

# Chemical Aspects of Diploxylon Pines

By N. T. MIROV

Institute of Forest Genetics, California Forest and Range Experiment Station<sup>1)</sup>

(Received for publication January 8, 1953)

Several systems have been developed for classifying the species of the genus *Pinus*; among the more recent are those of SHAW (29) and PILGER (28). SHAW'S classification appears to be the more natural of the two as it is based chiefly upon development of cones and seeds, while PILGER'S classification is based largely on the number of needles in a fascicle. The writer considers it to be more suitable as a basis for discussion of the chemical characters of pines.

SHAW'S classification of pines no doubt needs revision. Modern taxonomy requires that classification of plants be based not only on morphological characters, but also on anatomical, genetic, physiological, biochemical and even ecological and geographical characters. SHAW'S system was published in 1914. Since that time, as one could expect, certain points have been more fully elucidated.

Some new species have been described; Mexican pines have been studied more extensively by BLANCO (3) and by MARTINEZ (16), and later by LOOCK (15), who also studied pines of British Honduras. „Los Pinos Mexicanos“, published by MARTINEZ in 1938, and the second edition appearing in 1941, revealed many new facts about the taxonomy of pines. Recently, DUFFIELD (5) has subjected SHAW'S classification of Diploxylon pines to some changes, based on results of breeding tests at the Institute of Forest Genetics. There appeared in recent years several valuable works dealing with taxonomy of different pines and with natural pine hybrids (38). Anatomical characteristics of pines have been thoroughly studied by GREGUSS and VARGA (9). Chemical composition of the phenolic compounds of heartwood of pine species has been studied by ERDTMAN and his co-workers in Sweden (8); they were able to differentiate chemically between the two sub-genera: *Haploxylon* and *Diploxylon*.

It is not the purpose of the present paper to evaluate the abovementioned publications as to their validity in constructing an up-to-date system of classification of pines; the publications are mentioned merely to show how much valuable information has already been accumulated for use in revising the genus *Pinus*. In this paper some additional information of a chemical character is presented, in hopes that it also may be useful for a better understanding of relationships of pines. This information deals with the chemical composition of pine turpentines.

In his studies of the chemical composition of pine turpentines, the writer has not found any sharp distinction in the composition of turpentines of the two sub-genera; some compounds (saturated hydrocarbons, terpenes, and sesquiterpenes) are found in both. Chemical aspects of the *Haploxylon* pines have been already discussed elsewhere (22). It suffices to say here that the sub-genus *Haploxylon* seems to be linked with the sub-genus *Diploxylon*, through the group consisting of *Pinus cembroides* and related (pinon) pines and through the group of saturated-hydrocar-

bon pines (22). The chemical composition of turpentines of these two groups has much in common with the turpentine composition of the Diploxylon group *Macrocarpae*.

Systematic analysis of turpentines of pines has not yet been finished: some twelve species are still to be examined. But it appears that, even now, certain conclusions can be reached. The available results of chemical analyses of turpentines suggest some changes in SHAW'S classification. These changes are incorporated in Table 1. The species are numbered from 20 to 66 according to their arrangement in SHAW'S „*Genus Pinus*“. Thus, the numbers that are out of order designate species which have been rearranged.

It appears that such polymorphic species as *Pinus sylvestris*, *P. ponderosa*, *P. montezumae*, *P. pseudostrabus*, can no longer be considered simply as species. Rather, these are complexes, each embracing several recognized and not-yet-recognized varieties which differ one from another morphologically and chemically. *Pinus ponderosa* of SHAW'S system includes several pines which, in reality, are morphologically and chemically different. These varieties: *P. jeffreyi*, *P. apachea*, *P. engelmanni* are considered in this paper, as valid species. *P. ponderosa* itself is composed of several chemically different forms. Chemical and morphological analysis of *ponderosa* pine, now in progress, seems to indicate that the varieties from South Dakota, Arizona, or Utah are so different that it is not wise to lump them together under a single variety *scopulorum*, or, as SHAW did, to deprive them of even that much independence.

SHAW'S *Pinus montezumae* has been divided by MARTINEZ (16) into 5 species and 8 varieties and forms, i. e. into 13 morphologically recognizable entities. Opinions of botanists may differ from those of MARTINEZ, but a field acquaintance with the *montezumae* complex would convince anybody that *P. michoacana* or *P. rudis*, for instance, are truly different pines, and that they cannot be considered as mere forms of *P. montezumae*.

*Pinus durangensis* was placed by SHAW first with *P. montezumae* and later with *P. ponderosa*. In this paper it is considered as a species which is, perhaps, closer to *P. montezumae* than to *P. ponderosa*. *Pinus cooperi* was described by BLANCO (3) when SHAW'S „*Genus Pinus*“ had already been published; it is inserted in Table 1 of this paper near to the *montezumae* complex of the group *Australes*. *P. khasya*, *P. pithyusa* and *P. taiwanensis* each are given in this paper a specific status because of the chemical characters of their turpentines. *P. pithyusa* is considered by SHAW as a variety of *P. halepensis*. Presence of A-3-carene in *P. pithyusa* and its absence in *P. halepensis* caused the writer to put *P. pithyusa* closer to *P. sylvestris* than to *P. halepensis*; that is, to place *P. pithyusa* not in the group *Insignes*, but in the group *Lariciones*. PAPAJOANNOU considers *P. pithyusa* STEV. to be a synonym for *P. brutia* TEN. He further considers *P. brutia* and *P. halepensis* to be different species. His grounds for differentiating between the two pines are not only morphological but also chemical (27a). Camphor is more easily prepared from *P. halepensis* than from *P. brutia* because the turpentine of the former consists almost entirely of  $\alpha$ -pinene, while the turpentine of the lat-

<sup>1)</sup> The California Forest and Range Experiment Station is maintained by the Forest Service, United States Department of Agriculture, in cooperation with the University of California at Berkeley, California.

The work reported in this paper is part of a project aided through a grant from the Rockefeller Foundation.

CHEMICAL COMPOSITION OF TURPENTINES IN DIPLOXYLON PINES

Genus PINUS	ALIPHATIC HYDROCARBONS	ALIPHATIC ALDEHYDES	MONOCYCLIC TERPENES	BICYCLIC TERPENES		SESQUI-TERPENES	REMARKS
	heptane undecane		$\beta$ phellandrene limonene	$\alpha$ pinene $\beta$ pinene	$\Delta^3$ -carene	longifolene codinene	
Sub-genus DIPLOXYLON KOEHNIE*							
Sub-section Parapinaster							
Group VII - Leiophyllae							
20 leiophylla SCHLECT. & CHAM. (20)							
Group VIII - Longifoliae							
22 Roxburghii SARG. (35)							<i>P. longifolia</i>
23 canariensis SMITH (11)							1.5% ester of borneol
Sub-section Pinaster							
Group X - Lariciones							
25 resinosa AIT. (21)							*Unidentified sesquiterpene
26 tropicalis MORELET							Not investigated
27 Massoniana LAM.							Not investigated
28 densiflora SIEB. & ZUCC. (27)							Incomplete information; sesquiterpene suspected
30 montana MILLER							Not investigated
32 Thunbergii PARL. (36)							*Unidentified tricyclic sesquiterpene
33 nigra ARNOLD (6)							*Unidentified sesquiterpene
34 Merkusii DE VRIESE (33)							
35 sinensis LAM.							Not investigated
36 insularis ENDL.							Not investigated
36 khasya ROYLE (34)							Shaw's variety of <i>P. insularis</i>
50 pifyusa STEVEN (11)							Shaw's variety of <i>P. halapensis</i>
29 sylvestris L. (2)							Several varieties, needs thorough study
taiwanensis HAYATA (14)							Supposedly a variety of <i>P. densiflora</i> ; not in Shaw's classification
Group XI - Australes							
39 ponderosa DOUGL. (11)							
39 ponderosa (UTAH) (19)							
39 ponderosa (COLORADO) (26)							*Unidentified sesquiterpene
39 ponderosa (ARIZONA) (26)							*Unidentified sesquiterpene
39 ponderosa (S DAKOTA) (26)							*3% terpinolene; 3% unidentified sesquiterpene
39 ponderosa (IDAHO, N.) (26)							*Unidentified sesquiterpene
washingtonis MASON & STOCKWELL (11)							Possibly a hybrid; varying mixtures of $\beta$ -pinene and $\Delta^3$ -carene; traces of an $\alpha$ -pinene
39 Engelmanni CARR.							Shaw's variety of <i>P. ponderosa</i> ; not investigated
39 apACHECO LEMM.							Shaw's variety of <i>P. ponderosa</i> ; not investigated
Cooperi BLANCO (13)							Not in Shaw's classification
38 durangensis MART. (12)							Shaw's variety of <i>P. montezumae</i>
38 Montezumae LAM. (12,20) complex consisting of 5 species, 8 varieties and forms							Typical, from central Mexico; needs additional study
37 pseudostrabus LINDL. complex consisting of 3 species, 4 varieties and 1 form							Needs a thorough study; apparently crosses with <i>P. Montezumae</i>
40 taecole SCHLECT. & CHAM.							Not investigated
41 Lawsonii ROEHL.							Not investigated
42 occidentalis SWARTZ							Not investigated
43 palustris MILLER (4)							
44 caribaea MORELET (7)							
45 taeda L. (24)							
46 glabra WALTER (26)							
47 echinata MILLER (19)							
Group XII - Insignes							
48 Pringlei SHAW							Not investigated
49 oocarpa SCHIEDE (22)							From Michoacan, Mexico
49 oocarpa trifoliata MART. (12)							From Durango, Mexico; 5% unidentified terpene
50 halepensis MILLER (37)							*Unidentified sesquiterpene
51 pinaster AIT. (37)							Information incomplete; * sesquiterpene suspected
52 virginiana MILLER (24)							
53 clauso WASEY (32)							*10% camphene
62 attenuata LEMONN. (25)							
63 radiata D. DON (24)							
56 pungens LAM. (26)							
57 Banksiana LAM. (11)							
59 Greggii ENGEL.							Not investigated
60 patula SCHLECT. & CHAM.							Not investigated
61 muricata D. DON (N) (18)							*Less than 1% camphene
61 muricata D. DON (S) (18)							Not investigated
54 rigida MILLER (19)							
55 serotina MICHX. (11A)							Information incomplete
49 oocarpa SCHIEDE (a variety) (13)							From Chiapas, Mexico
58 contorta DOUGL. (23)							
58 Bolanderi PARL. (23)							Shaw's variety of <i>P. contorta</i>
58 Murrayana BALF. (30)							Shaw's variety of <i>P. contorta</i>
Group IX - Pineae							
24 pinea L. (6)							*Unidentified sesquiterpene
Group XIII - Macrocarpae							
39 Jeffreyi BALF. (31)							
64 Torreyano PARRY (10)							
65 Sabiniana DOUGL. (30)							
66 Coulteri D. DON (17)							
37 pseudostrabus oaxacana LINDL. (13)							From Chiapas, Mexico
38 Montezumae LINDL. (a variety) (12)							From Chiapas, Mexico
31 probably luchuensis MAYR.							In progress
21 probably Lutholtzii ROB. & FERN.							In progress

\*Subsections, Groups and numbers agree with Shaw. Rearrangement as noted by change of position of numbers is based on the chemical composition of turpentines. Italic numbers in parentheses refer to literature cited at the end of the paper

ter (if it is the same species as *P. pithyusa*) contains a considerable admixture of  $\Delta$ -3-carene.

*Pinus lumholtzi* is moved from group IX, closer to the group XIII, because it contains a considerable amount of limonene.

One pine, tentatively identified as „*P. montezumae* from Chiapas“ but chemically different from the typical *P. montezumae*, also was moved to the bottom of the table. The group *Pineae*, consisting of one species — *P. pinea* — was moved from its place in SHAW's scheme closer to the group XIII with which it has a great deal in common. *Pinus jeffreyi* was restored to its original rank of independent species from its position under SHAW as merely a variety of ponderosa pine. At present, most botanists and geneticists agree that this pine deserves a specific rank. Its chemical characteristics amply support this idea. On the basis of its chemical characters, the writer places *P. jeffreyi* in the group *Macrocarpae*. The aldehyde-containing (26) *P. luchuensis* known to SHAW „through MAYR's description and a single dried specimen“ (29, p. 56) and a heptane-containing pine from Chiapas — which is tagged for the time being as *P. pseudostrobus* var. *oaxacana* also are moved to the bottom of the table. In PILGER's classification (28), *P. pseudostrobus* is grouped with 2 other heptane-containing pines: *P. jeffreyi* and *P. torreyana*. As a whole, these changes are of a minor character and do not affect very much the structure of SHAW's system.

Turning to the chemical composition of the *Diploxylon*, the writer arranged the ingredients of the turpentine in order from the simplest to the most complicated, namely, the aliphatic hydrocarbons which are sometimes associated with aliphatic aldehydes; the monocyclic terpenes (chiefly limonene); the bicyclic terpenes:  $\alpha$ - and  $\beta$ -pinenes, and  $\Delta$ -3-carene; and the sesquiterpenes. Of these components, the two pinenes (especially,  $\alpha$ -pinene) are found in almost all pines. The exceptions are: *P. torreyana*, *P. sabiniana*, *P. jeffreyi*, and perhaps *P. serotina*. Some varieties of *P. ponderosa* have very small amounts of  $\alpha$ -pinene. *Pinus contorta* and its varieties have merely traces of this terpene.

A sesquiterpene longifolene originally discovered in turpentine of *P. roxburghii* (formerly known as *P. longifolia*) has been found during the life of this project in several other pines; it would seem to be the most common sesquiterpene of the *Diploxylon* pines. Sesquiterpenes are evenly distributed among the different groups of pines. In some species they are completely lacking.

When Table 1 is considered as a whole, it is evident that SHAW's classification, slightly modified, reveals certain chemical tendencies.

The group *Macrocarpae*, together with *P. jeffreyi*, forms a chemical group of pines possessing aliphatic hydrocarbons and in some cases aliphatic aldehydes. Monocyclic terpenes occur in some pines of this group in large quantities, but bicyclic terpenes are either completely lacking or (in one species) are subordinate. This group is composed of pines that are endemic. All four of them are restricted to the geographical region of California (which extends somewhat into the northern part of Lower California, southern Oregon, and western Nevada).

Adjacent to the aliphatic hydrocarbon pines, are found pines containing predominantly monocyclic terpenes — limonene (mostly) and phellandrene (rarely). Report on the Pacific coast *P. ponderosa* (11) containing 25 percent of limonene proved to be erroneous. This pine contains only 2 or 3 percent of this terpene. SHAW's groups *Laricionae*, *Au-*

*strales*, and *Insignes* remain almost intact. Only positions of some pines within a group were changed. At the top the group *Australes* there appears a bicyclic terpene,  $\Delta$ -3-carene. This terpene occurs also in several *Laricionae* pines and in *P. roxburghii* of the group *Longifoliae*, but not in any *Insignes* pines.

Although some 12 pines are yet to be investigated, it is almost certain that most of them will remain in the classification where SHAW put them.

There are several discrepancies in revision of SHAW's classification of pines as proposed by DUFFIELD (5), and as suggested by the present writer. In view of our not yet thorough understanding of the polymorphic pine species, and our not yet complete knowledge of the genetic and chemical relationships of pines, it is not surprising that there are some discrepancies. The surprising fact is how little disagreement there is between the results of DUFFIELD's genetic approach and the author's chemical approach in their attempts to contribute to the revision of the Genus *Pinus*.

### Zusammenfassung

Die einzelnen Kiefernarten des Subgenus *Diploxylon* werden auf die unterschiedliche Zusammensetzung ihrer Terpentine hin untersucht und danach in einem System angeordnet. Dieses System stimmt in großen Zügen mit dem von SHAW überein. In Tabelle 1 sind die Spezies entsprechend dem System von SHAW von 20 bis 66 nummeriert. Die hierbei nicht in der Reihenfolge stehenden Zahlen zeigen die durch die vorliegenden chemischen Untersuchungen begründeten Änderungen an. Die Anordnung weicht in einigen Punkten von der von DUFFIELD auf Grund von genetischen Analysen vorgeschlagenen ab, was mit den genetisch wie chemisch zum Teil noch unvollständigen Untersuchungen erklärt wird.

### Literature Cited

- (1) ARBUZOV, B. A.: Composition of turpentine of *Pinus pithyusa*. Zhurn. Prikl. Khimii 5: 787—89 (1932).
- (2) ARBUZOV, B.: A note on composition of Russian turpentine. Zhurn. Prikl. Khimii 7: 757—59 (1934).
- (3) BLANCO, CENOBIO E.: *Pinus cooperi* BLANCO. Sp. nova. Anales del Instituto de Biología 20: 185—87 (1949) and other articles in the same publication. Mexico City.
- (4) CHADWICK, T. C., and S. PALKIN.: Composition of American gum turpentine exclusive of the pinenes. U. S. Dept. of Agric. Bull. No. 749 (1941).
- (5) DUFFIELD, J. W.: Relationships and species hybridization in genus *Pinus*. Z. Forstgenetik 1: 93—99 (1952). (In English and German.)
- (6) DUPONT, G., and M. BARRAUD: Composition of pine oil from *Pinus pinea*. Bull. Soc. Ch. France 36, 625—31, 784—92 (1924).
- (7) DUPONT, G. and M. BARRAUD: Sur la composition de l'essence de térébenthine Américaine. Bull. Inst. Pin. 60: 155—156 (1929).
- (8) ERDTMAN, H.: Organic chemical research. Svensk Kemisk Tidsskrift 63: 43—66 (1951).
- (9) GREGUSS, P., and I. VARGA: Xylotomischer Bestimmungsschlüssel der *Pinus* Arten. Inst. der Universität Czegeged (Hungary). 162 pp. Illus. Czegeged (1950).
- (10) HAAGEN-SMIT, A. J., C. T. REDEMANN and N. T. MIROV: Composition of gum turpentine of Torrey pine. J. Am. Chem. Soc. 69: 2014—17 (1947).
- (11) HAAGEN-SMIT, A. J., C. T. REDEMANN, T. H. WANG, and N. T. MIROV: Composition of gum turpentine of pines: A report on *Pinus ponderosa*, *P. banksiana*, *P. canariensis* and *P. washoensis*. J. Am. Pharm. Assoc. Sci. Ed. 39: 260—265 (1950).
- (11a) HERTY, C. H., and W. C. DICKSON: The volatile oil of *Pinus serotina*. J. Am. Chem. Soc. 30: 872—4 (1908).
- (12) ILOFF, P. M., and N. T. MIROV: Composition of gum turpentine of pines. XVII. A report on *P. montezumae* from Chiapas, and *P. oocarpa* var. *trifoliata* and *P. durangensis* from Durango, Mexico. J. Am. Pharm. Assoc. Sci. Ed. (In press) (1953).
- (13) ILOFF, P. M., and N. T. MIROV: Composition of gum turpentine of Pines. XVI. A report on *Pinus oocarpa* and *P. pseudostrobus* var. *oaxacana* from Chiapas and *P. cooperi* from Durango. J. Am. Pharm. Assoc. Sci. Ed. 42: 46—49 (1953).
- (14) KAFUFU, K., N. ICHIKAWA, and R. KATO: Turpentine of *Pinus taiwanensis*. J. Chem. Soc. Japan 55: 185—89 (1934).
- (15) LOOCK, E.

E. M.: The pines of Mexico and British Honduras. Dept. of Forestry, Pretoria, South Africa, Bull. No. 35, 244 pp. Illus. (1951). — (16) MARTINEZ, M.: Los Pinos Mexicanos, 2nd Ed. Mexico 361 pp., Ediciones Botas (1948). — (17) MIROV, N. T.: Composition of gum turpentine of Coulter pine. Ind. Eng. Chem. 38: 405—8 (1946). — (18) MIROV, N. T.: Composition of gum turpentine of Bishop pine. J. Forestry 45: 659—60 (1947). — (19) MIROV, N. T.: Composition of gum turpentines of pines. A report on *Pinus echinata*, *P. rigida* and *P. ponderosa* from Utah. J. Am. Pharm. Assoc. Sci. Ed. 40: 410—13 (1951). — (20) MIROV, N. T.: Composition of gum turpentines of pines. XII. A report on *P. montezumae*, *P. oocarpa*, and *P. leiophylla*. J. Am. Pharm. Assoc. Sci. Ed. 40: 550—51 (1951). — (21) MIROV, N. T.: Composition of gum turpentines of pines. XV. A report on *P. resinosa* and *P. reflexa*. J. Am. Pharm. Assoc. Sci. Ed. 41: 677—79 (1952). — (22) MIROV, N. T.: Chemical aspects of white pines. Madroño, In press (1953). — (23) MIROV, N. T.: Unpublished data. — (24) MIROV, N. T., T. H. WANG and A. J. HAAGEN-SMIT: Chemical composition of gum turpentines of pines. A report on *Pinus strobus*, *P. cembra*, *P. taeda*, *P. radiata*, and *P. virginiana*. J. Am. Pharm. Assoc. Sci. Ed. 38: 403—07 (1949). — (25) MIROV, N. T., and A. J. HAAGEN-SMIT: Composition of gum turpentine of Knobcone pine. J. Forestry 47: 721—22 (1949). — (26) MIROV, N. T. and P. M. ILOFF: Yet unpublished (1953). — (27) Morioka Forest Exp.

Sta. Japan, Information received through Forestry Division, Natural Resources Section SCAP. (1950). — (27a) PAPAJOANNOU, J.: Über Artbastarde zwischen *Pinus brutia* TEN. und *P. halepensis* MILL. etc. Forstwiss. Centralbl. 58: 194—205 (1936). — (28) PILGER, R.: *Gymnospermae*. In Engler und Prantl: Die natürlichen Pflanzenfamilien. 2nd Ed. Leipzig. Vol. 13: 447 pp. (1926). — (29) SHAW, G. R.: The Genus *Pinus*. Arnold Arboretum Publ. No. 5. 96 pp. (1914). — (30) SCHORGER, A. W.: An examination of oleoresins of some western pines. U. S. Dept. of Agric., F. S. Bull. No. 119 (1913). — (31) SCHORGER, A. W.: The oleoresins of Jeffrey and Singleleaf pines. Ind. Eng. Chem. 5: 971—73 (1915). — (32) SCHORGER, A. W.: The oleoresin of Sand Pine. Ind. Eng. Chem. 7: 321—22 (1915). — (33) SIMONSEN, J. L.: Essential oil from *Pinus merkusii*. Ind. Forest Records 10 (4): 51—57 (1923). — (34) SIMONSEN, J. L., and M. G. RAU: The essential oil from oleoresin of *Pinus Khasya*. Ind. Forest Records 9 (4): 112—15 (1922). — (35) SIMONSEN, J. L.: The constituents of Indian turpentine from *Pinus longifolia* ROXB. J. Chem. Soc. 117: 570—78 (1920), 123: 549—60 (1923), 123: 2642—66 (1923). — (36) SHINOSAKI, Y.: Turpentine of *Pinus Thunbergii*. J. Soc. Chem. Ind. Japan, 21: 763—64 (1918), 22: 451—54 (1919). — (37) VEZES, N., and G. DUPONT: Résines et térébenthines. 656 pp. Bailliere et fils. Paris (1924). — (38) ZOBEL, B.: The natural hybrid between Coulter and Jeffrey pines. Evolution 5: 405—13 (1951).

(Aus dem Institut für Forstsamenkunde und Pflanzenzüchtung, München)

## Untersuchungen über den Ablauf der Meiosis bei *Pseudotsuga taxifolia* Britton

(Vorläufige Mitteilung)

Von URSULA ZENKE

(Eingegangen am 1. 3. 1953)

Die vorliegenden Beobachtungen wurden an Pollenmutterzellen in verschiedenen Entwicklungsstadien durchgeführt. Es handelt sich dabei noch nicht um vollständige und endgültige Untersuchungsergebnisse, sondern um vorläufige Befunde an einzelnen Meiose-Stadien, die ihrer Anschaulichkeit wegen beschrieben und mit Mikrophotographien belegt werden sollen. Unsere Untersuchungen werden fortgesetzt, und es ist beabsichtigt, sie in einer späteren Gesamtabhandlung über die Zytologie der Douglasie ausführlich zu diskutieren.

Als Untersuchungsmaterial wurden männliche Blütenknospen von *Pseudotsuga taxifolia* var. *viridis* verwandt, die von Bäumen aus dem Versuchsgarten Grafrath der Forstlichen Forschungsanstalt München gewonnen worden sind. Fixierung und Färbung geschahen in allen Fällen nach der Karminessigsäuremethode. Bei der Präparatstellung wurde die hierbei übliche Quetschtechnik angewandt. Als günstigster Zeitpunkt für die Fixierung erwies

sich unter den hiesigen Klimaverhältnissen die zweite Hälfte des Monats Januar.

Die Pollenmutterzellen lösen sich bereits in frühen Entwicklungsstadien (mit Ruhekernen) aus dem Archesporverband heraus. Sie sind zunächst noch nicht ganz abgerundet, sondern zeigen oft noch eckige Konturen. Die Zelle auf *Abbildung 1* befindet sich schon frei in der Antherenflüssigkeit. Der noch ruhende Kern hat durch Wasseraufnahme hier bereits an Umfang zugenommen. Der von granaartig gefärbtem Chromatin erfüllte Kernraum setzt sich noch deutlich gegen das übrige Zellplasma ab. Im Verlaufe der weiteren Auflockerung der Kernstruktur treten dann zwischen den Grana feine Fäden auf, d. h. Heterochromatin und Euchromatin werden unterscheidbar. Derartige Stadien stellen einen Übergang zur nächsten Phase dar. In *Abbildung 2* wird die zarte Fadenstruktur, die das Leptotän charakterisiert, deutlich.

Die *Abbildungen 3—4* zeigen bereits Zellen im Zygotän. Die typische Annäherung der homologen Chromosomenfäden und der noch in einzelnen Abschnitten parallele Verlauf ist an verschiedenen Stellen gut verfolgbar (siehe  $\curvearrowright$ ). Im Beispiel der *Abbildung 3* sind die Chromosomen A A (offenbar die SAT-Chromosomen) in ihrem mittleren Abschnitt schon gepaart und erscheinen daher dort als einziger Faden (siehe +).

In ihrer ganzen Länge gepaarte, dicker und einheitlich erscheinende Fäden, wie sie das Pachytän charakterisieren, gibt die *Abbildung 5* wieder. An einigen wenigen Stellen, an denen zwei parallel gelagerte Chromomeren sichtbar werden, tritt ihre Doppelnatur zu Tage (siehe  $\curvearrowright$ ).

Der weitere Verlauf, nämlich die nun wieder erfolgende Trennung der gepaarten Homologen, wird an verschiedenen Stellen der *Abbildung 6* ersichtlich. Dort lassen sich auch bereits einzelne Chromosomenenden (siehe  $\curvearrowright$ ) und

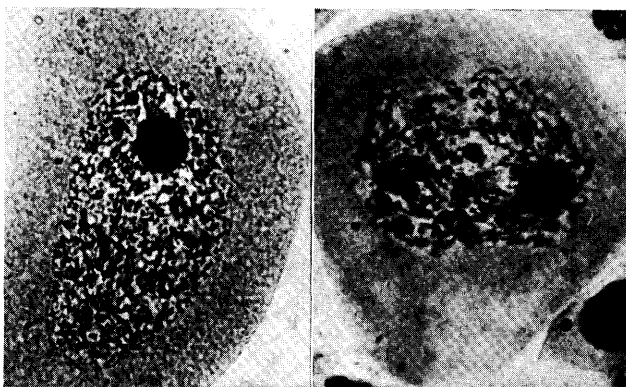


Abb. 1—2. — Vergr. 720 $\times$ .