

PLANT PARASITES.

EXPERIMENTAL PARASITISM IN THE HIGHER PLANTS.

BY DR. D. T. MACDOUGAL.

FLOWERING plants which live as parasites upon other organisms are exemplified to the common observer by the mistletoe, and the farmer has further unwelcome knowledge of the yellowish cord-like stems of the various species of dodder which infest his fields of wheat and flax. These and other seed plants which are parasitic on crops are a serious economic menace in places. About 2,500 species of parasitic seed plants are known, which are included in two hundred genera, representing ten great families. All degrees of dependence are exhibited by the members of these families, some having a normal green color, and capable of independent existence when they do not readily find a host, while others have lost their chlorophyll, and with it the capacity for building up complex foods. Degeneration and atrophy have been carried so far in some cases, that the entire plant including the flowers and ovaries does not come above the surface of the ground.

The shoots and aerial parts of plants are subject to constant scrutiny, so that parasitism on the branches of trees and other large forms is readily detected. The underground members are not so well known. The careful examination of the root systems of a few desert plants by Dr. W. A. Cannon at the Desert Laboratory has resulted in the discovery that *Krameria*, a small leguminous shrub, is parasitic on a number of hosts, a fact that has hitherto eluded observation, although the roots have been used to furnish color adulterants for many years. Thorough examination of the common plants would doubtless result in evidence that would double the number of parasites, and give a total that would include above five per cent of all flowering plants which exhibit dependent nutritive habits.

Any study of parasitic plants leads to a consideration of the mycorrhizal forms, or plants which form associations with filamentous fungi in which the thread-like hyphae enwrap or penetrate the roots of the higher plants. Such partnerships generally result in some advantage to the higher plant, and are followed by immediate changes similar to those exhibited by species known as parasites. These changes include a lack of differentiation of the tissues, even in the seed and embryo; a lessened development of the shoot and root, a reduction of the leaf surface, and diminished production of chlorophyll. Taken together, the parasitic plants and those which enter into partnerships with fungi in the soil, comprise nearly half of the seed plants of the world. It is evident that the existence of a tendency affecting half of the higher plants, which leads toward atrophy of the vegetative organs and the development of specializations of structure and habit seen in associations and dependent nutrition, must have a tremendous significance for the student of evolution.

Singularly enough, the changes shown by parasites are not due directly or alone to the food received by the host or symbiont, as no similar changes may be seen when plants are fed with solutions of organic materials which might be obtained by parasitism. The entire set of complicated conditions furnished by active association with a living host or co-operating organism seems to be necessary to induce the changes described.

The studies of the general anatomical features presented by the families, the members of which exhibit parasitism, have so far failed to yield any conclusions as to the morphological features which might be favorable to such arrangements. The specialization of tissue which ensues when a seed plant becomes parasitic fortuitously, is far more striking than any simple anatomical character which might be interpreted to indicate a predisposition to the dependent habit of nutrition in autophytes.

Theoretical considerations lead to the belief that it is to purely physiological features and to the habits of green plants that we must look for the conditions favorable to the origination of parasitism. Evidence to the effect that a number of green plants may take inorganic compounds through their membranes is increasing, and this capacity would facilitate parasitism as at present understood. The course of development of the absorbing organs, their mechanical relations to the bodies of other plants, and the concentration of the fluids in the cells of the possible parasite, would be features to which attention would naturally be directed in any attempt to ascertain the method of origin of this method of nutrition. Some results of importance with respect to this matter are presented herewith.

The mechanical adhesion of the bodies of seed

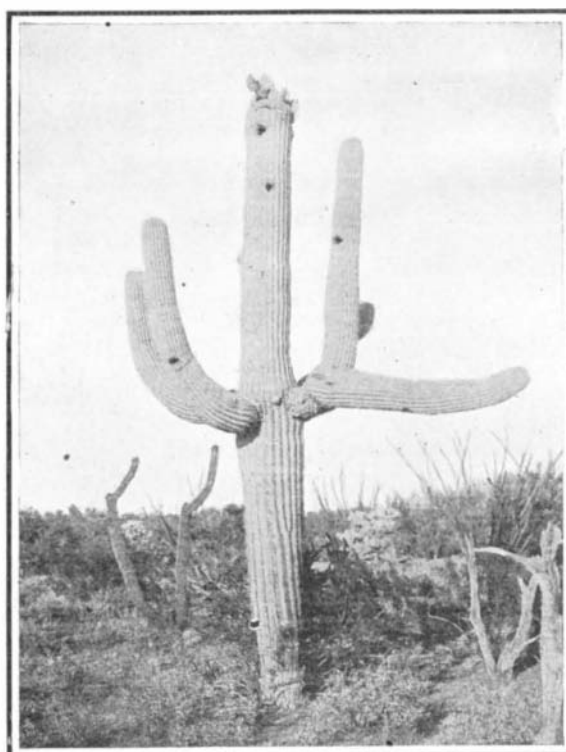
plants which would make parasitism possible, might be brought about by three different ways. The roots growing thickly interlaced in the soil might unite or penetrate each other, or adventitious roots arising from internodes any place on the aerial stems might pierce the bodies of other plants, or seeds lodging in the bark or in the wounds of a plant might germinate



MEXICAN GRAPEVINE GROWN ON PRICKLY PEAR FOR ONE YEAR.

ate and send absorbing organs into the tissues of the possible host. Of these methods, that of incidental root parasitism seems to bear the greater probability of recurrence, and to be illustrated by some very striking examples. Peé-Laby has recently described a case in which the main root of a plant of a passion-flower vine has become attached to a root of Japanese burning bush, forming a specialized absorptive tissue, and undergoing general atrophy of its own root system, in a manner suggestive of a highly developed degree of parasitism, although but little indication of this was to be seen in the shoot of the *Passiflora*.

The germination of seeds on the bodies of other plants might result in mechanical parasitism, the ad-



PRICKLY PEAR GROWING ON GIANT TREE CACTUS.

vantage being purely one of position with respect to light, and this feature is illustrated by many hundreds of examples, particularly abundant in tropical forests. The development of any form of nutritive dependence out of such purely mechanical relations has not yet been demonstrated, although various workers, notably Peirce, have made extensive demonstrations of the

possibility of short-lived annuals completing their entire cycle of existence as parasites upon enforced hosts, in the tissues of which their seeds were germinated, or were set at an early stage of their existence.

It is also reported that grape culturists in France insert seeds of the vine in old living stems of the same plant a short distance above the ground, and that the developing plantlets send roots through the tissues which eventually reach the soil and ramify in it. Many of the phenomena consequent upon grafting operations also are of interest in this connection. Such unions may be of all degrees of intimacy varying from perfect grafts, where the vessels unite, to other cases in which the scion is separated from the stock by a layer of dead tissue, through which there can be no free interchange of material as between a branch and a main stem, but instead a phase of parasitism exists. These arrangements in fact present the simplest accomplishments of parasitism artificially produced.

A large number of instances are known in which the scion after uniting with the stock, or during the process, sends out adventitious roots, which strike downward and penetrate the tissues of the host, simulating parasitism mechanically, as would be done whenever the roots of any plant accidentally bore through those of another. No real or important transfer of food material has been demonstrated in such cases, and the roots showed no prolonged existence.

The whole subject thus illustrated seemed to offer unusual opportunities for the study of the origin of "adaptations" or of acquisition of specialized characters. Various stages of parasitism are known, ranging from plants which derive only a small amount of nutrition from some incidental host to instances where everything is taken from the supporting organism. The induction of even a slight degree of dependence of one seed plant upon another or the intensification of the habit in a form already showing a tendency to parasitism would be taken as evidence of first-class importance in the interpretation of the way in which new characters are acquired and developed in the history of the plant.

In the organization of an experimental attack on this problem at the Desert Laboratory, it was thought advantageous to use plants furnished with a large water balance, and hence capable of existence for extended periods, independent of any additional supplies. Such forms have great inertia; that is, cuttings or sections of the body may carry on existence in a fairly normal manner for a long time without additional supplies, and during this time regeneration and the formation of new absorbing organs may take place with adjustment to conditions of parasitism. Observations on material of this character might well furnish exceptional opportunities for detecting the conjunction of conditions or developmental stages which would facilitate the assumption of dependent relations in nutrition. The use of massive plants also rendered it easy to make the chemical analyses necessary to determine the concentration of the cell sap, which was thought to be of importance in this connection. The most direct method of ascertaining the relative osmotic value of the sap of two plants would be by freezing tests of the expressed juice.

The native flora around the Desert Laboratory at Tucson, Arizona, is rich in succulents which furnish the conditions noted above and the material chosen for experimentation in the present work included chiefly several *Opuntias* which were used as both host and parasite, normal and in etiolated condition: *Carnegiea gigantea*, exclusively as host, *Echinocactus wislizenii* as host, *Fouquieria splendens* as both host and parasite, *Cissus digitata* and *C. laciniata* from Southern Mexico, *Agave americana*, *Cotyledon macrantha*, and *Tradescantia* as parasites, in addition to a number of other forms, of which but slight use was made. After some preliminary tests, the arrangement of the material in the dependent relation was begun seriously in January, 1908, and many hundreds of preparations have been set up since then.

The methods of experimentation employed consisted in making cuttings of the joints of prickly pears, Mexican grapevine, agave, and of other plants which were to be induced to live parasitically, and thrust these into a bed of sand until the raw surfaces were healed and regeneration with root formation had begun. Next a suitable cavity was cleanly cut in the flesh of a giant cactus or barrel cactus, or in the plant to be used as host, into which the base of the slip of the "xeno parasite" was thrust. The insertion was held in place by an adequate setting of plaster of Paris, and

the whole preparation was cared for as to shade and temperatures. If the inserted slip was capable of immediate adjustment to the new conditions, interesting results followed. The transfer of a plant from its original state to experimental arrangement described, however, is an extremely radical one, and involves serious disturbances of a group of functions. Thus, in the insertion of slips of one plant in the body of another, the development of the roots would necessarily be carried on in confined wound cavities, in which the only free oxygen available from the growth of these organs would be that coming from the intercellular spaces of the host and by transfusion. The lack of this substance alone would operate to prevent parasitism, while in other cases the speedy formation of oxidases and peroxidases in the wound tissues, together with the ready formation of corky layers and mucus, would hinder root formation.

None of these factors would be detrimental to actual grafting, since in this case the union of living cells and the intermediate tissues would proceed best when free aeration was prevented.

Some of these experimentally arranged parasites have endured for more than two whole seasons, forming roots which penetrated the soft bodies of the hosts in some instances, while other species absorbed juices directly through the epidermal surfaces of the healed bases of the slips inserted.

The spread and surface leaves and branches developed from the inserted parasitic slips were in all cases less than that of similar parts which still formed a part of the original plant from which cuttings were made. The lessened size and reduced leaf surface characteristic of parasites was thus seen as a direct response of the individual to dependent nutrition, foreshadowing the degradation or atrophy which reaches advanced stages in species which have followed a long course of parasitism.

After a great number of experimental trials had been made in which the failures proved no less interesting than the successes, a series of analyses was made to determine the concentration or osmotic activity of the sap of the species used in the tests.

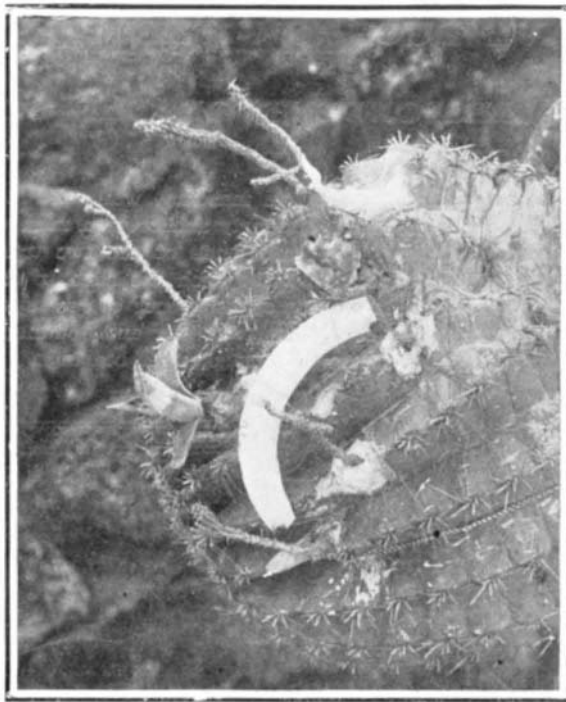
The results of these analyses and of the general observations show that the Mexican grapevine with an osmotic activity of 15 (?) atmospheres was successfully parasitic on a small prickly pear (*Opuntia blakeana*) in which the mucilaginous juice had a pressure of 9 atmospheres and on the barrel cactus (*Echinocactus*) at a pressure of 6 atmospheres, but not on the giant tree cactus (*Carnegiea gigantea*) at 7 atmospheres by reason of the copious gummy exudation and fermentation products which follow wounds in making the necessary incision in the body of the host. Rooted joints of the prickly pear were parasitic on the barrel cactus (see above), especially when the slender cylindrical joints produced by the prickly pear when it is grown in darkness were used as parasites. The cylindrical prickly pear (*Opuntia veriscolor*) with a juice showing a pressure of 12 atmospheres was successfully parasitic on *Carnegiea*, and on *Echinocactus*. (See above.) Rooted cuttings of agave, or the common century plant, maintained themselves for extended periods upon *Carnegiea* and *Opuntia*, as it had a pressure of about 11 atmospheres.

A careful consideration of all the details gathered from the experiments showed that one plant might become parasitic upon another only when it possessed a sap having a higher osmotic activity and hence being capable of withdrawing sap from the body of the possible host. Other causes might intervene to prohibit parasitism even when the relative osmotic pressures were favorable, but such inequality was a necessity in all cases. It is to be noted that the pressure of the sap changes unequally in different species with the seasons, and that a plant which might have a higher osmotic pressure at one season would be incapable of acting as a parasite during other seasons with respect to any given host. The plants used in the tests were natives of arid areas and accumulate a relatively great amount of surplus water at times, thus lowering the osmotic activity of the sap, while during the drier seasons water is lost in such quantity as to increase the osmotic pressure. In none of the analyses of desert plants hitherto made has the sap been found to show a higher activity than that of the common lilac and other plants which have been known to display an activity equivalent to 25 atmospheres and even higher. It is to be noted also that many plants show a capacity for increasing the osmotic activity of the sap when the solution in the substratum becomes more concentrated, and this may play a very important part in the origination and development of parasites.

The relative acidity of the sap of two plants appeared to be of no importance in the determination of their capacity to enter into parasitic relations, quite contrary to a common supposition. The ready formation of wound tissue or the exudation of enzymatic products would act as a deterrent to a possible parasite, while the capacity for formation of adventitious roots or of absorptive organs from the surfaces of stems would be an opposing factor in the development of

parasitic relations. The more important features of the specialization by which parasitism ensues may thus be put in the form of an algebraic equation, the reduction of which should indicate with some certainty the possibility of dependent nutrition between two plants.

Many instances of singular arrangements of two species were seen during the course of the observations in connection with the investigations described above. A large prickly pear with several well-de-



AGAVE AND OPUNTIA GROWING PARASITICALLY ON BARREL CACTUS. SCALE PLACED FOR NOTING NUTATION OF STEM.

veloped joints was seen growing from the summit of a tall tree cactus 80 miles west of Tucson, in November, 1907. An individual of a smaller species was found occupying a cavity in an old knothole of a palo verde (*Parkinsonia microphylla*) near the Desert Laboratory, while another occupied a similar position on an acacia tree a few miles to the eastward. The unceasing distributional movements of species over the face of the world would undoubtedly operate to bring new pairs of species constantly under test conditions, and it is in accord with the known facts to suppose that new parasitic unions are being formed frequently in almost all kinds of habitats, while on the other hand, it is to be kept in mind that extinction lies beyond parasitism, as the inevitable atrophies which follow dependent nutrition must in the end bring the species to a precarious condition, in which the slightest untoward variation in its highly complicated environment would end its existence.

The changes ensuing when a plant becomes parasitic may include some startling phenomena, as was illustrated by the action of the prickly pear used in the

movements hitherto described by the fact that they were not accompanied by growth in length. So far as could be determined, the curvatures resulted from rhythmic alterations in the turgidity or osmotic activity of the cell sap on opposite sides of the thin stems, thus setting up a movement utterly foreign to the ordinary habits of the plant, and purposeless so far as its environmental relations were concerned.

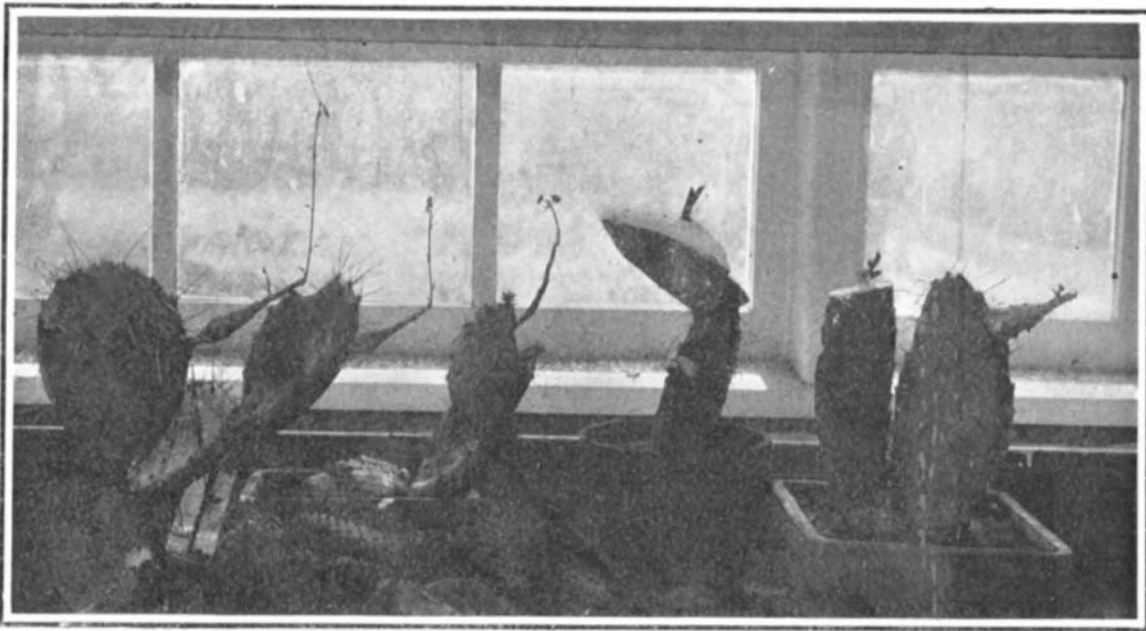
The results of this and previous studies allow us to recognize the limiting factors, the operative conditions, and some of the facts as to the physiological nature of parasitism. Few specializations present their main features so clearly to the student. When the total body of evidence, however, is evaluated in the light of current theories, it is found that it is no easy matter to decide by what main methods of evolutionary procedure this adjustment or "adaptation" is attained, and how it is advanced from stage to stage.

Some alterations such as that of *Passiflora* on *Euonymus* are distinctly discontinuous, but in this particular instance it can not be shown that any permanent results would follow the occurrence of the dependent relation. Some features, however, such as the development of *Haustoria* on roots and stems would be a distinct mutation and well illustrated by *Krameria*, and supposedly also by *Cuscuta*. The taking on of absorptive functions by the epidermal cells of xeno parasites, as described in the present paper, is to be recognized as a distinct mutatory alteration.

A direct and immediate atrophy of the various organs of the shoot ensues as a result of the assumption of the parasitic relation, but the extreme stages of such reduction appear to have been reached by gradual changes although it is evident that such a conclusion is almost wholly inferential. The transition from autophytism to complete parasitism with attendant habitual characters appears to have been gradual, since species may be cited to illustrate all degrees of the alteration; but on the other hand, it is not impossible that the complete change may have been made at once in some forms. Nothing in the entire matter suggests progression or retrogression of all of the involved characters by one method alone.

Viewed from another angle, it may be seen that some of the alterations described may be taken to be directly interlocking, or reactive, essential and practically irreversible. Correlated with these, having no direct connection with originating external causes or limiting conditions, but inevitably consequent upon the primary alterations, are a number of secondary changes which may be the most obvious, but in reality of lesser importance. Modifications of the absorbent organs and of the nutritive systems would be included in the first, while incidental atrophies and other characters such as the striking nutatory movements described would be examples of the second. The ingenious and intricate and strained interpretations made to include all of the phenomena displayed by organisms which bear specialized relations to other organisms or to environmental factors, are in striking contrast with this view.

A good mechanical illustration of the alterations in an organism is of a drop of liquid, such as water, when allowed to rest upon a rough surface, which it will not wet. Under equable external conditions, such



CUTTINGS OF MEXICAN GRAPEVINE GROWING IN JOINTS OF PRICKLY PEAR.

experiments. The structure of the heavy succulent jointed stems of the prickly pears presents no features which suggest movement, yet when etiolated cylindrical branches of these plants were inserted in the fleshy bodies of the barrel cacti, and had become well established, sweeping nutatory movements like those of a vine were set up which carried the tips through an arc of 180 degrees in thirty-six hours, the complete nutation occupying twice that length of time. Furthermore, these movements differed from other nutatory

a drop would be approximately globular with all of its sectors practically equivalent. When placed upon a roughened surface, the shape of the drop would be altered, the sectors in contact with the hard external body would be markedly modified, the position of the centroid would not be the same as that of the free drop, and the non-engaged sectors would be altered to a degree corresponding to the directness of their connection with those in contact with the hard external objects.

With the further application of this illustration the study of the mode of adjustment of an organism to an environmental factor would entail a determination of the changes in the engaging sectors or engaging characters, the measurement of the effects of

the external factors, an estimation of the limiting conditions, and the detection of connected variations in the other sectors, functions, or qualities of the living drop. Among the many other suggestive parallels that might be drawn is to be mentioned the mechanical

fact that under the altered conditions of surface tension ensuing from contact with one set of hard objects, the drop is much more liable to be changed further, or to be broken up by other agencies acting upon the free or unengaged surfaces.

A N O T A B L E B R I D G E.

THE ASSOPOS VIADUCT ON THE PIRAEUS RAILWAY.

BY THE ENGLISH CORRESPONDENT OF THE SCIENTIFIC AMERICAN.

ONE of the most notable works on the Piraeus railway, which has recently been opened in Greece, is the viaduct spanning the Assopos torrent and gorge between Dadi and Lianokladi. The country traversed by the line is among the most rugged in the Balkan peninsula; the mountains rise sharply, the spurs are steep and broken, and torn with deep, wide gulches. The most difficult of these proved to be the Assopos gorge, where it was seen that the structure necessary to span the ravine would have to be of large dimensions, entailing a considerable span in the main section, while the task of erection, owing to the nature of the site, would offer many interesting problems. In order to secure the best type of structure, the railway company decided to invite public competition, and the foremost bridge builders of France and other countries submitted tenders and designs. The successful tender was that of the Société de Construction des Batignolles of Paris. The general features of their design may be gathered from the accompanying illustration, which shows the bridge completed amid its wild surroundings. Through the courtesy of the builders we are enabled to give the following particulars:

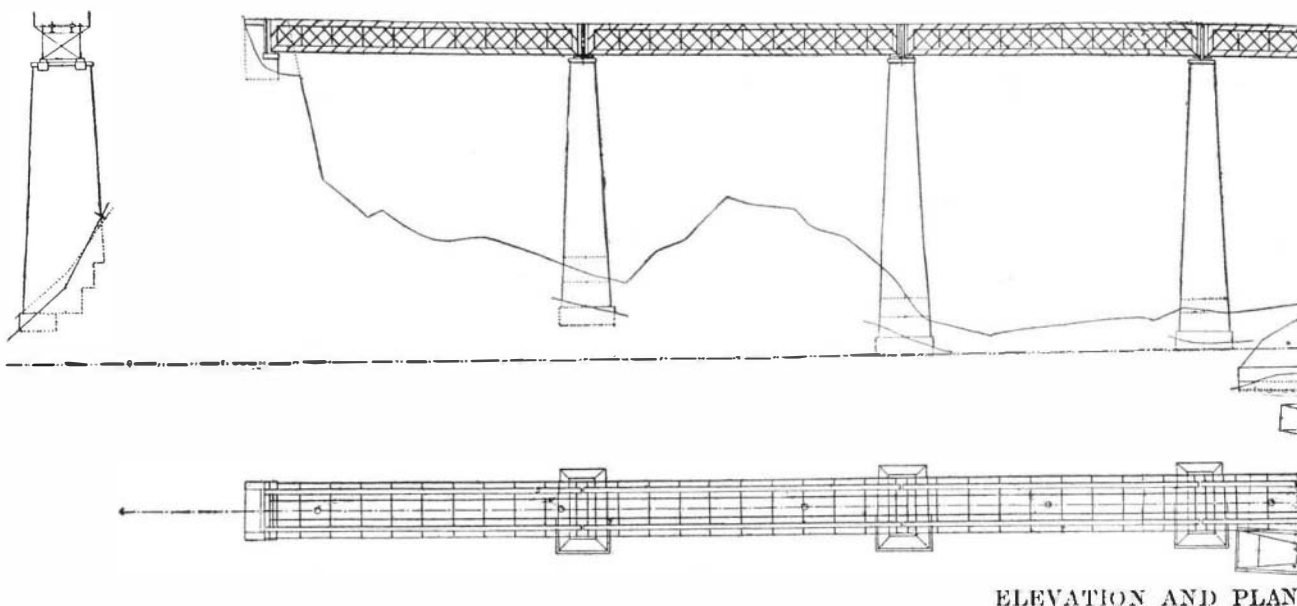
The total length of the structure is 576 feet, the span of the main arch between the anchorages is 240 feet, and the height of the rails above the anchorages is nearly 80 feet. The rails are 330 feet above the bed of the torrent. The viaduct, which carries a single track, is situated upon a curve of about 1,330 feet radius, and has a grade falling toward Lianokladi of 1.875 per cent. The design finally adopted was prepared by M. Paul Bodin, the engineer in chief of the construction company. Broadly speaking, the main opening resembles the feet of a broadly-spread letter A with the floor system forming the crosspiece. The outer arms are perfectly straight and square, while the inner arms have a slight graceful curve to their central point of connection. The net results gained by this design are not only extreme lightness, consequent upon the lesser quantity of metal required, but great stability, with an appreciable economy in first cost.

On the Dadi side there are three approach spans of the deck truss type, each about 86½ feet in length, carried on masonry piers. The latter are of rectangular section, have practically a uniform height—about 80 feet—and have a batter on all sides of one in twenty. The width between trusses is 10 feet, by 14 feet over all at rail level. The extreme abutments of the via-

duct are also carried out in masonry, while the feet of the arched span are similarly anchored in massive masonry plinths. The inner ends of the two truss spans which connect with the arch are fixed to the steelwork of the latter, the opposite ends of each span and truss resting on the masonry pier and abutment, respectively, and having the usual roller bearings.

inches in diameter, one-half of the steel bearing being attached to the extremity of each half of the arch.

The erection of this bridge at the gorge was beset with numerous difficulties. The task was aggravated by the fact that the viaduct is entered from either side of the gorge through a tunnel, which somewhat handicapped movement. Working spaces, however,



ELEVATION AND PLAN

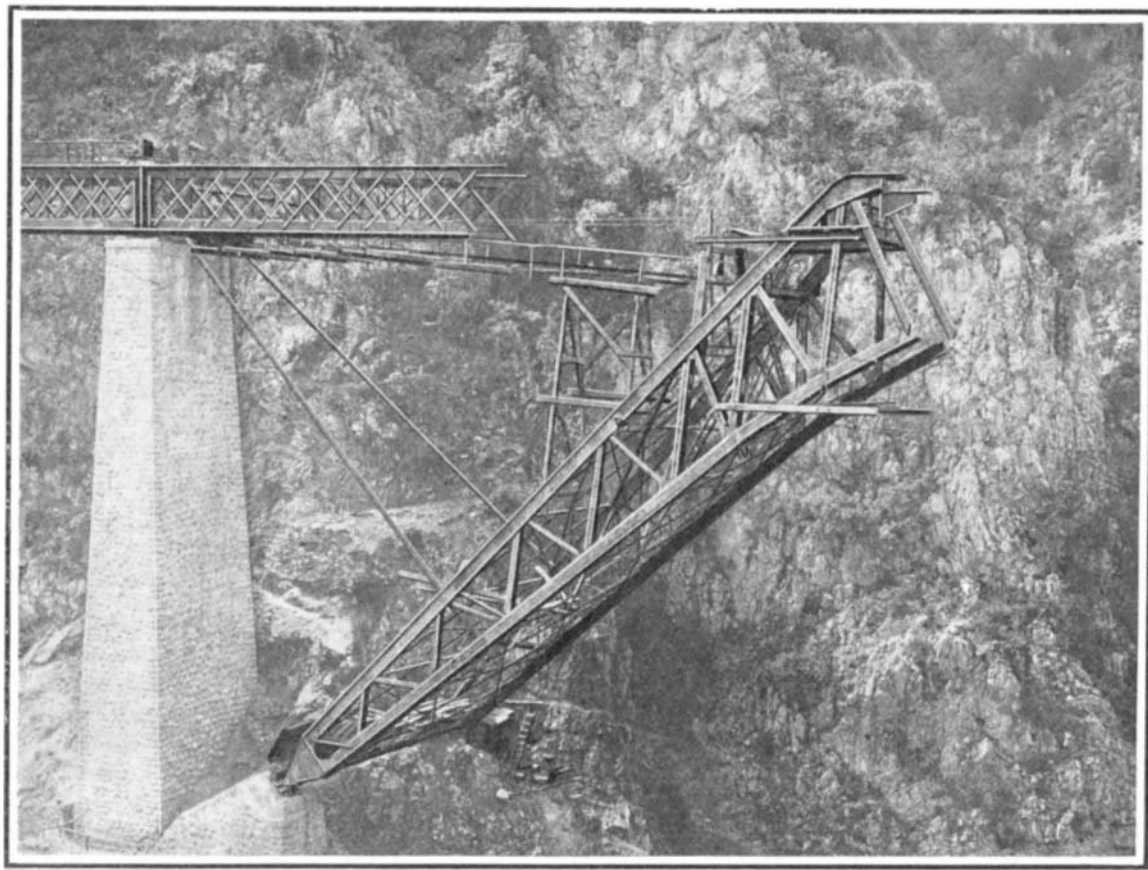
The main or arched span is built up of two sections of identical design, connected at the crown. Each leg is anchored to a solid masonry foundation, and the feet are spaced about 40 feet apart, center to center. The extrados comprises straight members set at an angle of about 45 degrees from the horizontal, while the lower members describe a parabola. The greatest distance between the upper and lower girders is at the point where the extrados meets the horizontal truss, the depth of the truss at this point being about 22½ feet. The legs have a taper of 14 per cent, so that at rail level the width conforms with that of the straight spans. The upper and lower girders of each truss was vertically divided into N panels, while horizontally the bracing is of the simple cross diagonal type. The feet are anchored to the masonry foundations by pins having a diameter of about 12 inches, while the connecting pin at the crown is about 6½

were cut in the mountains on either side of the ravine. An overhead cableway was set up spanning the gorge and the site. The material was brought up to the entrance to the tunnel, through which a temporary track was laid, and transported on to special cars which hauled the material to the foot of the works. Here each piece was picked up by hoisting tackle on the overhead cableway, and by means of a second hauling cable was transported from one side of the ravine to the other, or set exactly where required.

The straight deck spans were erected in the usual manner. It was the erection of the main span that occasioned the greatest difficulty. On the Dadi side, a timber falsework was erected around the anchorages to support the first sections of the arch. When the feet were anchored and the cross bracing riveted up, it was possible to continue the erection upward without further scaffolding to the level of the second verticals from the base. The inclined section was then temporarily secured by diagonal chords connecting with the outer members of the arch and the under side of the first panel of the overhanging straight span at the adjacent masonry pier, as shown in the accompanying illustration. This enabled erection to be continued up to the point where the inclined section met the rail level, and then similar temporary chords, practically horizontal, and carried to the same points as the temporary diagonal chords beneath the fixed span at the tower, were fixed to hold the whole section rigid. The same principle was adopted on the Lianokladi side, in which case, however, the straight deck span springing from the abutment to its connection on the arch timber falsework had to be set up. The second section of each half of the arch was then set in position and finally connected at the crown, a special arrangement devised by the engineer in chief, Paul Bodin, being adopted for this purpose.

The bearings for the straight spans, where they connect with the arch span on either side, are formed by vertically continuing the verticals of the N panels of the inclined members, and at this point the straight spans rest on rollers for temperature expansion and contraction movements. The arched span is set on the curve of about 1,330 feet radius, and makes an angle of 3 deg. 10 min. with the tangent on the Dadi, and of 5 deg. 30 min. on the Lianokladi side, respectively.

The total amount of steelwork in the whole structure is about 400 tons, of which the arch span comprises 190 tons, and the five straight spans, complete, the balance. The construction and erection of the bridge occupied thirteen months.



ERECTING ONE HALF OF THE MAIN ARCH.