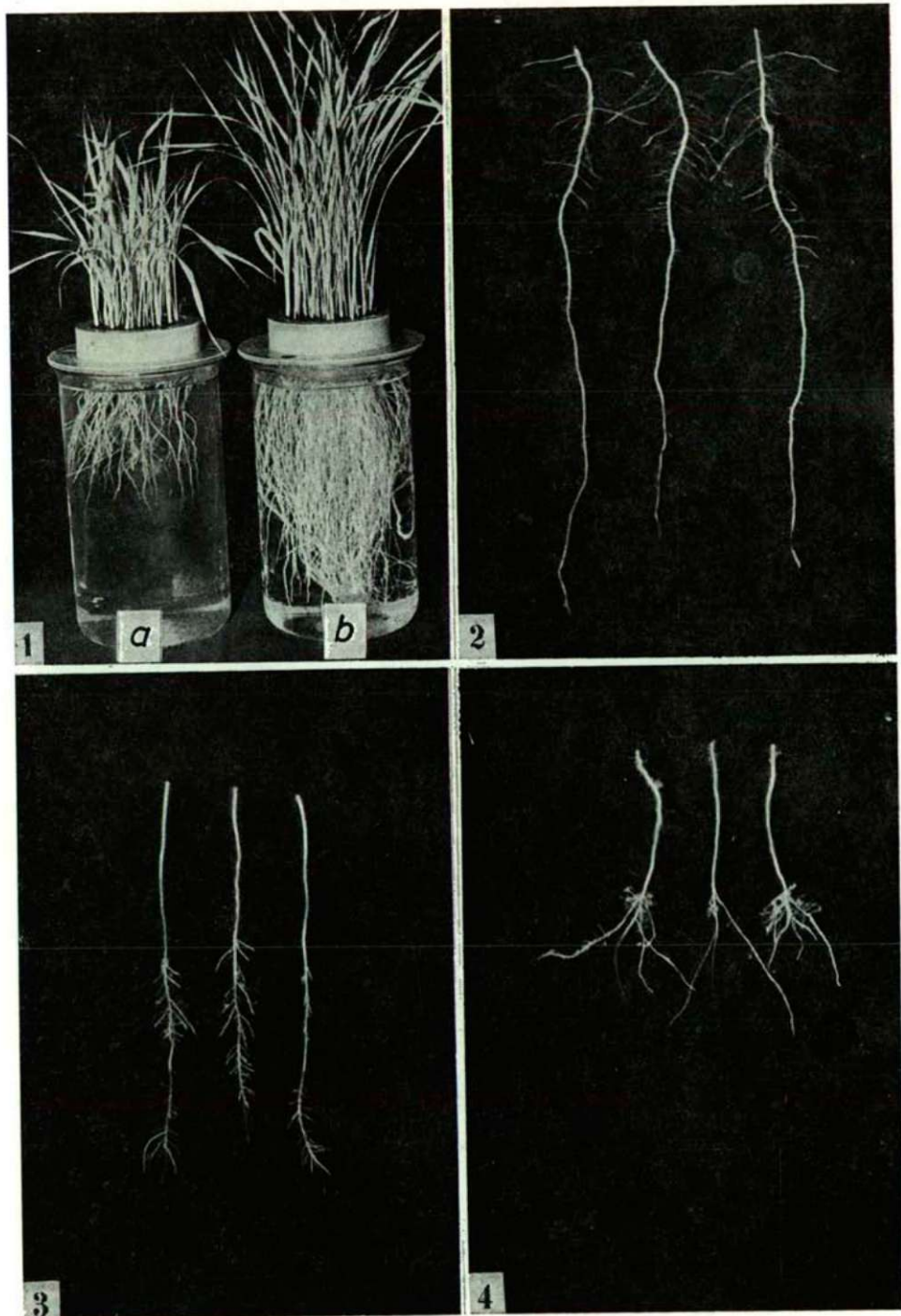


Fig. 2. The manifestation of brief chilling treatment in the growth of rice and winter wheat seedlings on the second day after treatment. From left to right: 1. rice (control); 2. rice (5-hours chilling treatment at 0 °C); 3. winter wheat (control); 4. winter wheat (5-hours chilling treatment at 0 °C).

Plate 1 shows rice plants on the ninth day following cold treatment. Comparing the photos seen in Fig. 3 and Plate 1 it is very clear that: 1) the roots of cold-treated rice plants remained practically the same length (no elongation growth); 2) as a result of low temperature stress an intensive development of side-roots occurred.

In 8–9 days after the cold treatment we detected that the roots having a length of 9–10 cm and that the tips of the side roots became discolored to a pale yellow, and later gradually decayed. From this fact we can conclude that there may be considerable differences between the different root segments (organizational conditions) as regards cold sensitivity. In connection with this we must draw the attention to the changes occurring in the fine structure of the cell membranes (permeability) after the cold stress. This is considerably influenced by its chemical composition e.g. the proportion of saturated and unsaturated lipids and fatty acids (FARKAS et al. 1975, FARKAS et al. 1977, LYONS 1973, ROCHE et al. 1975).

- Plate 1. Fig. 1. The manifestation of brief chilling on the growth of rice seedlings on the fourteenth day after treatment. From left to right: a) untreated (control); b) chill-treated. Fig. 2. Untreated rice roots, age: 21 days, growing in water culture. Fig. 3. Chill-treated rice roots on the ninth day after treatment with intense side-root formation above the root tips. (After chilling treatment seedlings were cultivated in a diluted Hoagland solution, i.e. at a "low-salt condition"). Fig. 4. Chill-treated rice roots on the fourteenth day after treatment with strong side-root formation above the destroyed root tips. (After chilling treatment seedlings were cultivated in tapwater, i.e. at a "high-salt" condition)





3. Anatomical studies: Microscopic investigations demonstrated that 2 or 3 days after the cold treatment a considerable change in construction and disorganization occurred in the roots (Plate 2). The hexarch type rice roots, secondarily still unthickened showed the changes in the following ways:

*a)* as an effect of cold treatment the root hairs, and the underlying 4–5 cell-layers of the primary cortex, died. At the same time we could not detect changes in the stele of the roots. The primary cortex seemingly protected the interior tissue-layers from being damaged;

*b)* besides this, the meristem layers of the root tips also showed some disorganization.

After the mentioned tissue-decay the stele of the roots behaved as it does when the roots begin thickening under optimal conditions. At the distance 2–3 cm from the root tips — as it was mentioned earlier — still in zone of root hairs, an intensive side-root development started. This process could be detected later in zones farther from the tip too. The newly developed side-roots which were nearer to the tips developed more vigorously.

On the third day after the cold treatment the development of side-roots from the one layer pericycle started at many places. This development of side-roots, however, differed from normal side-root development in the following:

*a)* the supplementation of the decayed tips began in the root-hair zone;

*b)* the cell-division started at more places at the same time than under normal conditions;

*c)* in spite of the fact that the side-roots formation can be detected almost the whole length of the cold-treated roots, they formed not basiton system, but temporarily an acroton type root system because the side-roots formed closer to the tip and grew faster. One of these (Plate 1) later usually overgrew the others and somehow took the guiding role. Thus the destroyed root tip became regenerated;

*d)* the above side-root formation was strongly influenced through the salt concentration of the cultura medium too. (Compare Figs. 3 and 4 in Plate 1).

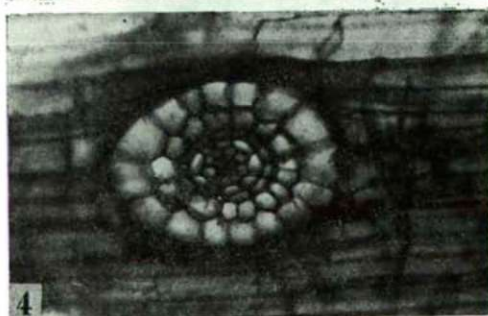
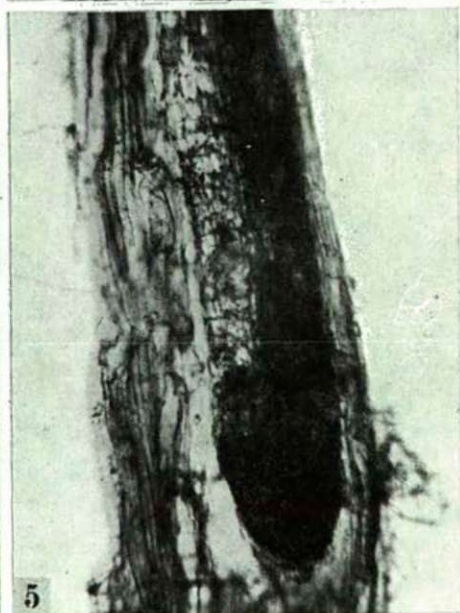
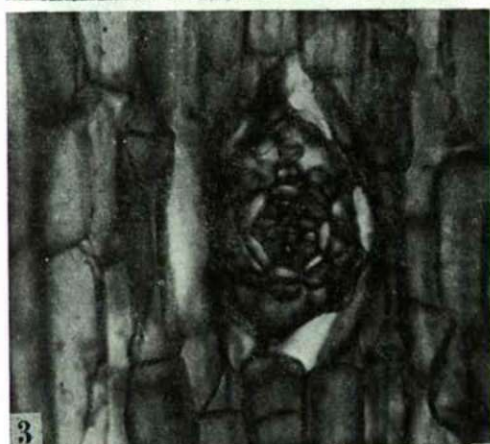
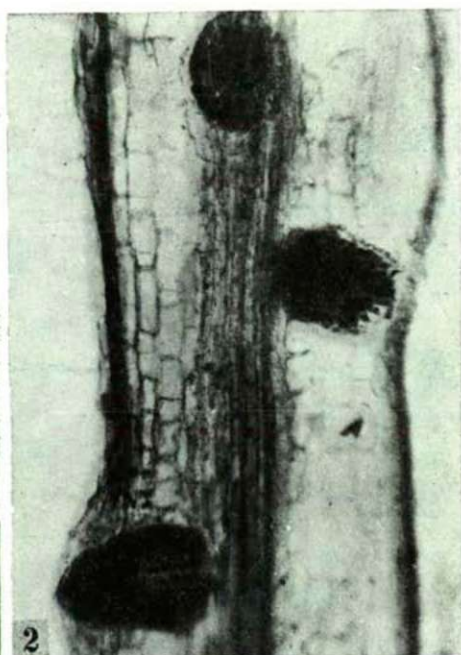
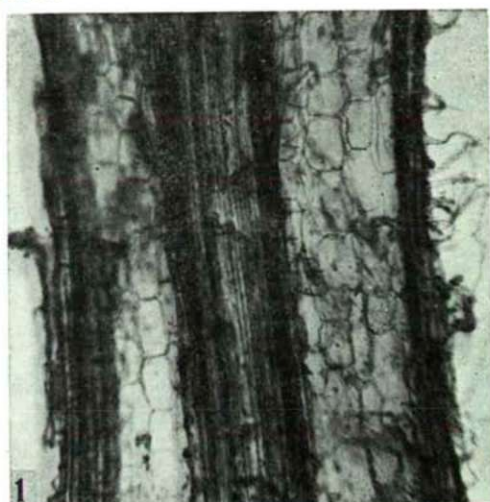
An interesting observation is that the substitution of the "lost" root tip can be so intensive that some of the newly developed roots, immediately after their formation, grow not in a sidewise direction but perpendicularly downward directly into the decayed cortex of the old roots. The regeneration of the cold-treated roots is completed when we observe basiton type roots externally, too, about 14–16 days after cold stress.

### Conclusions

1. On the basis of  $K^+$  uptake and efflux after a sudden fall in temperature, i.e. cold stress, plants can be divided into two large groups. One group (the thermophilic rice belongs into this) show a  $K^+$  uptake anomaly and a large scale structural change

- Plate 2. Fig. 1. The external layers of rice cells, exposed to cold stress, began disorganizing (x370).  
 Fig. 2. The side-root formation begins at many places from the pericycle on the third day after cold treatment (x370).  
 Fig. 3. Cross-section of the tip of a young side-root (x370).  
 Fig. 4. Cross-section of an older side-root (x370).  
 Fig. 5. Side-root developing the closest to the decayed apical meristem grows downwards through the decayed tissues (310)

Plate 2





and disorganization in the roots after cold stress. This phenomenon cannot be observed with the other group (in our case winter wheat) under the same experimental conditions.

2. The after-effects of the cold-stress, that is the changes in the ion uptake and especially in the root structure draw attention to the important role played by cell membranes in the course of cold resistance (damage).

3. Important differences appeared in the cold damage of some of the root segments (zones). On account of this it is necessary to do some comparative examinations of the segments in the course of which we can get more concrete information about the chemical composition of cell membranes (segments) and in this way about the biochemical background of cold resistance.

4. The disorganization of the apical meristem is explained by the considerable change in membrane permeability accompanying cold sensitivity and by the  $K^+$  leakage afterwards. Under such conditions the  $K^+$  concentration, having crucial importance to the metabolic processes, cannot be provided just in the apical meristem.

5. As it is well known that auxin plays a chief role in the initiation of roots, we must not forget about the possible role of growth-regulators in connection with the irregular side-root formation as a result of cold stress. Obviously it is not by chance that after the cold stress of the apical meristem (i.e. the supposed place of auxin synthesis), elongation growth ceases and that after this the structural changes leading to side-root formation occur and are preceded by the occurrence of a convenient hormone level.

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## SOME DRYINIDS FROM MALAYSIA (HYMENOPTERA)

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### Abstract

Dryinids parasites of rice-feeding Cicadellidae: *Nephotettix nigropictus* (STÅL), *N. virescens* (DISTANT), *Recilia dorsalis* (MOTSCHULSKY) and Delphacidae: *Nilaparvata lugens* (STÅL), *Sogatella* sp. are listed hereunder along with some new species: *Chelogyne ephippiger* (DALMAN), *Pseudogonatopus hospes* PERKINS, *Ps. sarawaki* sp. n., *Ps. ponomarenkoi* sp. n. from Sarawak.

Dr. D. D. MUNROE, Agricultural Research Centre in Semongok (Sarawak), studied the parasites of Cicadellidae and Delphacidae living in rice and he also reared some Dryinid specimens. The latter were identified by me whose list follows together with hosts and other data.

#### Subfam. Anteoninae:

*Chelogyne ephippiger* (DALMAN), 1818

*Gonatopus ephippiger* DALMAN, 1818, K. Vetensk. Acad. Handl., 8 (4): 81 ♀

*Chelogyne ephippiger*: 1914, KIEFFER, Das Tierreich, 41: 179

*Anteon (Chelogyne) ephippiger*: 1939, RICHARDS, Trans. R. ent. Soc. Lond., 89 (8): 267 ♀ ♂

*Chelogyne ephippiger*: 1975, Ponomarenko, Ins. Mongolia, 3: 315

Specimens examined: Sarawak, 3<sup>d</sup> Div., Ng. Tada, Sq. Kabah, 1. ii. 75 Hill. Padi leg.  
D. D. MUNROE 2 ♀

Distribution: From Lapland to Germany, Malaysia, Mongolia.

#### Subfam. Gonatopodinae:

*Pseudogonatopus hospes* PERKINS, 1912

*Pseudogonatopus hospes* PERKINS, 1912, Bull. Rep. Expt. Sta. Hawaii Sugar Plntrs Ass., 11: 12 ♀

Specimen examined: Sarawak, 1st Div., Payah Paloh, 22—23. vii. 76, ex *Nilaparvata lugens* (STÅL) (Delphacidae), emerged 12. viii. 76, D. D. MUNROE 1 ♀

Distribution: China, Java, Malaysia.

#### *Pseudogonatopus sarawaki* sp. n.

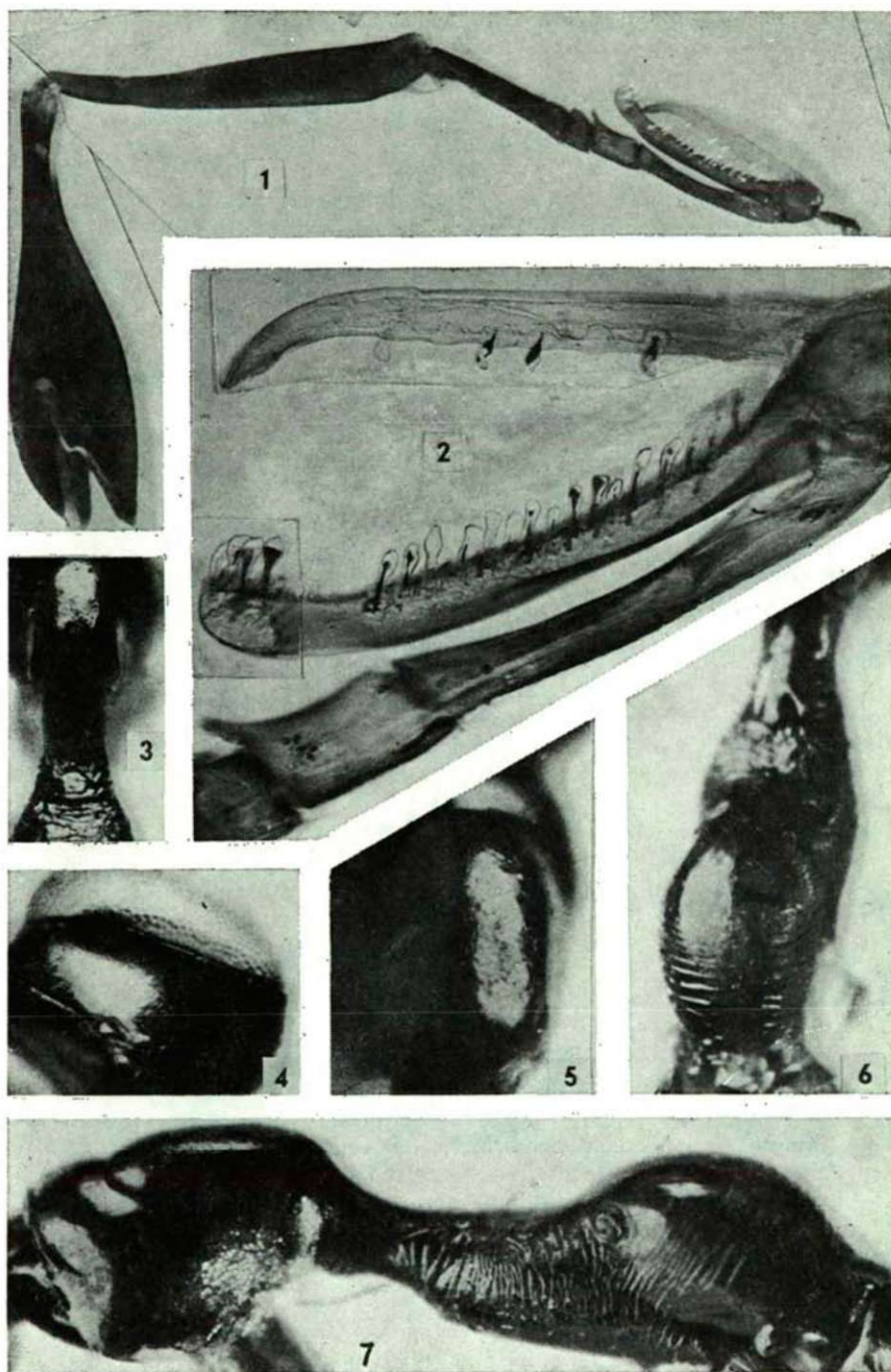
♀—Length 4 mm. Black; face around antennae, clypeus, mandibles, except red teeth, antennal joints 1—2, lateral margin of pronotum, fore coxae and trochanters, upper side of fore tibia, fore tarsal joints 2—3, apical part of joint 4, enlarged claw, middle and hind trochanters, as well as, tarsal joints, posterior margin of abdominal segments 5—6, an irregular transversal streak before posterior margin of segment 4 and last abdominal segments yellowish to yellowish red; flagellum brown; poste-



rior side of head, posterior part of pronotum, postnotum, propodeum, middle and hind coxa, femora, partly tibia, middle of abdominal segment 1, small spots on segments 2-4 dark red to reddish translucent. Body with trace of silvery short microscopic pubescence, ventral side of thorax and abdomen with sparse light hairs.

Head including eyes, in frontal view, about two-thirds as long medially as broad (15:23), widely excavated posteriorly, temples strongly broadened, largest diameter of eye and temple, in lateral view = 9:5. Frons with a short and a narrow keel beginning at fore ocellus, surface finely alutaceous, shining (Fig. 4), frons steeply bent towards clypeus, deeply impressed between eyes. Half frons distinctly narrower than eye, width of half frons at fore ocellus: width of eye (viewed from above) = 4:7. Eyes conspicuously converging towards clypeus. Ocelli in an acute angle, anterior one touching keel, POL:OOL = 1:3.5. Clypeus triangular, sharply protruding. Mandibles with four teeth, lower one about twice as long as broad at base. Maxillary palp with 4(2+2), labial palp with 2 joints. Malar space as long as length of the antennal joint 2. Antennal joint 1 (scape) little bent, more than twice as long as 2, thicker than joint 3, which being the narrowest joint, joint 3 twice as long as scape. further joints gradually thickened to last joint, penultimate joint more than 15, times as long as broad, length and breadth proportions of antennal joints 1-11 = 5(2):3(1.5):10(1):4.5(1.5):4.5(1.5):4.5(1.5):3.5(1.5):3.5(1.5):3.5(2):3.5(2):5(2.) Length proportions of pronotum:mesonotum:scutellum:metanotum:propodeum (viewed from above) = 15:5:3:4:16. Pronotum with a conspicuous transverse furrow at about anterior third, clearly dividing an anterior area from a tumescent posterior area (Fig. 7), nearly quadrate, almost as broad as long (14:15), and nearly as long as propodeum; pronotal collar and disc shining, with scattered very fine punctures, only just at base of disc and pronotal collar laterally, before posterior margin densely punctured (Fig. 5). Mesonotum quadrate, as long as broad before scutellum (Fig. 3), finely shagreened medially and laterally, with some transversal wrinkles towards lateral side of scutellum (Fig. 7). Scutellum not sharply defined especially in front, with some punctures, shining only medially. Upper surface of metanotum shagreened and wrinkled medially (Fig. 3), densely and rather deeply transversally wrinkled laterally (Fig. 7), continuing stronger and denser on mesopleuron. Propodeum nearly two-thirds as broad as long (10:16), in dorsal view, sides equally converging in front as behind, in profile rising to a point about two-thirds of its length (Fig. 7), then sinking to orifice, rising distinctly higher than pronotum, dorsal surface shining, anterior part unsculptured, laterally deeply and densely wrinkled, posterior surface, also declivous part sparsely and transversally wrinkled (Fig. 6). Fore coxae thick, more than twice as long as broad (13:6); fore trochanters as long as coxae, distinctly less thickened distally, length:breadth of trochanter = 13:3.5, thin proximal stalk as long as distal thickened part; fore femora (Fig. 1) strongly thickened and clavate basally, thickest part of femora nearly one-quarter of its length (7:27); fore tarsi with joints 1-4 together as long as tibia (9+2+3+9=23), joint 1 (basitarsus) and 4 of equal length, joint 3 a little longer than 2, joint 3 produced into a strong proximal anterior (inner) hook (Fig. 1); articulated (mobile) part (Fig. 2) distinctly longer than enlarged claw (13:11),

Fig. 1-7. *Pseudogonatopus sarawaki* sp. n., 1: fore leg, 2: chela, 3: pronotum-scutellum, 4: frons, 5: pronotal disc, 6: propodeum, 7: thorax in lateral view. (Orig.)





articulated part with two rows of 13 lamellae, latter expanded at the tip and with a distal group of about 8 lamellae; enlarged claw with 6 large lamellae (Fig. 2), with one bristle in front and with a subapical tooth. Middle and hind femora strongly thickened on its proximal two-thirds. Abdomen finely alutaceous, weakly shining, last abdominal segment compressed laterally.

Specimen examined: "Sarawak 1st div., Payah Paloh, 23. vii. 76", "ex *Nilaparvata lugens* (Stål) 22. vii. 76, S. KUEH" 1 ♀ holotype Hym. Typ. No. 3658 Budapest.

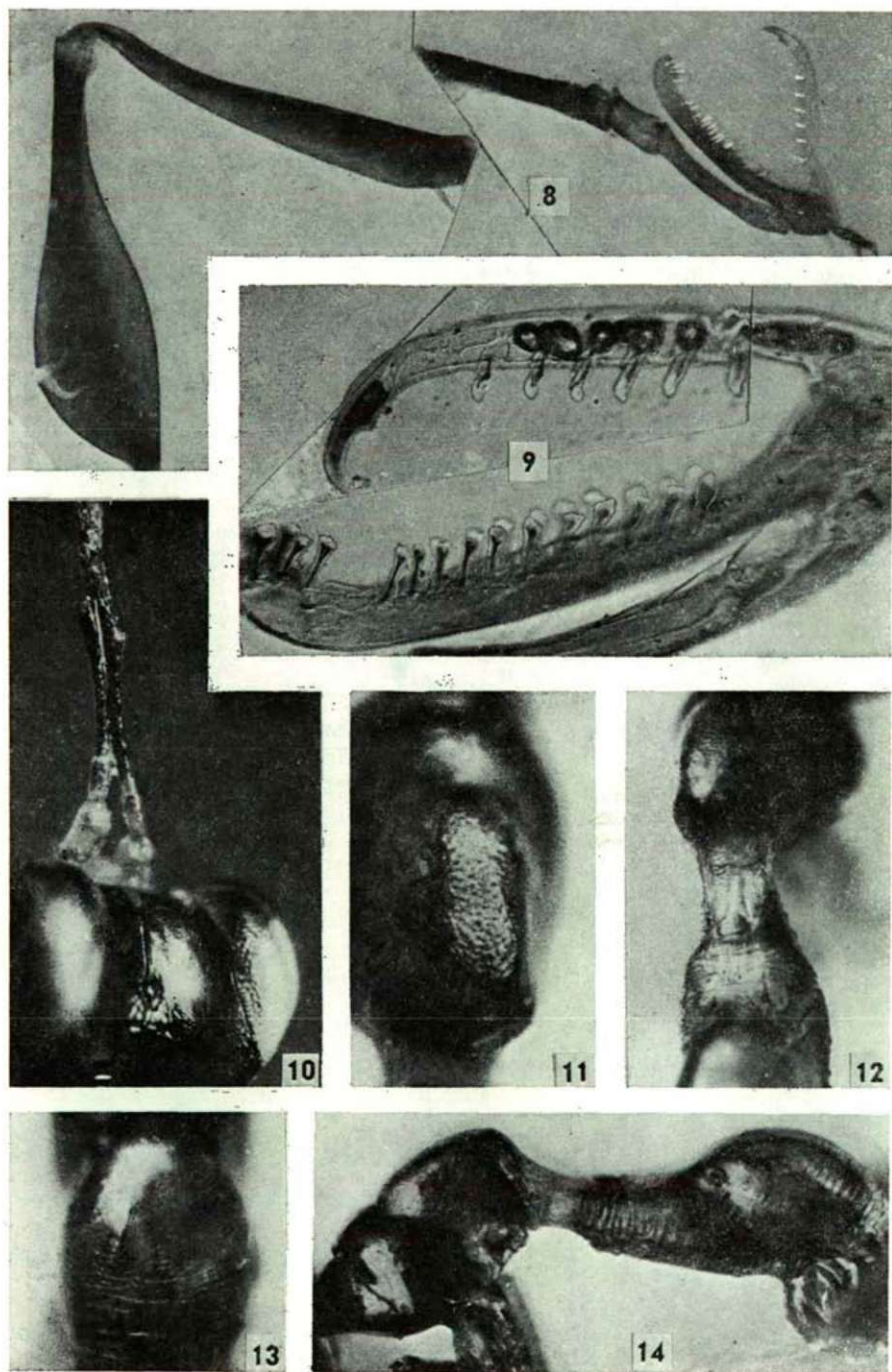
This species is related to *Ps. nudus* PERKINS, 1912, but differs especially by its larger size, not 2.75 mm, by the colour, by the sculpture of pronotum. It differs from *Ps. dichromus* PERKINS, 1905, by the length proportions of the antennal joints, namely, the third joint is distinctly longer than scape, by the sculpture of head, by the distinct and dense punctures of pronotum.

#### ***Pseudogonatopus ponomarenkoi* sp. n.**

♀-Length 3.8 mm. Head, abdomen largely black, thorax almost entirely yellowish brown. Lower face of head and scape (Fig. 10) yellowish; occiput, posterior side of head and antennal joint 2 yellowish red. Anterior margin narrowly, as well as, postero-lateral margin of pronotum black (the whole pronotal collar dark brown on paratype); postero-lateral part of mesonotum, scutellum and mesopleuron darker brown to black (or black together with small basal ring on paratype). Legs largely yellowish brown; lower side of fore coxae, as well as tibia and basitarsus, middle and hind trochanters entirely light yellowish; lower side of fore trochanters, fore femora, upper side of fore tibia and metatarsus, as well as posterior ends of middle and hind femora, a long streak on hind tibia more or less darker brown. Middle of abdominal segment 1, last segments partly (as well as a narrow streak on tergites 2-4 of paratype), yellowish red. Body with some scattered silvery short hairs.

Head deeply excavated and strongly emarginate behind, two-thirds as long as broad including eyes (in frontal view 14:21), temples strongly broadened, largest diameter of eye and temple in lateral view = 9:5; eyes strongly converging towards clypeus; surface of frons shining, finely alutaceous, with a weak central keel beginning at fore ocellus (Fig. 10), vertex and declivous part of frons towards clypeus finely shagreened, only moderately shining. Clypeus convex, semicircularly protruding. Mandibles with four teeth, lower one about twice as long as broad at base, 1st very small. Maxillary palp with 4(2+2) joints, labial palp with 2 joints. Malar space as broad as length of scape (5) or twice and a half longer than width of mandible basally. Antenna rather short, scape and pedicel thicker, joint 3 the slenderest (Fig. 10), flagellum moderately thickened beginning with joint 4, all joints at least twice as long as broad except penultimate one, last joint clavate, nearly as broad as scape, scape little bent, distinctly shorter than twice length of joint 2 (pedicel), joint 2 longer than its twice width, joint 3 twice as long as scape, joints 4-6 as long as joint 2, last joint as long as scape, length (and breadth) proportions of antennal joints 1-11 = 5(2): 3.5(1.5): 10(1): 3.5(1.2): 3.5(1.3): 3.5(1.3): 3.5(1.5): 3.5(1.5):

Fig. 8-14. *Pseudogonatopus ponomarenkoi* sp. n., 8: fore leg (tibia separated from tarsal joints), 9: chela, 10: head (view from above) with first antennal joints, 11: pronotal disc, 12: pronotum-scutellum, 13: propodeum, 14: thorax in lateral view. (Orig.)





3.5(1.5):2.5(1.7):5(1.7). Pronotum shorter than propodeum and distinctly broader in front than its length medially, length (and breadth) proportions of pronotum: mesonotum: scutellum: metanotum: propodeum (viewed from above) = 12(15): 5(5 basally):1.5:5:14(9.5). Pronotum with a conspicuous transverse furrow at about its anterior third, clearly dividing an anterior area from a tumescent posterior area (Fig. 14), pronotal collar smooth shining, with some scattered punctures laterally, disc densely distinctly punctured (Fig. 11), only weakly shining on its upper surface, finely punctured and striated laterally. Mesonotum granulated and with about 6 distinct transversal wrinkles laterally (Fig. 14). Scutellum rather well distinct, anterior margin semicircularly rounded (Fig. 12); mesopleuron densely transversally wrinkled (Fig. 14); base of propodeum smooth, weakly shining (Fig. 13) only very finely punctured. Upper side of metanotum (Fig. 12) as well as declivous part of propodeum partly striated, partly finely wrinkled (Fig. 13), posterior part of propodeum, lateral part in front more distinctly transversally wrinkled (Fig. 14). Fore coxae thick nearly along its whole length, about three times as long as broad (14:5); fore trochanters almost as long as coxae and only distally thickened about one-third of its length (4:13); fore femora strongly thickened and clavate basally, (Fig. 8), thickest part of femora nearly one-quarter of its length (6:24); fore tibia hardly longer than fore tarsal joints 1-4(23:9+1.5+2.5+8), joint 1 hardly longer than joint 4(9:8), joint 2 nearly as long as broad (1.5:2); joint 3 nearly twice as long as joint 2(2.5:1.5), produced into a strong proximal anterior (inner) hook

(Fig. 8); articulated (mobile) part longer than enlarged claw (13: 12), articulated part with two rows of 11 lamellae (Fig. 9), latter expanded at the tip and with a distal group of about 5 lamellae; enlarged claw with 6 large lamellae (Fig. 9) and with a subapical tooth. Middle and hind femora conspicuously thickened on its proximal two-thirds. Abdominal tergites smooth, finely alutaceous, only weakly shining, last segment compressed laterally.



Specimens examined: "Sarawak 1st Div., Payah Paloh, 14. xii. 76", "ex *Sogatella* sp. 15. xii. 76 D. D. MUNROE" (=Delphacidae) (Fig. 15) 1 ♀ holotype Hym. Typ. No. 3659 Budapest; "Sarawak 1st Div., Payah Paloh, 12. viii. 76", "Probably ex *Nephotettix nigropictus* (STÅL), S. KUEH", (=Cicadellidae), 1 ♀ paratype Hym. Typ. No. 3660 Budapest.

I have named this species in honour of the Dryinids specialist Dr. N. G. PONOMARENKO of Moscow, who kindly took part in the separation of the new species.

This species is related to *Ps. dichromus* PERKINS, 1905, but differs from it by the length proportions of the antennal joints, since joint 3

Fig. 15. *Sogatella* sp. (Delphacidae) with *P. ponomarenkoi* sp. n. pupa (Orig.)

is remarkably longer than scape; by the colour, by the densely punctured pronotum, by the not smooth and shining metathorax, etc.

It also differs from *Ps. ortholabis* KIEFFER, 1906, by the less dense transversal wrinkles of the lateral side of mesonotum, mesopleuron and propodeum, by the lack of the longitudinal shallow furrow on the propodeal disc, by the less densely punctured propodeal disc, by the enlarged claw, by the lighter colour, etc.

It further differs from *sarawaki* sp.n. by the sculpture of the pronotal disc, by the wrinkles of the mesopleuron and by the much finer wrinkles of the propodeum, by the fore tarsal joints, by the colour, etc.

### *Neogonatopus lunatus* (KLUG), 1810

*Gonatopus lunatus* KLUG, 1810, Beitr. Naturh., 2: 164 ♀

*Neogonatopus lunatus*: 1939, RICHARDS, Trans. R. ent. Soc. Lond., 89 (8): 216 ♀

*Neogonatopus lunatus*: 1965, MÓCZÁR, Ann. Hist.-nat. Mus. Nat. Hung., 57: 401

*Neogonatopus lunatus*: 1975, OLMI & CURRADO, Boll. Mus. Civ. Venezia, 27: 58 ♀

*Neogonatopus lunatus*: 1975, PONOMARENKO, Ins. Mongolia 3: 316

Specimens examined: Sarawak, 1st Div., Payah Paloh = vii. 76, ex *Nephotettix nigropictus* (STÅL), 14. ix. 76, S. KUEH, 1 ♀; 23. viii. 76, ex *N. nigropictus*, nymph, 13. ix. 76, S. KUEH, 10 ♀; 4. viii. 76, ex *N. nigropictus*, S. KUEH 1 ♀; as above except 8. viii. 76, 1 ♀; 20. vii. 76, swept from padi with *N. nigropictus*, S. KUEH 1 ♀; 6. x. 76, B. H. VOON 1 ♀; x. 76, ex *Recilia dorsalis* (MOTSCHULSKY) B. H. VOON 2 ♀; as above except 1. x. 76, 1 ♀; 23. viii. 76, ex *Recilia dorsalis* 12. ix. 76, S. KUEH 1 ♀; 4. viii. 76, ex *N. virescens* nymph, 25. viii. 76, S. KUEH 1 ♀; as above except 25. viii. 76 and 13. ix. 76, 3 ♀; as above except 28. viii. 76, and 15. ix. 76, 1 ♀; as above except 25. viii. 76 and 14. ix. 76, 1 ♀; as above except 25. viii. 76 and 23. ix. 76, 1 ♀.

Distribution: Europe, Central Asia, Mongolia.

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## SPECIAL MITOCHONDRIAL TRANSFORMATION IN THE INNER SEGMENT OF VISUAL CELLS

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### Abstract

The fairly dense mitochondria in the inner segment of one type of visual cell in the retina of a 6 to 8 days old chick form a close association with large lipid droplets. Another type of visual cell is without lipid droplets. Their granular central substance derives from the breakdown the mitochondria. Apart from mitochondria, the appearance of vesicles and granules and the ribbon lath was also observed in the young visual cells by the authors.

### Introduction

Knowledge of the retina of animals standing taxonomically at widely different levels of advancement has been brought about by a large number of light- and electron-microscopic morphological, histochemical and experimental physiological investigations. Valuable handbooks and compendia by BLOOM and FAWCETT (1964), DOWING and BYKOTT (1963), EAKIN (1963), POLYÁK (1957), De ROBERTIS (1969), VILLEGAS (1960) are available to those who are interested in the very complicated process of the mechanism of vision. Yet, it should be stated that there are several unsolved problems in its physiology. Very different theories have emerged on the question of colour vision. Knowledge of the characteristics of the photoreceptor cell structure is very defective and uncertain, as it is almost everywhere in want of a morphological basis. On the basis of our investigations, we want to describe, with some pictures, a peculiarity of receptor cells perceiving the first signs of light or colour in a very early phase of the post-embryonic development: mitochondrial transformations in the inner segment.

### Materials and Methods

The material of our investigation is the visual cells of the retina of 6—20 days old chicks. After removal of the eye, the retina was removed from the concentric outer coats with a lancet. 0.5—1 mm pieces of retina cut from the equatorial plane, after being prefixed in glutaraldehyde, were fixed with 1 percent osmium tetroxide, buffered according to Millonig. After being dehydrated, they were embedded in araldite. Sections were made, with the aim of culting in the tangential direction, by setting a Tesla BS 478 electron microtome according to the results of semi-thin sectioning. Photographs were made with a BS 500 electron microscope.

### Results

The cross-section of the retina of the young chick is very narrow. The stratification of its structure can be observed only with difficulty. The structural density of



the plexiform layers and the lack of pigmentation are the more important differences from the state in the adult animals.

In our examined material differences within, visual cells are striking in the semi-thin sections, and even more in the photographs from low magnification (Fig. 1-2). The distal part of the visual cells is a peripheral photoreceptive lamellar termination, well-demarcated from the inner segment which is rich in mitochondria and named the oval body.

In the early phase of development, these segments of visual cells, show another structure than in adults well-known from the literature.

The visual cells are close to one another: there is no connection between them. The transversely flattened light-receiving lamellae are fewer in the rod cells than in the cone cells but they are more protruding than in the cone cells (Fig. 1, 2, above). Between the lamellar systems the processes of the pigment epithelium are easily visible but they contain no pigment granules. The difference between the inner segments of the distal processes of visual cells is the most striking. The rod cells in the inner segments have lipid droplets of remarkably large size. The diameter of the lipid droplets vary (7-800 nm). Very many mitochondrion was always to be seen in their oval body. The visual cell rich in broad lipid droplets and long situated mitochondria in its inner segment is the rod cell, according to the data of De ROBERTIS (1958), COHEN (1961), NILSSON (1964), VILLEGAS (1960). The young chick has quite other characteristic ultrastructural organization in this cell.

The other visual cell to be seen in the lower part of the picture (Fig. 1-2) is most easily distinguished by the lack of inner-segment lipid droplets. On the basis of this peculiarity and published data, these cells in the oval body rich in mitochondria and can be distinguished by their large nucleus in the cell, by their wider perikaryon and wider proximal central process, we designated them as cone cells.

The differences of visual cells seems to be connected with the age. The functional mechanisms commencing from the visual cells particularly called attention to the formation of mitochondria. In the inner segment of both types of visual cell, there are several mitochondria, as in the visual cells of man and mammals generally. But the facts that the mitochondria are arranged perpendicularly to the longitudinal axis of the segment and that gaps are to be seen in the longitudinal arrangement, do not present themselves at all in the visual cells of the young chicken. The shape and density of the mitochondria of scattered situation remarkably differ in the inner segment.

### Rod cell

In case of the rod cell, as seen in photograph 2, above and even more clearly in the subsequent photograph (Fig. 3), the mitochondria which are of nearly identical diameter, form a mitochondrial grouping in the peripheral part of the inner segment.

The mitochondria of the inner segment of the rod cell, investigated carefully, show well limited double membranes. The inner membrane does not show any crista-like intussusception. Rather the matrix of the mitochondrion is filled in with a formation of tubuli touching both side-walls of the mitochondrion. These mitochondria may be as shown in our picture, in a close physiological connection with the lipid droplet (Figs. 2-4). It is often to be seen that one or other mitochondrion

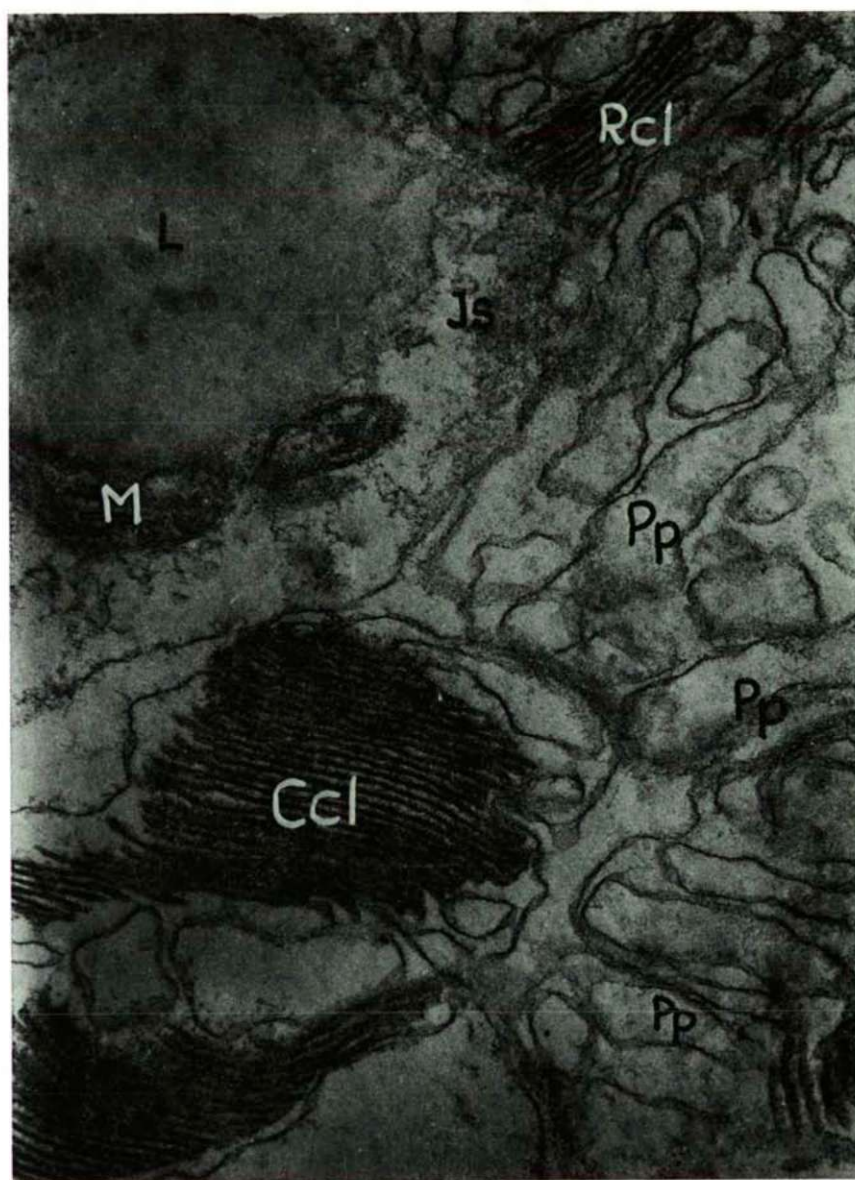


Fig. 1. Formation of the lamellar system of outer segment and of the inner segment of *Gallus domesticus* (6-day old). Rcl=rod-cell lamellae, Ccl=cone-cell lamellae, Js=inner segment, L=lipid droplet, M=mitochondrion, Pp=processes of pigment epithelia. Electron micrograph: x48 000.



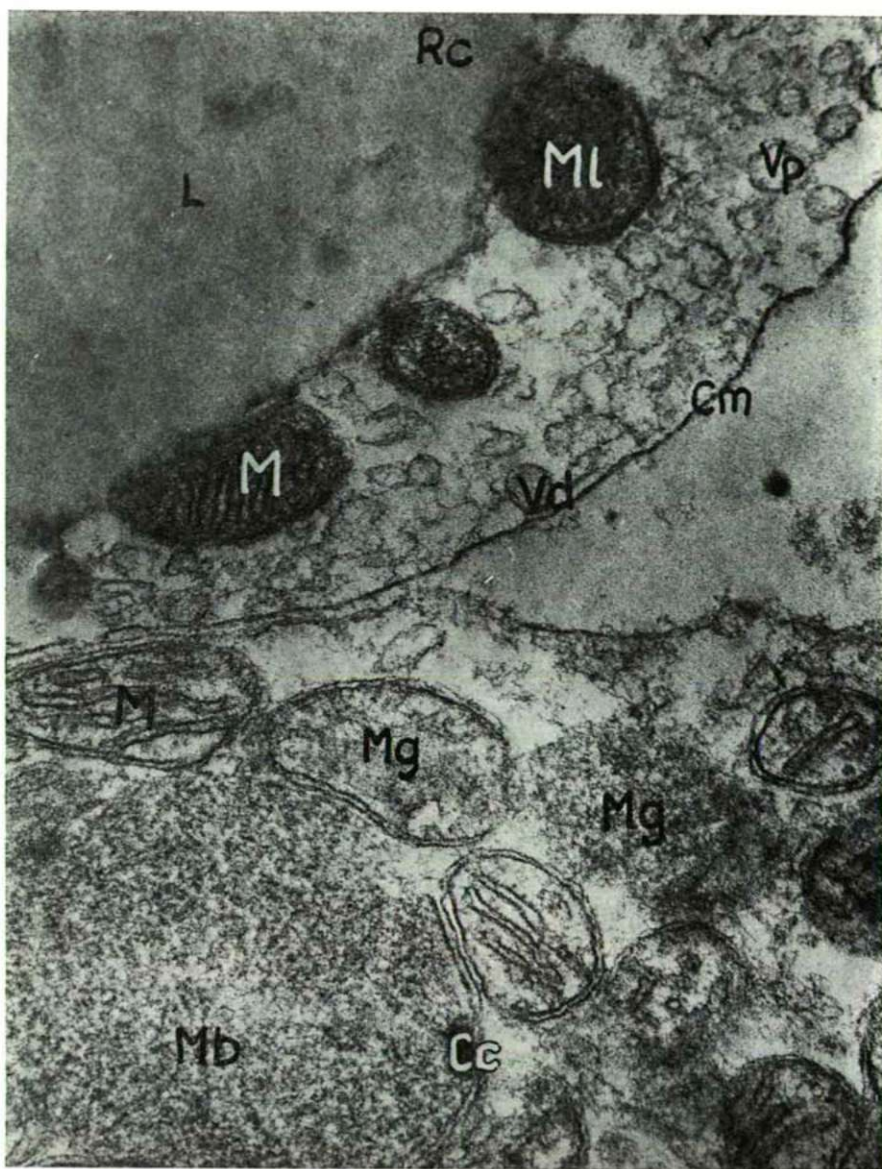


Fig. 2. Details of inner segments of the different types of visual cells of *Gallus domesticus* (8-day old). Rc=rod cell, Cc=cone-cell, L=lipid droplet, Mb=granulated central body, M=intact mitochondria, Ml=merging mitochondria undergoing granulation, Vp=cytoplasmic vesicle, Vd=vesicle for transmitting stimuli, (synaptic vesicle). Electron micrograph: x64 000.

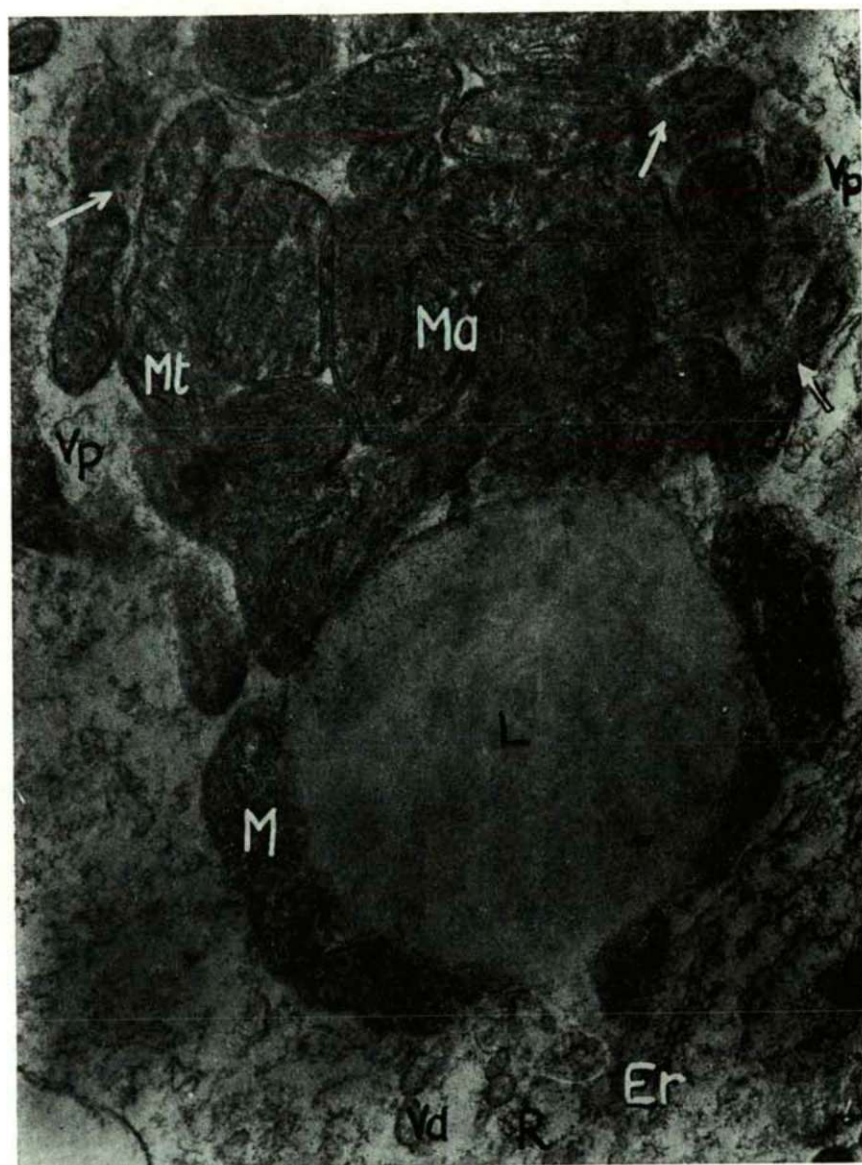


Fig. 3. Inner segment of a rod cell of *Gallus domesticus* (8-day old). L=lipid droplet, M=mitochondria, Ma=Aggregate of mitochondria, Mt=mitochondrial tubules, Er=rough endoplasmic reticulum, R=free ribosome, Vp=cytoplasmic vesicle, Vd=synaptic vesicle. (Arrows indicate constricted mitochondria.) Electron micrograph: x36 000.



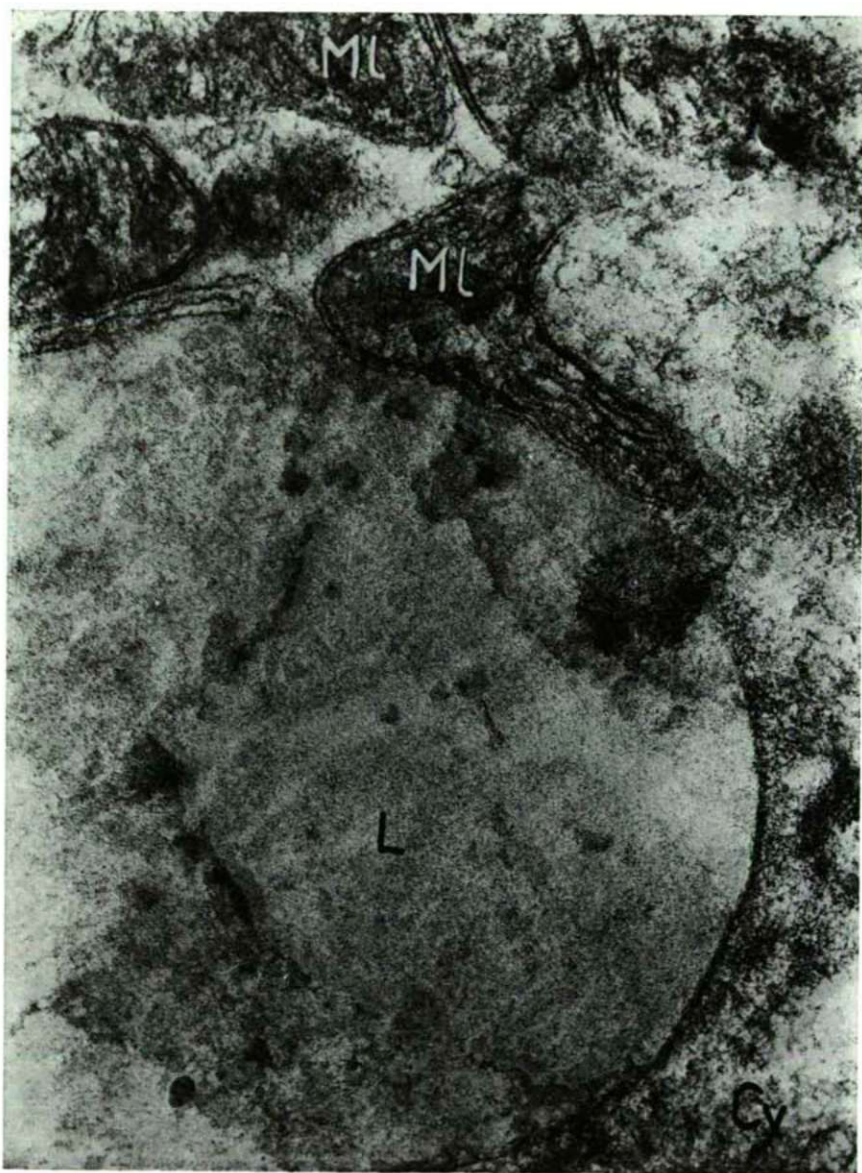


Fig. 4. Inner segment of a rod cell of *Gallus domesticus* (8-day old). Cy=cytoplasm, L=lipid droplet, MI=mitochondrion merged into a lipid droplet. Electron micrograph: x64 000.

penetrates into the lipid droplet. Before the penetration, in the basic substance of mitochondria the decomposition of the tiny granules can be noticed, then the membrane opens and we may suppose that the contents run into the lipid droplet. The size of the lipid droplet can be increased permanently by the presumably very rapid metabolism and transport of materials, and it may also be observed in semi-thin sections that the lipid droplets are "spotted". The merging mitochondria are replaced by intact mitochondria migrating from the periphery to the lipid droplets. We have frequently seen constricted mitochondria among the grouping places indicated with an arrow (Fig. 3). Similar phenomena can never be observed in the older longish mitochondria or in the nuclear region.

### Cone cell

In the cytoplasm of the inner segments, of the cells classed cone cells, there is no lipid droplet. There is a group of mitochondria, here also, situated towards the peripheral outer process, but they do not cohere. The mitochondria to be seen here are much more distinct. Their membrane consists of closed, double membranes, similar to the mitochondria of the rod cell, but the inner tubular structure is less. Gradual fusion of the cone cell mitochondria and the rearrangement of their lamellar systems maintain a centrally situated, strongly granulated "central body". The mitochondrial fusion can be seen particularly well in our Fig. 5. The granules of the central body migrate in part of the nuclear portion of the cone cell by cytoplasmic streaming but many more granules can be seen migrating towards the periphery and this suggests it is possible that play an important role in starting off the pigment production of the cells of the pigment epithelial cells.

### Basal parts of the visual cells

The rod cell has, as is well known, a longish nucleus and a thin perikaryon. With its process of fairly thin (450 Å) diameter it penetrates deeply in the direction of the bipolar cells and gets in synaptic touch with its rod bipolar cell by means of its very small spherule. In the nuclear region of the rod cell a weakly developed endoplasmic reticulum is noticeable. Along the cisternae of the endoplasmic reticulum some ribosomes appear, and at the basal end irregular groups of these are also visible. Apart from the ribosomes there are round dark granules of small size (250 Å) and larger ones (380 Å). Some lighter "cytoplasmic vesicles" which are ovoid usually occurred. The darker vesicles run in the direction of the spherula they are, therefore, to be considered as synaptic vesicles. It is interesting that already in the vicinity of the nucleus a strong, dense membrane fragment appears (Fig. 6). This lathlike formation may aptly be named a "ribbon lath". Similar laths appear, but only much later, in the perikaryon of cone cells, mainly in the thick proximal process of this, forming its continuation, which, with its enlarged peduncle, shows a number of synaptic connections with the strongly ramifying dendrite ends of the cone bipolars (Fig. 7).

### Discussion

The development of the young visual cells, sharply separated from one another and from the processes of the pigment epithelium, varies greatly in respect of the inner segment, at the beginning of the post-embryonic development. Among



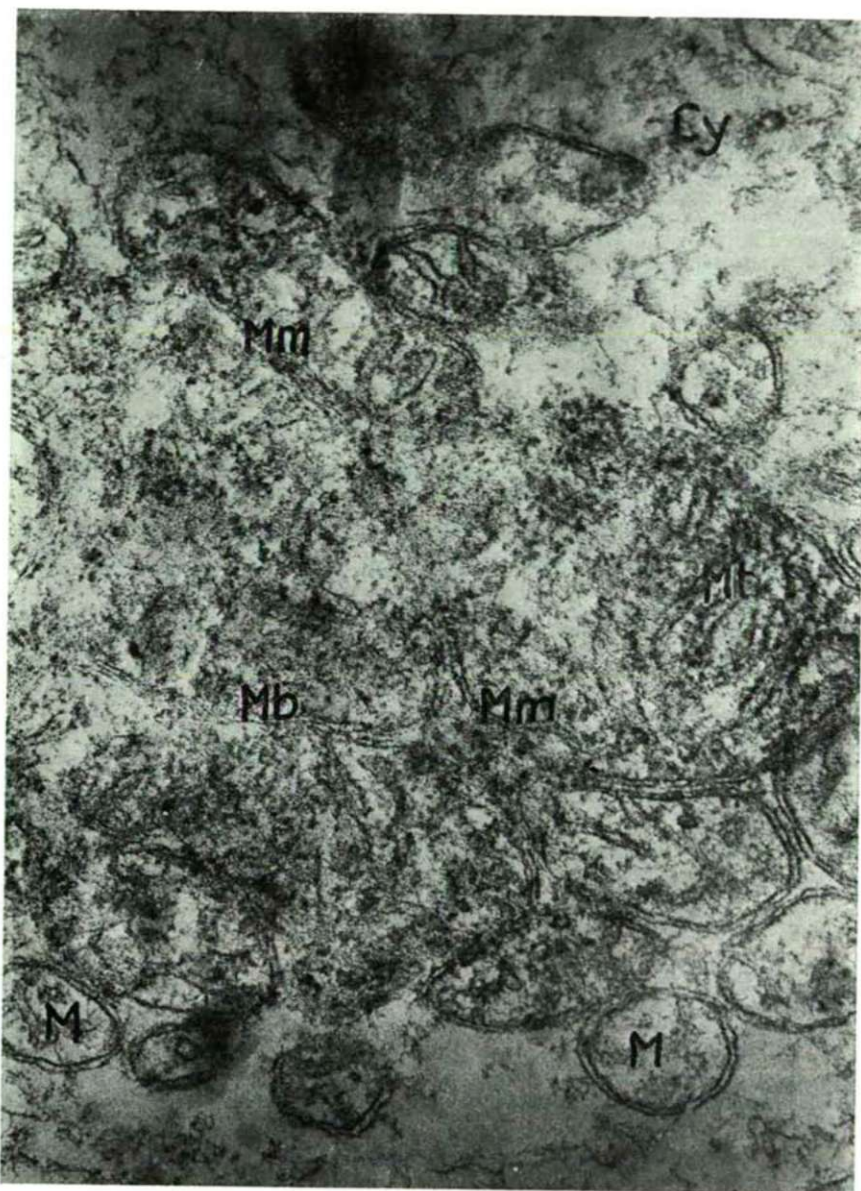


Fig. 5. Inner segment of a cone cell of *Gallus domesticus* (6-day old). Cy=cytoplasm, Mb=granulated central body, M=intact mitochondria, Mt=mitochondrial tubulus, Mm=mitochondrial membrane. Electron micrograph: x64 000.

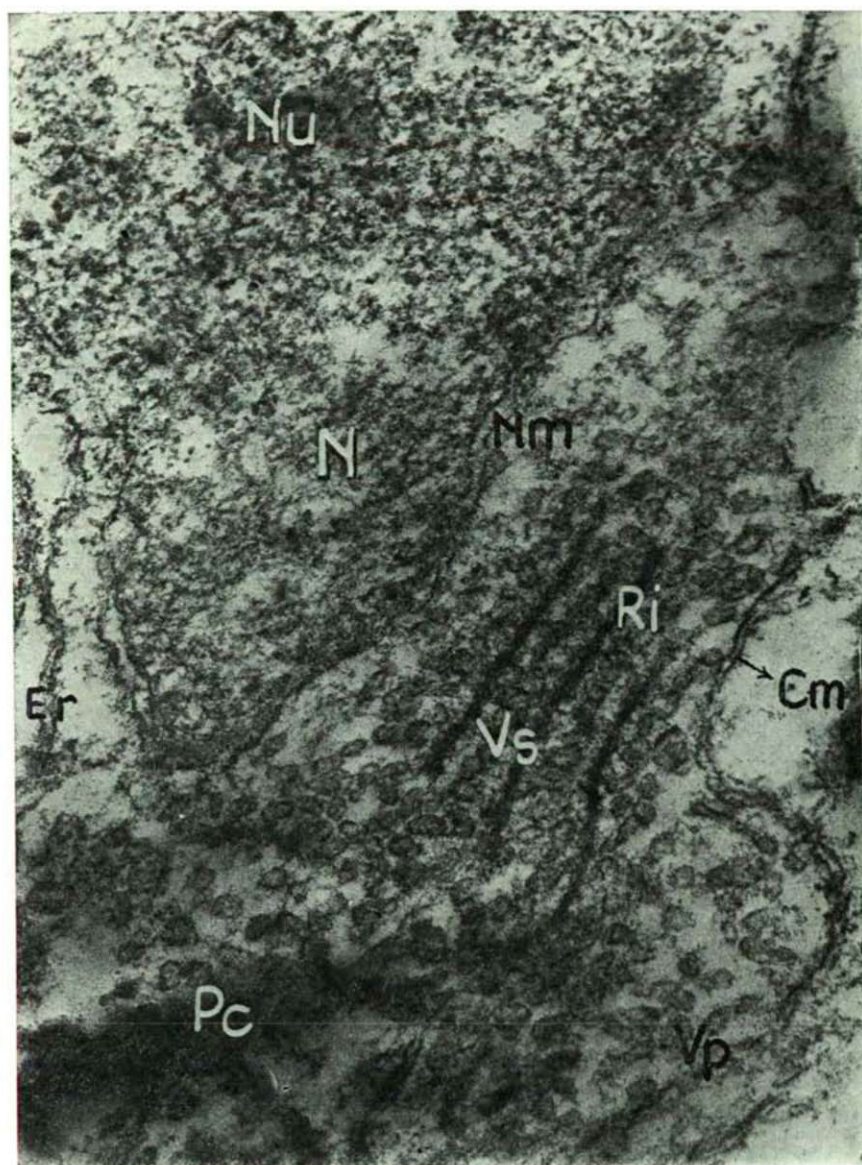


Fig. 6. Ending of the proximal central process (Pc), of a rod cell of *Gallus domesticus* (8-day old). Cm=cell membrane, N=cell nucleus, Nm=nuclear membrane, Nu=the separated chromatin of the nucleus, Er=endoplasmic reticulum, Vp=cytoplasmic vesicle, Vs=synaptic vesicle, Ri=ribbon precursors. Electron micrograph: x64 000.



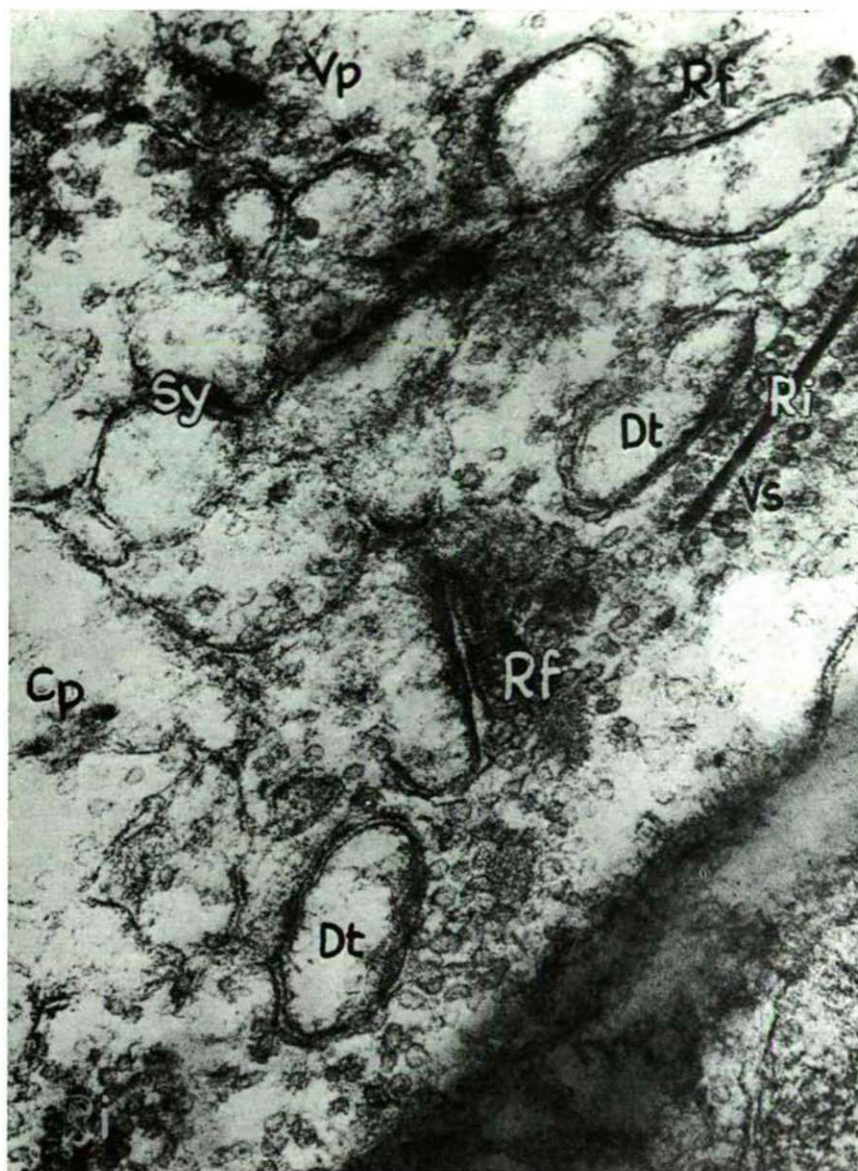


Fig. 7. Peduncle of the central process (Cp), of the cone cell of *Gallus domesticus* (20-day old) Ri=actual ribbon, Rf=ribbon in formation, Vs=synaptic vesicle, Vp=cytoplasmic vesicle, Dt=dendrite process, of bipolar, Sy=synapse. Electron micrograph:  $\times 64\,000$ .

cytoplasmic organelles of rod cells, the mitochondria are connected with a lipid droplet of large size, merging gradually into that. The lipid droplet, indicating to the presence of some rhodopsine may persuade us to suppose that the rod cells may have a primary role in transmitting and transforming photons. The light stimulus is directed by two lateral ribbon lath at the proximal end.

In the inner segment of the rod cell there are also several mitochondria but of a different nature. The limiting membranes of mitochondria being decomposed, the central granulated body takes shape; its tiny granules primarily migrate towards the pigment epithelium and the result is possibly the inception of pigmentation. The granules can be discovered only later in the perikaryon of the cone cell, which is wider and rich in the usual cell organelles. Here apart from the cytoplasmic vesicles, a great number of slightly darker synaptic vesicles also appear. The investigation of these can be continued in the "ribbon synapses" between the peduncle of the cone cell in the retina of 20 days old chick (Fig. 7) and the cone bipolar cell forming rich penetration with their protrusions.

It may be supposed that during the transmission of the colour stimulus the ribbon systems, which lie in several directions, allow the "polarisation" of different colours in one direction. As seen in Fig. 7, it seems that the thickened synaptic membrane becomes the ribbon lath.

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## A NON-METRIC EXAMINATION OF THE RELATIONSHIPS BETWEEN OSTEOLOGICAL REMAINS FROM HUNGARY REPRESENTING POPULATIONS OF AVAR PERIOD

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### Abstract

A sample of 317 crania representing 6 populations of the Avar period were scored for 42 non-metric cranial traits in order to generate the biological distances between these groups. The basic statistic used to measure the divergence between these groups was the Grewal-Smith statistic with some modification. Additionally, numerical taxonomic computer programs were utilized to display the relevant associations among these groups. The population samples under study were further elaborated to show the affects of side-to-side frequency differences, sex dimorphism, and age dependency of the traits utilized. This material is elaborated and presented as a preliminary report of biological divergence among the population samples tested. Continuing research is suggested to compare the non-metric analysis with traditional typological analysis.

### Introduction

In recent years non-metric, i.e. qualitative variation, has become quite popular in analyzing osteological remains at the population level. Those who utilize these means suggest that the population distances generated reflect something real about the biological similarity of the populations involved and indeed can be used to show migration patterns (FINNEGAN, 1972) between populations, microevolutionary changes (JANTZ, 1970; ORTNER—CORRUCCINI, 1976) and has been used as a useful tool in the placement of one individual into its logical population group (SJOVOLD, 1975a; FINNEGAN, 1975). Most of these workers have studied regional and/or continental populations and have utilized cranial non-metric traits to these ends. Each author justifies this approach by quoting BERRY and BERRY (1967) and OSSENBERG (1970) who suggest that, 1) the traits are highly genetic in nature; 2) that populations vary in frequencies between even closely related populations; 3) that some consistency is seen without regard to environmental variation; 4) the traits do not vary significantly with age; 5) show little sex difference; 6) show little correlation between the traits used; and 7) are easily defined and large samples can be studied in a short period of time. This by way of justification is then contrasted with the usefulness of metric traits in understanding a population or population groups. Although all of these assumptions do not hold for most populations (see below) there are many populations which can be studied utilizing these techniques or where the data can be standardized in some form to allow for any sex and age differences.

These above assumptions have been tested on many populations, most of which originate in North America or in Western Europe. However, some of the most interesting migrations and settlements are seen in Central Europe. These populations



have been analyzed by other osteological techniques, the archeology is well done, with documentation and excellent provenience, the bone material is in excellent condition, and the cultural variables have been studied in some depth.

The purpose of this paper is to utilize non-metric trait analysis in analyzing populations from the Avar period in Hungary and associated populations separated both by time and space.

### Materials and Methods

A sample of 317 crania were studied for 42 non-metric cranial traits. The sample was divided into six subsets composed of 31 Kunszállás individuals, 11 male and 22 female, as reported by LIPTÁK and VARGA (1974). The second subset was that of Mélykút—Sáncdűlő showing 30 individuals evenly divided between male and female (MARCSIK, 1971). The third subset is composed of 8 males and 14 females of the Árkus—Homokbánya group as elaborated by LIPTÁK and MARCSIK (elaboration in process). The fourth subset composed of 21 males and 28 females is known as the Madaras—Téglavető elaborated by LIPTÁK and MARCSIK (1976). The fifth group and the largest subset of the current study is that of Fehértó—A—Szeged comprised of 50 males and 50 females as reported by LIPTÁK and VAMOS (1969). The final group, Szeged—Kundomb, is composed of 41 males and 40 females and was reported by LIPTÁK and BOROSNÉ MARCSIK (1966).

Each of the above crania was scored for the following 42 cranial traits as reported by FINNEGAN (1972) (Fig. 1).

#### 1. Highest nuchal line present

The inferior and superior nuchal lines form well marked ridges running laterally across the occipital bone inferior to the external occipital protuberance. The highest line, when present, arises with the superior line at the external occipital protuberance, and arches anteriorly and laterally providing attachment for the epicranial eponeurosis. Many times it is more easily felt than seen. (Refer to figures for location)

#### 2. Coronal ossicles present

Single or multiple ossicles are sometimes found in the coronal suture.

#### 3. Ossicle at bregma present

An ossicle (the bregmatic or interfrontal bone) may be present at the junction of the sagittal and coronal sutures.

#### 4. Sagittal ossicles present

Single or multiple ossicles are sometimes found in the sagittal suture.

#### 5. Ossicle at lambda present

A separate bone may be observed the junction of the sagittal and lambdoid sutures. This is distinguished from an Os Inca (number seven below). An ossicle at the lambda occurs in the occipital fontanel, and is generally smaller than the Os Inca and must articulate with both parietals and the occipital bones.

#### 6. Lambdoid ossicles present

One or more ossicles may occur in the lambdoid suture on the left side, right side or both sides. These may only articulate with one or the other parietal bones and the occipital bone.

#### 7. Os Inca present (interparietal bone)

The portion of the occipital bone which ossifies in membrane may persist as a separate bone. The suture separating the Os Inca from the occipital bone generally runs from asterion to asterion.

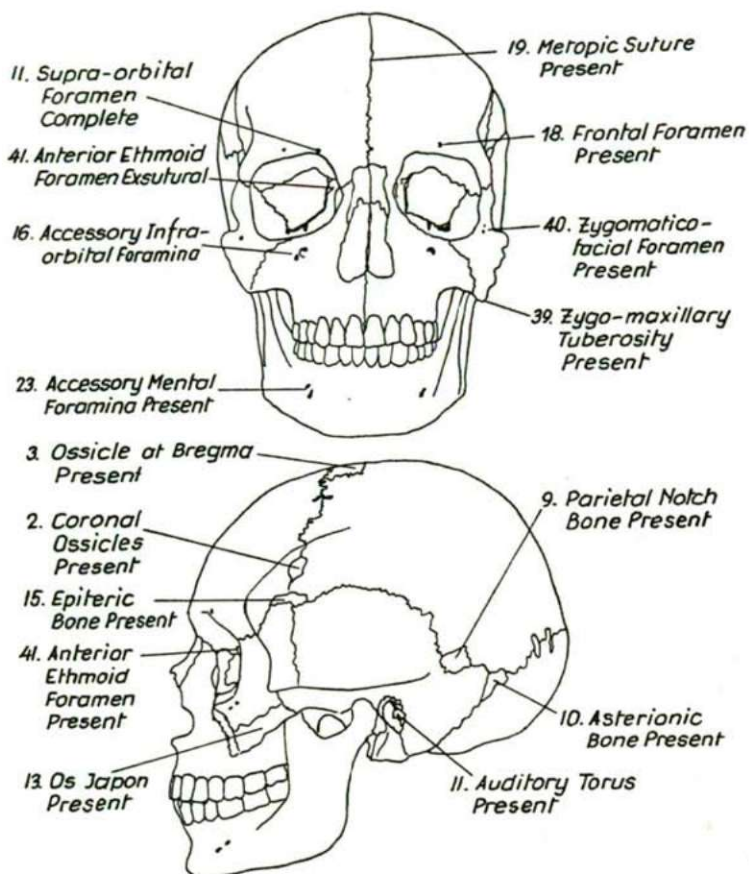


Fig. 1. Normal frontal and normal lateral views of the cranium depicting the location of non-metric traits used in this study.

#### 8. Parietal foramen present

A foramen may occur in the parietal bone near the sagittal suture and a few centimeters above the lambda. When present, this foramen transmits a small emissary vein to the superior sagittal sinus.

#### 9. Parietal notch bone present

A separate bone may occur in the parietal notch. The notch is defined as that part of the parietal bone that protrudes between the squamous and the mastoid portions of the temporal bone.

#### 10. Asterionic bone present

A separate bone may occur at the junction of the lambdoid, occipito-mastoid and parieto-mastoid sutures.



## 11. Auditory torus present

A bony ridge may occur on the anterior or posterior walls or on the floor of the external auditory meatus.

## 12. Malar tubercle present (maxillary torus) Fig. 2.

The malar tubercle is a bony ridge running along the lingual aspects of the roots of the molar teeth.

## 13. Os Japon present (os japonicum)

A separate bone may occur as the product of the subdivision of the malar bone by a suture passing from the temporo-zygomatic suture to the zygo-maxillary suture, with some variations.

## 14. Pterion form (fronto-temporal articulation)

Normally the frontal bone is separated from the squamous part of the temporal bone by the greater wing of the sphenoid and the anterior inferior angle of the

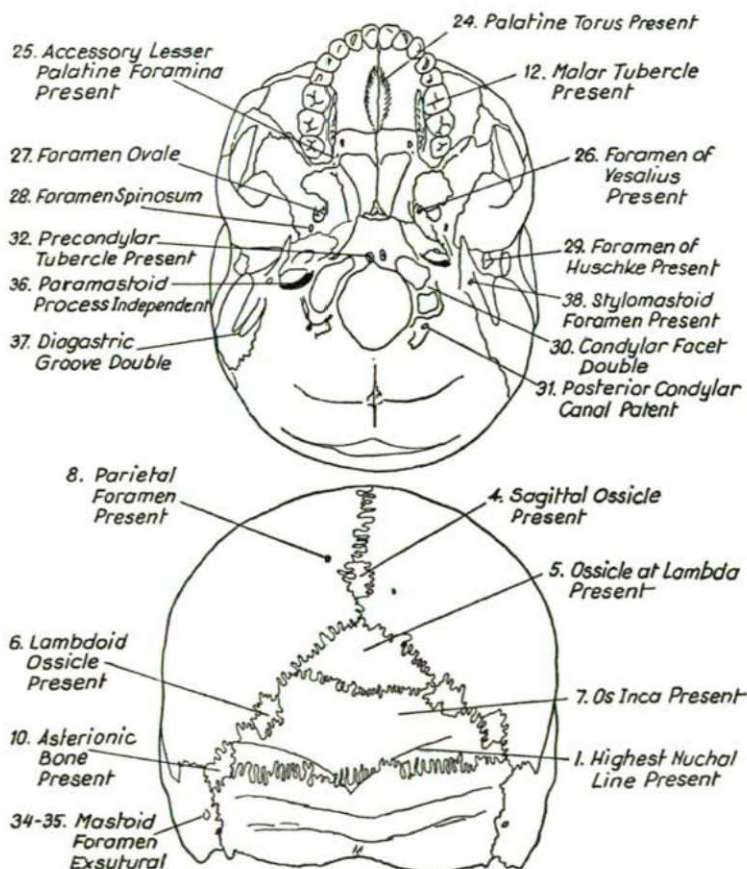


Fig. 2. Normal basilar and normal occipital views of the cranium showing the location of non-metric traits used in this study.

parietal bone. Occasionally the frontal and temporal bones are in direct contact at a point (X-form) or a line (K-form), forming a fronto-temporal articulation (not shown).

15. Epipteric bone present

An epipteric bone or pterion ossicle may be present between the parietal bone and the greater wing of the sphenoid. When large, it may also articulate with the squamous portion of the temporal bone.

16. Accessory infra-orbital foramina

One or more accessory foramina may lie immediately adjacent to the infra-orbital foramen.

17. Supra-orbital foramen complete

The supra-orbital foramen is either complete or open, in which case it is called a notch. The foramen or notch transmits the supra-orbital vessels and nerve.

18. Frontal notch or foramen present

A secondary foramen may be present lateral to the supra-orbital foramen. Frequently a cluster of pin-sized holes may occur in this area, but only a well developed foramen was scored.

19. Metopic suture present

The medio-front suture usually disappears in the first two years of life. When this suture persists into adult life, it is called metopism and is scored.

20. Mandibular foramen double

Sometimes the mandibular foramen is double or bipartite at its opening.

21. Mylohyoid groove closed (mylohyoid bridge)

A bony bridge may occur over the mylohyoid groove on the internal aspect of the ascending ramus. When this bony bridge occurs, the normally open groove is considered closed.

22. Mandibular torus present

One or more discrete bony tori occur on the internal aspect of the body of the mandible, usually below the canine and premolars.

23. Accessory mental foramina present

Accessory mental foramen may occur immediately adjacent (superiorly and posteriorly) to the primary foramen.

24. Palatine torus present

A bony ridge may run along the mid-sagittal line of the hard palate.

25. Accessory lesser palatine foramina present

Usually a single lesser palatine foramen is found immediately posterior to the greater palatine foramen and transmits the lesser palatine nerves. When more than one of these foramina are present, it is scored as accessory.

26. Foramen of Vesalius present

A small foramen may occur medial to the foramen ovale. When present, it may be seen opposite the root of the pterygoid process. It opens below, near the sphenoid fossa, and transmits a small vein from the cavernous sinus. (The position of this foramen is highly variable.)

27. Foramen ovale incomplete

Rarely, the postero-lateral wall of the foramen ovale is incomplete such that it is continuous with the foramen spinosum.



## 28. Foramen spinosum open

Sometimes the posterior wall of the foramen spinosum is corroded and incomplete.

## 29. Foramen of Huschke present (dehiscences of the tympanic plate)

The floor of the external auditory meatus contains an opening at birth, but only occasionally does it persist past the fifth year. When it does, it is scored as present.

## 30. Condylar facet double

Rarely, the articular surface of the occipital condyle is divided into two distinct facets.

## 31. Posterior condylar canal patent

The posterior condylar canal usually pierces the condylar fossa which lies immediately posterior to the occipital condyles. Sometimes this canal ends blindly in the bone. This can be scored as patent only when a seeker can be passed through the canal.

## 32. Precondylar tubercle present

A bony tubercle may lie immediately anterior and medial to the occipital condyle.

## 33. Anterior condylar canal bipartite (foramen hypoglossi) Fig. 3.

A bony septum may occur in the anterior condylar canal dividing it into two discrete parts. In some cases this septum is only partial, but this character is not scored unless the septum is complete.

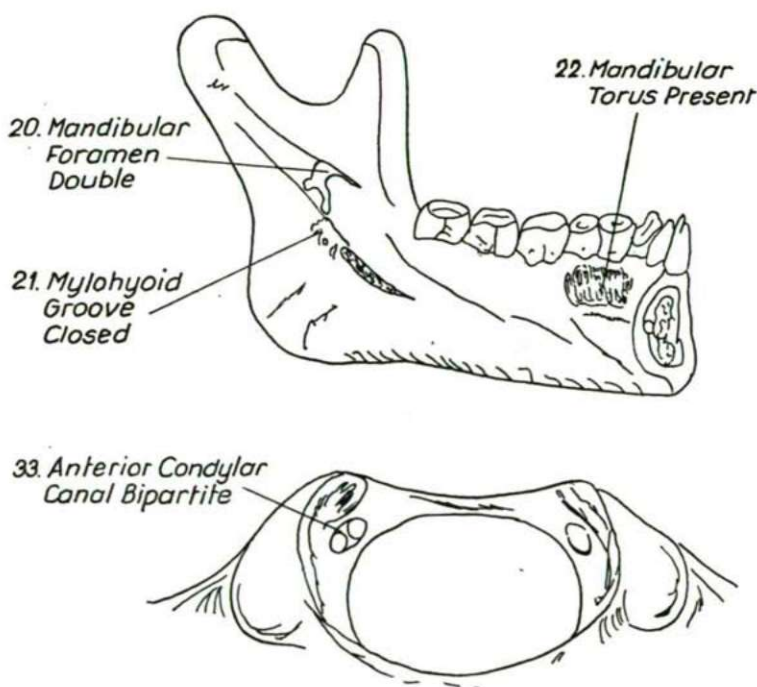


Fig. 3. The medial aspect of the left half of the mandible and the inferior anterior view of the occipital bone and occipital condyles showing non-metric traits used in this study.

## 34. Mastoid foramen absent

This is scored when the mastoid foramen cannot be found (See # 35).

## 35. Mastoid foramen exsutural

When present, the mastoid foramen lies in the occipito-mastoid suture. Sometimes it lies in the mastoid portion of the temporal bone and very rarely in the occipital bone adjacent to the occipito-mastoid suture.

## 36. Paramastoid process independent

This is scored when a definite downgrowth from the jugular process just medial to the mastoid process is observed.

## 37. Diagastric groove double

This is scored when the diagastric groove appears to be bipartite. This judgment is difficult as there is, in the same immediate area, an occipital groove for the occipital artery.

## 38. Stylo-mastoid foramen present

When present, this foramen lies immediately posterior to the styloid process. (Although it has been reported as absent to a small frequency in some populations, it was found absent in only one of the present study.)

## 39. Zygo-maxillary tuberosity present

Often a roughened downward projection at the lower end of the junction between the zygoma and the maxilla.

## 40. Zygomatico-facial foramen absent

There are usually one or more small foramen which pierce the zygomatic bone opposite the junction of the infra-orbital and lateral margins of the orbit. When present, it transmits a nerve and small artery.

## 41. Anterior ethmoid foramen exsutural

The anterior ethmoid foramen usually lies on the suture between the frontal and ethmoid bones. It is scored when it emerges above the suture.

## 42. Posterior ethmoid foramen absent

When present, the posterior ethmoid foramen lies on the fronto-ethmoid suture behind the anterior ethmoid foramen. (Numbers 41 and 42 are very difficult to score unless the orbits are in very good condition.) For other cranial and infra-cranial non-metric traits, see Finnegan and FAUST (1974).

The basic statistic used in generating the biological distances was developed by C. A. B. SMITH and used by GREWAL (1962). This statistical technique is based on the transformed frequencies of observed non-metric traits as seen by the following equation:

$$\frac{\sum_{i=1}^R [\theta_{1i} - \theta_{2i}]^2 - (1/\bar{N}_{1i} + 1/\bar{N}_{2i})}{R}$$

where  $\theta_{1i} = \sin^{-1}(1 - 2P_{1i})$  and

$r_{1i}$  = transformation angles of first sample  $i$ th trait

$i$  = trait # under summation

$\bar{N}_1$  = total crania in sample 1

$\bar{N}_{1i}$  = crania of sample 1 with observable trait  $i$



$$P_{1i} = \% \text{ of trait } i \text{ in sample } 1 = \left( \frac{K1i}{N1i} \right)$$

$R$  = # of traits for particular data set

$K$  = count of positive observations for trait  $i$ .

(See Finnegan and COOPRIDER (1978) for alternative statistical forms.)

The first use of the Grewal—Smith statistic on human non-metric traits was produced by BERRY and BERRY (1967) and subsequent researchers developed variations of this statistic or used other statistics entirely. Some slight variations of the Grewal—Smith statistic were utilized by FINNEGAN (1972), BUIKSTRA (1972) while others, SUCHY (1975), SJØVOLD (1973, 1975b, 1977) and GREEN and SUCHY (1976) suggests modifications by using alternate transformations or corrections to the transformation used above. ZEGURA (1973) utilized the equation of Balakrishnan and Sanghvi's  $B^2$  rather than the Grewal—Smith equation in order to analyze his data. Although the statistical work by GREEN and SUCHY and SJØVOLD suggest that theoretical problems exist in the comparison of tabulated frequencies where various transformations and statistics have been employed in the final Grewal—Smith statistic, the recent work of FINNEGAN and COOPRIDER (1978) suggests that the results of empirically testing a variety of statistical transformations show no departure, one from the other, in analyzing this type of non-metric data. For these reasons the above statistic and transformation of the GREWAL—SMITH statistic were utilized.

The usefulness in the present study of non-metric traits is seen in the early justification for this method based on BERRY and BERRY (1967) and GREWAL (1962). They believe that non-metric traits may have a high genetic determination, maintain consistency in and do not suffer duress under various environmental conditions and are sensitive to frequency differences between closely related populations. Each individual who has utilized the non-metric approach justifies this approach on a quasi-genetic basis quoting Berry and BERRY (1967) and OSSENBERG (1970). Other researchers, however, have questioned many of the basic assumptions seen in the above papers asking to what degree the sides and the sexes can be pooled in making comparisons between various population samples. Also to what extent the traits are age dependent. KOREY (1970) studied side independence, sex independence, and age dependency, while BUIKSTRA (1972) studied the age correlation of non-metric traits and CORRUCINI (1974) made a detailed investigation of side and sex dimorphism and age dependency in regard to 72 non-metric cranial traits. Many of these questions have been satisfactorily answered for a number of populations utilizing non-metric cranial studies. However the same considerations will have to be demonstrated in terms of the present paper.

Additionally world-wide continental and local population samples have been studied and offer basic data on both the traits used and total population comparisons. These are seen in the studies of Berry and BERRY (1967, 1971, 1972), CZARNETZKI (1971, 1972, 1975), KNIP (1970, 1971), LARNACH and MACINTOSH (1966, 1970, 1971, 1972), LARNACH (1974), BRUNNER (1972), PUCCIARRELLI (1972), SUBLETT (1965), BIRKBY (1973), MCWILLIAMS (1970, 1974), and ARENSBURG et al. (1977). The data presented in the present paper will help elaborate the cranial non-metric distributions for more populations from an unreported important time and area.

## Results

The basic data for the six subsets currently under study are presented in Table 1. It is interesting to note that the trait *Os inca* and the trait auditory torus was not present in any of the six subsamples. This is an interesting departure from much of the North American native samples as seen in FINNEGAN (1972, 1974) and CYBULSKI (1975). As suggested above a number of tests on the data seen in Table 1 must be utilized prior to the acceptance of this data for the Grewal-Smith statistic.

### Side-to-Side Differences

Although a number of traits show left-right side dimorphism in the female samples as determined by the presented  $X^2$  values (See Table 2) it should be noted that as a group we would expect at least two differences at the .01 level and over 12 significant differences at the .05 level due to chance alone. This suggests that while some of the female samples show unique and in some cases consistent dimorphism from side-to-side, the dimorphism does not exceed chance expectations. In comparison, we note that in Table 3 the males display less side-to-side dimorphism than the females. Again, taking the male sample together, we find that the significant differences do not exceed chance expectations. We also see that the pattern of traits showing dimorphism are quite different between the males and females. The only trait that shows any side dimorphism in both males and females is the parietal notch bone which shows a significant side dimorphism in the female sample of the Szeged-Kundomb. In the males, a significant side dimorphism for this trait, at the .5 level, exists in the Szeged-Kundomb, Fehértó-A-Szeged and in the Kunszállás.

Inasmuch as the observed significant differences do not exceed the chance expectation for significant difference, we suggest that the sides can be statistically summed in our analysis. The reason for doing this is not only statistical but logical as well. We feel that by using only one side of the crania, we have lost some important biological data. The argument against summing the sides can be seen in the fact that where great similarity exists from side-to-side, we have increased our sample size and supposedly, artificially, decreased the variance. This is not however strictly true in that although we have few significant differences side-to-side, we have at the same time very few traits which show absolute asymmetry. It is our belief that if  $X^2$  values are above 0.0, some difference is noted and that using one side only we would lose some biological information.

### Sex Dimorphism

In comparing the sexes both left side and right side (Table 4 & 5 respectively) it was found that many traits were involved in sex dimorphism at or above the .05 and .01 level of significance. Indeed, in each group taken by itself we find that the .05 level of significance exceeds chance expectation both on the left and on the right side. At the .01 level of significance we find that only the left side exceeds chance expectations. In this case 25 of the 42 traits show a significant difference in one or more samples either on the left or the right side at the .05 or .01 level. Although the significant difference is not consistent for any particular trait over all six sub-



sets, both left and right, some comments have to be made based on this significance and the fact that it exceeds chance expectations.

Before utilizing this data with these significant differences, we obviously have to make some corrections or considerations before the sexes can be summed legitimately and used in our GREWAL—SMITH distance statistic. Various ways of doing this have been proposed. FINNEGAN (1972, 1978) has suggested that if we keep the number of males and females nearly equal in each population sample, we have adequately corrected for frequency differences displaying sex dimorphism. GAHERTY (1974) suggests that males and females could be summed for all traits which did not show sex dimorphism, and only the male or female samples be used for those traits that do display significant sex dimorphism. Gaherty's reasoning seems quite justifiable with the only disadvantage being a reduction in sample size for those traits which do show significant sex dimorphism. JANTZ (1970) attacked the sex dimorphism problem by eliminating all sexual dimorphic traits before his distance statistic was applied. Again, this can be justified, but much information is lost by the exclusion of these traits. In the present analysis 25 of the 42 traits show significant sex dimorphism in one or more subsets under study. If we were to discount the sex dimorphic traits, we would be left with a trait list of 17 traits rather than the original 42 traits. Additionally KELLOCK and PARSONS (1970) and FINNEGAN (1972) conducted principal component analysis of non-metric trait variation in human crania from a number of diverse populations and found that the largest Eigen value, accounting for the greatest percentage of total variance, was indeed a sex dimorphic trait. Each of these studies found that four traits out of the top twelve traits, in terms of the principal component analysis, were sex dimorphic. It seems clear that if we exclude the sex dimorphic traits from the current analysis, we have excluded those traits which best distinguish and define the affinities among the subsamples in question. It therefore seems necessary that we include the traits which are sex dimorphic, but that we control to some extent the numbers of males and females within each population.

In the present study most of the populations are very evenly balanced relative to sex. Three samples, Mélykút—Sáncdűlő, Fehértó—A—Szeged and Szeged—Kundomb are evenly represented by the number of males and females. Three samples, Kunszállás, Madaras—Téglavető, and Árkus—Homokbánya show about a .60/.40 split in the sexes in each population. However in each of these populations the male frequency is the lower frequency, suggesting that a balance exists in terms of proportions between males and females in these three populations. This suggests that we can allow the summing of the sexes for use in our GREWAL—SMITH statistic. Additionally, as shown above, we feel it is legitimate to sum statistically the side as well as the sexes for our final frequency. These summed frequencies are presented in Table 1.

### Age Dependency

Relatively little work has been done on age dependency in these non-metric traits. OSSENBERG (1970) suggests that a relatively small amount of age dependency would not greatly alter the significance of genetic distance studies between populations at least with regard to anthropological studies. On the other hand KOREY (1970) and BUIKSTRA (1972) suggest that age dependency of cranial traits do show some age dependency, and this dependency must be considered before distance statistics



are applied among population samples. The rationale for this by KOREY (1970) is his feeling that significant frequency correlation over the entire age range for a number of cranial traits would adversely effect an analysis of distance between populations, particularly where the age profiles in the samples under question were dissimilar. This assumption however is not totally supported in that simple age correlation will not show the magnitude of difference. This is to say that age dependent traits could be highly correlated, but frequency difference between the earlier age groups and older age groups might not be significantly different, based on a  $X^2$  test. This technique, which is more robust than correlation, was applied by FINNEGAN (1978) to a number of populations in documenting the nature of infracranial non-metric traits. FINNEGAN found that while the correlation between age and the expression of non-metric traits were significant, the  $X^2$  examinations, between youngest and oldest groupings within each sex, side, and race, showed the number of significant differences fell below that we would expect due to chance alone. His work suggests that the age dependent nature of infracranial traits could not be fully expressed in terms of correlation coefficients and he makes the recommendation that the age regressive nature of infracranial traits does not warrant any correction in applying distance statistics unless the combined samples generate a distinct bimodal age distribution. Also, if the traits utilized between the populations can be shown to be more or less homogeneous with respect to age, then correction for age dependency is not necessary. This however may not be entirely true of cranial traits as shown by CORRUCINI (1974).

In the present analysis, although we do not have mean ages for males and females in each subsample, we suggest that the age profile are more or less homogeneous between the sexes and among the subsamples. From the above, therefore, we determine that age dependency is not so great as to warrant a selection in the basic sample in order to match age criteria.

### Distance Values

Biological distances generated by the Grewal—Smith statistic among the sample subsets is presented in Table 6 with an estimate of the variance beneath. In each possible pairings the level of significance is  $P < .01$ . With this number of population pairs it becomes increasingly difficult to represent all possible associations in a two dimensional graphic representation. However there are a number of numerical taxonomic methods which can be utilized to reduce this six dimensional array to a two dimensional plot. Among these are the phenogram, compiled by average linkage methods (SOKAL et al, 1963), and a stereogram of plotted eigen values (ROHLF, 1967).

The present analysis was generated based on the statistical programs offered by ROHLF et al. (1974). In this, the data from Table 6 of distances between all population pairs, were subjected to a TAXON analysis which is a sequential agglomerative hierarchical cluster analysis. In this analysis we used the unweighted pair-group method using arithmetic averages, where the lowest values are considered for similarity. This program produces a phenogram which is presented in Figure 4. The second step was to run the routine MXCOMP which is here used to compare the matrices for congruence. The elements of the first matrix are plotted against the corresponding elements in the second matrix and displayed as a bivariate scatter diagram as is



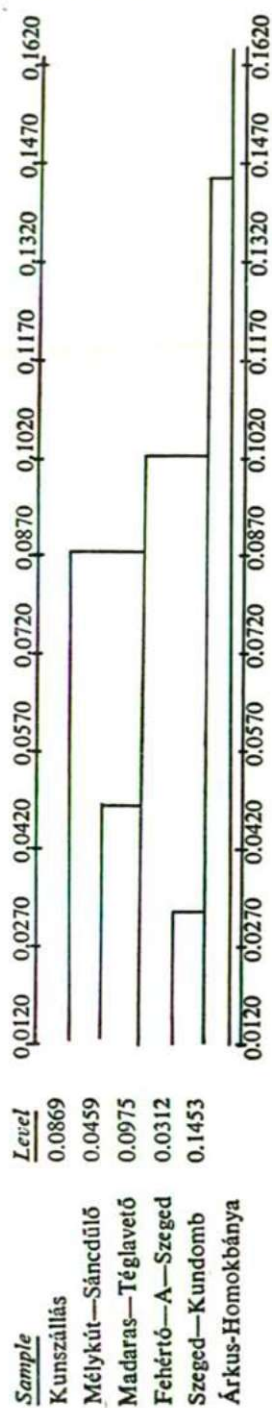


Fig. 4. A phenogram, based on the clustered distance matrix using the unweighted pair-group method with arithmetic averages. Low values were specified to indicate correspondent distance similarities.

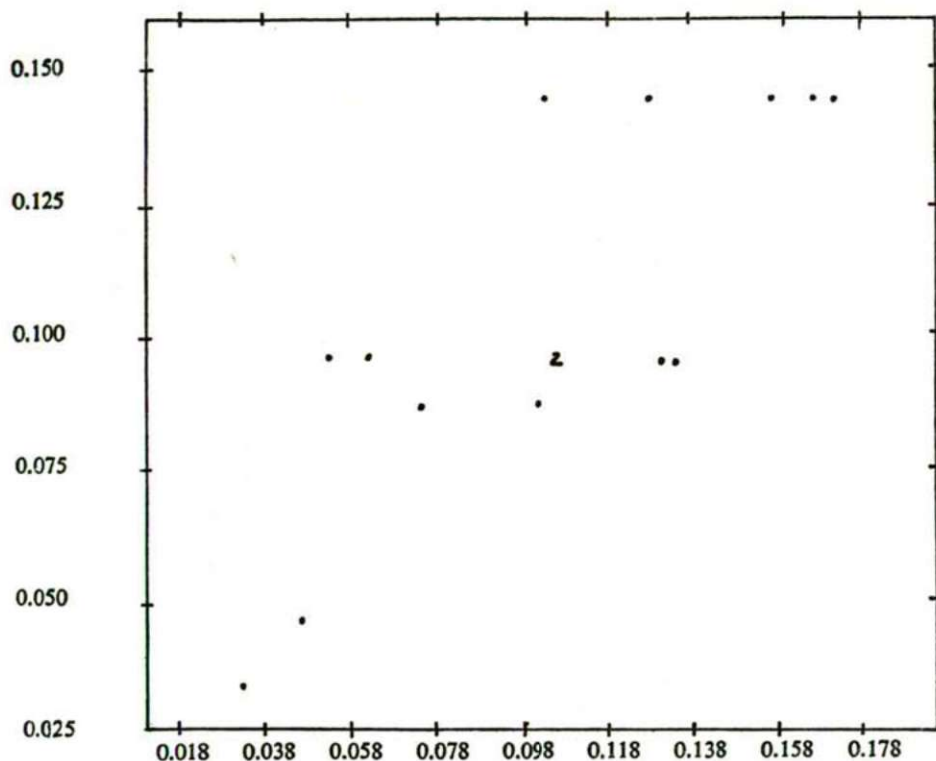


Fig. 5. A stereogram of the distance value matrix plotted against the cophenetic value matrix determined by arithmetic averages and the unweighted pair-group method. This clustering is done in order to test for the amount of distortion present in the cluster analysis. Correlation = 0.808.

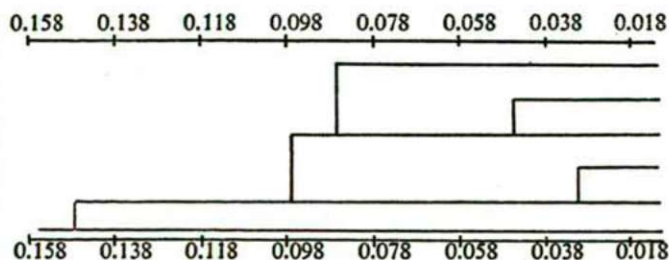


Fig. 6. A phenogram derived from the matrix of cophenetic values. When comparing this with figure 4, we find little distortion in the phenogram which produces little distortion in the cluster analysis seen in figure 5.



shown in Figure 5. The correlation between these two matrices was also computed and was found to be 0.808, which showed a highly successful plot. This shows the distance matrix as being clustered using the unweighted pair-group method with arithmetic averages and a cophenetic value matrix is plotted against the original distance matrix in order to test for the amount of distortion present in the cluster analysis. The cophenetic matrix is again reduced to a phenogram, based on the average linkage method and is produced in Figure 6.

As seen in Figure 4, the greatest similarity is shown in the primary groupings of the Fehértó—A—Szeged and the Szeged—Kundomb at the 0.312 phenon level. Secondly, the hierarchical grouping is the pair made up of Mélykút—Sáncdülő and Madaras—Téglavető at the .0459 phenon level. The Kunszállás joins the secondary group at the .0869 phenon level and these join the primary group at the .0975 phenon level. All of the above groups finally join the Árkus—Homokbánya at the .1453 phenon level. This indicates a relatively close relationship exists between Mélykút—Sáncdülő and Madaras—Téglavető population samples and between Fehértó—A—Szeged and Szeged—Kundomb samples, with the latter pair being more closely associated.

These two pairings join at a much lower phenon level than the inclusion of the Kunszállás or the Árkus—Homokbánya samples.

The same data is essentially presented in Table 6, where the matrix is converted into a phenogram called the BDIST, which is the cophenetic matrix displayed in the phenogram and is essentially the same output as seen in Figure 4, with the exception that the interval has been generated at 100 units instead of a random unit generation.

### Discussion

These data, presented in Table 6 and Figures 4, 5 and 6, should be taken at face value with little emphasis on the size of the numerical representation. Rather, the important aspect of this type of analysis is the relative numerical distance between the various population pairs. These data must at the present time speak for themselves, but we anticipate comparisons of this form of analysis with the existing traditional typological approach. It must also be noted that although the use of numerical taxonomy has produced a great deal of research in both method and technique and has been widely used in the classification of species and seriation of artifacts, tool types, etc., there are nonetheless problems connected with hierarchical ranking of various taxa. These problems are best summarized by Sokal and Sneath:

"Those who have devised techniques for numerical taxonomy have suggested that they can be used to decide the rank of the taxa which they yield, and some suggestions have been made that agreement might be reached by biologists on the similarity levels which should define the categories of rank. To say that this is premature is to state the obvious, but the likely developments deserves some discussion. SNEATH has pointed out that there is a lower limit to the groupings which can be fitted into a nonarbitrary hierarchy. For example, different mutants of one species cannot be so arranged; it is impossible to decide whether white cats are of higher rank than long-haired cats. Such groups are not phenetic taxa; they are "rankless taxa" and cannot be satisfactorily handled

by hierarchic subspecific nomenclature. Many so-called subspecies are of this nature." (SOKAL and SNEATH, 1963).

Although we are not here dealing with subspecies in the technical sense, but rather isolate populations, spacially separated or not, and temporarily located or not, we still must consider the underlying assumptions both of the techniques and methods in numerical taxonomy of a statistical nature and the assumptions underlying the trait list used in this study in order to hierarchically rank these populations. We suggest that the populations are of equal hierarchical rank, but that we are showing the genetic similarity or closeness of fit by utilizing these numerical taxonomic techniques. We believe that by utilizing the techniques outlined in this paper we have successfully shown the genetic relationships among the populations sampled. It is now left to our future work and the work of our colleagues to document the cultural relationships relative to the biological relationships we have here defined.

#### Acknowledgments

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Table 2. Chi-square values for each trait in each population comparing left and right sides in females only. Significance levels: \* = .05; \*\* = .01

Variable	Kunszállás	Mélykút— Sáncdűlő	Árkus— Homokbánya	Madaras— Téglavető	Fehérbő— A— Szeged	Szeged— Kundomb
Highest Nuchal Line	0.000	0.135	0.000	0.085	0.059	0.068
Coronal Ossicle	0.000	0.000	0.000	2.023	0.354	0.338
Ossicle at Bregma	0.000	0.000	0.000	0.000	0.000	0.000
Sagittal Ossicle	0.000	0.000	0.000	0.000	0.000	0.000
Ossicle at Lambda	0.000	0.000	0.000	0.000	0.000	0.000
Lambdoid Ossicles	0.387	0.853	4.299*	0.497	0.000	0.016
Os Inca	0.000	0.000	0.000	0.000	0.000	0.000
Parietal Foramen	0.909	3.152	0.007	0.182	0.000	0.000
Parietal Notch Bone	1.184	0.000	0.000	2.139	2.427	6.167*
Asterionic Bone	0.000	0.000	0.000	1.713	0.729	3.385
Auditory Torus	0.000	0.000	0.000	0.000	0.000	0.000
Malar Tubercle	0.363	0.000	0.000	0.000	0.000	0.000
Os Japonicum	1.996	0.000	0.000	0.000	0.000	1.992
Pterion Form (x, k)	0.000	1.682	0.000	1.921	0.000	0.183
Epipetric Bone	0.001	0.000	0.275	1.362	0.081	0.203
Accessory Infra-Orbital Foramen	1.985	0.000	0.000	3.919*	0.785	0.421
Supra-Orbital Foramen						
Complete	2.973	1.250	2.708	0.798	0.299	0.965
Frontal Foramen	0.384	8.214**	0.223	1.342	0.000	2.450
Metopic Suture	0.000	0.000	0.000	0.000	0.000	0.000
Mandibular Foramen Double	0.000	0.000	2.105	4.028*	6.041*	4.221*
Mylohyoid Groove Closed	0.007	3.746	0.000	2.067	0.377	0.443
Mandibular Torus	0.085	0.000	0.000	0.000	0.118	0.000
Accessory Mental Foramen	0.426	4.211*	0.000	4.270*	3.288	2.046
Palatine Torus	0.000	0.000	0.000	0.000	0.000	0.000
Accessory Lesser Palatine						
Foramen	0.628	0.032	0.014	1.994	0.056	0.317
Foramen of Vesalius	0.658	1.816	0.724	0.835	0.003	0.235
Foramen Ovale Incomplete	0.488	0.068	0.056	1.597	0.680	0.000
Foramen Spinosum Open	0.071	0.173	0.753	1.962	3.072	0.325
Foramen of Huschke	0.409	0.098	0.942	0.363	0.380	3.141
Condylar Facet Double	0.000	0.000	0.000	0.000	2.030	3.957*
Posterior Condylar Canal Patent	0.904	1.824	0.004	0.109	0.185	2.410
Precondylar Tubercle	0.000	0.000	0.000	0.000	0.000	0.000
Anterior Condylar Canal						
Bipartite	2.372	3.509	0.167	0.418	0.208	2.414
Mastoid Foramen Absent	0.116	0.134	0.566	3.648	0.026	0.091
Mastoid Foramen Exsutural	0.011	0.227	0.501	0.618	0.259	0.000
Paramastoid Process Independent	0.010	0.000	0.000	0.000	0.000	0.007
Diagastric Groove Double	0.130	0.750	0.404	0.039	0.951	0.688
Stylo-Mastoid Foramen	1.982	0.000	0.000	0.000	0.000	0.000
Zygo-Maxillary Tuberosity	0.000	0.351	0.421	0.197	0.007	1.088
Zygomatiko-Facial Foramen	0.004	0.611	4.253*	0.006	0.100	0.804
Anterior Ethmoid For. Exsutural	2.963	3.030	2.043	0.011	0.644	0.140
Posterior Ethmoid For. Absent	1.535	2.043	0.000	0.006	3.326	0.132

Table 1. Proportions of each trait in ea  
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Non—Metric Variable	K
Highest Nuchal Line	3
Coronal Ossicle	1
Ossicle at Bregma	
Sagittal Ossicle	
Ossicle at Lambda	
Lambdoid Ossicles	1
Os Inca	
Parietal Foramen	3
Parietal Notch Bone	
Asterionic Bone	
Auditory Torus	
Malar Tubercle	
Os Japonicum	
Pterion Form ( $x, k$ )	
Epipteric Bone	
Accessory Infra-Orbital Foramen	
Supra-Orbital Foramen	
Complete	2
Frontal Foramen	2
Metopic Suture	
Mandibular Foramen Double	
Mylohyoid Groove Closed	
Mandibular Torus	1
Accessory Mental Foramen	
Palatine Torus	
Accessory Lesser Palatine	
Foramen	1
Foramen of Vesalius	1
Foramen Ovale Incomplete	
Foramen Spinosum Open	1
Foramen of Huschke	1
Condylar Facet Double	
Posterior Condylar Canal	
Patent	1
Precondylar Tubercle	
Anterior Condylar Canal	
Bipartite	
Mastoid Foramen Absent	4
Mastoid Foramen Exsutural	1
Paramastoid Process	
Independent	
Diagastric Groove Double	1
Stylo-Mastoid Foramen	
Zygo-Maxillary Tuberosity	3
Zygomatiko-Facial Foramen	
Anterior Ethmoid For.	
Exsutural	1
Posterior Ethmoid For. Absent	3



Table 4. Chi-square values showing sex dimorphism within each population sample utilizing the left side only. Significance level: \* = .05; \*\* = .01

Variable	Kunzállás	Mélykút— Sáncdűlő	Árkus— Homokbánya	Madaras— Téglavető	Fehértó—A— Szeged	Szeged— Kundomb
Highest Nuchal Line	0.747	0.430	2.228	3.609	3.425	0.885
Coronal Ossicle	0.000	0.000	0.000	1.722	0.000	0.003
Ossicle at Bregma	0.000	0.000	0.000	2.337	1.993	0.000
Sagittal Ossicle	2.565	0.000	2.660	1.722	0.299	0.396
Ossicle at Lambda	1.504	1.985	4.468*	0.755	2.293	1.185
Labdoid Ossicles	0.216	0.530	17.351**	0.110	0.379	1.573
Os Inca	0.000	0.000	0.000	0.000	0.100	0.000
Parietal Foramen	0.257	0.164	0.462	0.603	0.000	0.813
Parietal Notch Bone	1.504	0.000	0.000	0.000	0.100	12.493**
Asterionic Bone	0.000	2.268	0.000	1.751	0.354	0.686
Auditory Torus	0.000	0.000	0.000	0.000	0.000	0.000
Malar Tubercle	0.002	0.000	0.000	0.000	0.000	0.000
Os Japonicum	1.370	0.000	0.000	0.000	1.953	2.097
Pterion Form (x, k)	5.528*	2.132	0.000	1.638	0.354	2.285
Epipteric Bone	1.468	0.000	2.393	3.688	0.950	2.717
Accessory Infra-Orbital Foramen	0.000	1.566	0.000	3.919*	0.001	0.000
Supra-Orbital Foramen						
Complete	0.067	0.025	0.004	7.236**	0.002	1.490
Frontal Foramen	0.294	1.961	0.004	2.555	0.655	0.054
Metopic Suture	0.007	0.000	2.507	1.671	0.545	0.333
Mandibular Foramen Double	0.000	1.961	0.000	0.081	8.055**	0.003
Mylahyoid Groove Closed	1.678	0.000	0.000	0.000	0.000	0.438
Mandibular Torus	0.674	0.000	0.000	5.146*	2.184	0.338
Accessory Mental Foramen	0.030	4.492*	2.552	0.081	1.103	4.154*
Palatine Torus	0.159	1.481	3.568	0.063	2.904	0.693
Accessory Lesser Palatine Foramen	0.011	0.783	0.041	0.562	0.354	0.135
Foramen of Vesalius	2.353	2.240	0.690	0.458	0.364	0.032
Foramen Ovale Incomplete	0.273	2.587	3.840*	1.909	0.332	0.311
Foramen Spinosum Open	0.205	1.759	0.036	1.794	0.660	1.066
Foramen of Huschke	0.147	1.336	4.922*	2.416	0.188	10.576**
Condylar Facet Double	0.000	1.792	0.000	0.000	6.179*	4.068*
Posterior Condylar Canal Patent	0.057	0.180	0.436	0.127	3.121	2.112
Precondylar Tubercle	1.645	1.910	0.000	0.715	0.552	2.244
Anterior Condylar Canal						
Bipartite	0.151	0.006	0.000	5.489*	1.996	1.193
Mastoid Foramen Absent	0.019	0.348	1.043	0.792	3.439	0.518
Mastoid Foramen Exsutural	1.403	0.163	3.631	2.071	4.560*	3.609
Paramastoid Process						
Independent	0.086	5.600*	0.000	8.065**	1.591	1.360
Diagastric Groove Double	0.560	0.712	0.019	1.260	2.248	1.794
Stylo-Mastoid Foramen	0.000	0.000	0.000	0.000	0.000	0.000
Zygo-Maxillary Tuberosity	0.313	0.237	6.601*	0.603	6.423*	1.599
Zygomatiko-Facial Foramen	0.000	0.012	0.362	0.330	0.544	0.625
Anterior Ethmoid For. Exsutural	0.140	0.000	0.000	0.211	0.184	1.953
Posterior Ethmoid For. Absent	3.012	0.022	0.000	0.163	4.508*	2.071

Table 5. Chi-square values showing sex dimorphism within each population sample utilizing the right side only. Significance level: \* = .05; \*\* = .01

Variable	Kunszállás	Mélykút— Sáncdűlő	Árkus— Homokbánya	Madaras— Téglavető	Fehértó—A— Szeged	Szeged— Kundomb
Highest Nuchal Line	0.010	1.025	2.228	4.712*	3.191	1.815
Coronal Ossicle	0.000	0.000	0.000	0.000	4.054*	0.002
Ossicle at Bregma	0.000	0.000	0.000	2.337	1.993	0.000
Sagittal Ossicle	2.565	0.000	2.660	1.722	0.299	0.396
Ossicle at Lambda	1.504	1.985	4.468*	0.755	2.293	1.185
Lambdoid Ossicles	0.395	0.433	19.831**	0.013	0.379	0.084
Os Inca	0.000	0.000	0.000	0.000	0.000	0.000
Parietal Foramen	0.039	4.268*	0.134	0.402	1.007	0.952
Parietal Notch Bone	0.028	2.132	0.000	0.006	0.729	1.262
Asterionic Bone	0.000	0.000	0.000	0.231	0.122	2.146
Auditory Torus	0.000	0.000	0.000	0.000	0.000	0.000
Malar Tubercle	0.282	0.000	0.000	0.000	0.000	0.000
Os Japonicum	0.000	0.000	0.000	0.000	1.993	0.000
Pterion Form (x, k)	2.716	0.000	0.000	0.000	1.993	1.262
Epiteric Bone	0.209	1.566	0.984	0.146	0.081	2.250
Accessory Infra-Orbital Foramen	1.068	0.000	0.000	2.202	0.000	0.134
Supra-Orbital Foramen						
Complete	2.067	0.018	8.512**	0.898	0.299	0.054
Frontal Foramen	1.516	0.112	1.458	0.206	0.299	1.804
Metopic Suture	0.007	0.000	2.507	1.671	0.545	0.333
Mandibular Foramen Double	0.000	0.000	1.263	2.348	0.137	3.964*
Mylohyoid Groove Closed	0.125	3.900*	0.000	1.697	0.001	0.001
Mandibular Torus	0.332	0.000	0.000	5.146*	3.321	3.244
Accessory Mental Foramen	2.809	1.986	2.658	2.407	0.338	2.118
Palatine Torus	0.159	1.481	3.568	0.063	2.904	0.693
Accessory Lesser Palatine						
Foramen	0.099	1.850	1.946	0.361	0.033	0.841
Foramen of Vesalius	0.011	0.794	0.439	1.214	0.826	0.978
Foramen Ovale Incomplete	1.346	4.253*	1.755	1.186	0.729	0.299
Foramen Spinosum Open	0.037	2.502	0.253	3.876*	0.386	0.325
Foramen of Huschke	2.119	0.512	2.279	0.301	4.488*	0.003
Condylar Facet Double	0.000	1.640	0.000	0.000	0.000	0.003
Posterior Condylar Canal Patent	0.189	2.341	0.179	0.066	0.423	0.544
Precondylar Tubercle	1.645	1.910	0.000	0.715	0.552	2.244
Anterior Condylar Canal						
Bipartite	1.178	3.677	0.027	0.117	0.545	2.105
Mastoid Foramen Absent	4.302*	2.416	3.872*	0.657	0.062	0.091
Mastoid Foramen Exsutural	1.770	0.859	0.464	0.505	3.257	0.104
Paramastoid Process						
Independent	0.037	5.040*	0.000	4.910*	0.886	0.411
Diagastric Groove Double	0.008	2.748	0.006	0.275	2.202	0.832
Stylo-Mastoid Foramen	1.444	0.000	0.000	0.000	0.000	0.000
Zygo-Maxillary Tuberosity	0.051	0.038	0.799	0.000	5.768*	1.678
Zygomatico-Facial Foramen	0.003	0.000	0.000	0.001	6.386*	0.015
Anterior Ethmoid For. Exsutural	0.297	4.743*	1.021	0.120	0.388	0.097
Posterior Ethmoid For. Absent	0.795	2.724	0.000	1.022	0.058	2.597



Table 6. Measures of divergence between population samples used in this study. The underwritten italicized figures are estimates of the variance. In each case these show the measure of divergence to be significant at or above the .01 level. Measures of divergence and estimates of the variance are based on the Grewal-Smith statistic

Population Sample	Kunszállás	Mélykút—Sáncdülő	Árkus—Homokbánya	Madaras—Téglavető	Fehértó—A—Szeged
Mélykút—Sáncdülő	.100 .002				
Árkus—Homokbánya	.156 .004	.131 .003			
Madaras—Téglavető	.074 .001	.046 .000	.104 .002		
Fehértó—A—Szeged	.131 .002	.135 .002	.166 .004	.060 .001	
Szeged—Kudomb	.104 .001	.104 .002	.169 .004	.050 .000	.031 .000

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