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The Journal of the Indian Botanical Society

(Formerly "The Journal of Indian Botany")

VOL. XXVIII] AUGUST, 1949 [No. 3

THE GENUS ANABÆNA, WITH SPECIAL REFERENCE TO THE SPECIES RECORDED FROM INDIA AND FROM THE ADJACENT ASIATIC MAINLAND

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(with 101 figures in the text)

(*Received for Publication on May* 26, 1949.)

In connection with De's (1939, p. 125) investigations on the rôle of Blue-green Algæ in the fixation of nitrogen in rice-fields, a number of species of *Anabæna* were grown in pure culture, viz. *A. gelatinosa* n. sp. (=*A. Oryzæ* n. sp., cf. below), *A. naviculoides* n. sp., *A. variabilis* Kütz. var. *ellipsospora* n. var., *A. torulosa* (Carm.) Lagerh., forma, and *A. thermalis* Vouk var. *indica* n. var. (=*A. anomala* n. sp., cf. p. 147). All of these were raised from samples of Faridpur soil. Although provisional diagnoses, prepared by me, were included in De's thesis, they were not incorporated in the published paper.

The material, upon which these diagnoses was based, was in part obtained from old cultures which were no longer completely pure. Some of it was preserved in 4% formalin, and the present paper furnishes the results of a more detailed study of this interesting material. The full descriptions of the various species found in the Faridpur soils are followed by a consideration of specific characters within the genus *Anabæna*, and a review of the species of the genus so far recorded from the Indian sub-continent and adjacent parts of the Asiatic mainland.

I. The Species of Anabæna found in the Faridpur Soils

Anabæna Oryzæ n. sp. (figs. 1-16).

(Syn. : *A. gelatinosa* Fritsch in De, 1939, p. 125 ; non *A. gelatinosa* Reinsch ; non *A. gelatinosa* Wood)

Stratum molle, viride, gelatinosum, membranaceum, patens. Trichomatibus brevibus, sæpe rectis, subdense aggregatis, plerumque parallelis et vaginis propriis præditis. Cellulis 2·5-3 μ latis, plus minus doliiformibus, 1½-2plo longioribus quam latis. Heterocystis terminalibus et intercalaribus, paullo latioribus quam cellulis aliis, 3-3·5 μ latis ; iis terminalibus in fine utroque trichomatis vel in uno fine solum, conicis,

ad 2plo longioribus quam latis, singulis vel binis vel (raro) triseriatis ; iis intercalaribus plerumque doliiformibus, interdum sphæricis, semper singulis. Sporis (akinetis) raro singulis heterocystis terminalibus appositis, vulgo intercalaribus heterocystis remotis, singulis vel 2-7 seriatis, subsphæricis vel breviter ellipsoideis, exosporio luteo-fusco. Dimens. akinet., 5×5, 6·5×7, 5×5·5, 5×6·5, 5×6μ.

The specific name *gelatinosa* given to this species has already been used twice for species of *Anabæna* and cannot therefore be employed for the Faridpur form.

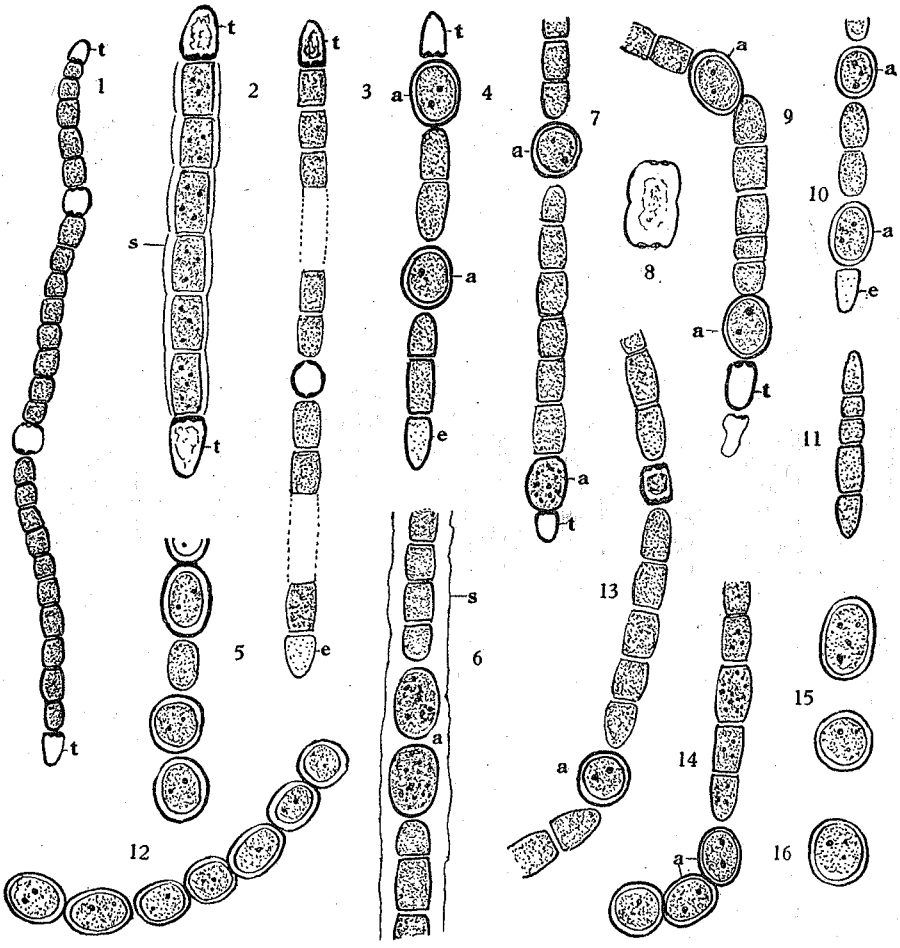

Fig. 1-16.—*Anabæna Oryzæ* n. sp. **1-4,** older germlings ; in **1** and **2** with terminal heterocysts at each end ; in **1** and **3** with intercalary heterocysts ; in **4** with two akinetes (*a*). **5, 7, 9, 10, 13, 14,** parts of threads with mature akinetes. **6,** thread with mucilage-sheath (*s*) and two young akinetes (*a*). **8,** intercalary heterocyst formed from a dividing cell. **11,** 5-celled germling. **12,** chain of akinetes. **15, 16,** akinetes of different shapes. *a,* akinetes ; *e,* end-cells ; *s,* mucilage-sheath ; *t,* terminal heterocysts. (**1, 11** ×655 ; **8** ×1636 ; the rest ×980).

The trichomes in the cultures of this species were in general rather short and often tended to be straight and rather densely aggregated. After staining with ruthenium red a mucilage-sheath, which either fits closely (fig. 2) or is rather wide (fig. 6), becomes obvious around many of the trichomes ; it seems that it is often specially marked in such as are forming akinetes. The cells are usually elongate and slightly barrel-shaped (figs. 1—3), although isodiametric after division; they are separated from one another by thick septa, and there is only slight constriction between them.

The young trichomes seem usually to be pointed at each end (fig. 11). In longer ones the end-cells are usually constituted by conical terminal heterocysts (figs. 1, 2, *t*), that at one end seemingly for the most part developing rather sooner than that at the other end (figs. 3, 4). In older threads (fig. 1) there are also several intercalary heterocysts which sometimes seem to develop before the terminal ones (fig. 3) and are barrel-shaped (figs. 1, 13) or, more rarely, spherical (fig. 3). Not uncommonly there are two, and sometimes even three, terminal heterocysts at the end of a thread (fig. 9). Conical terminal heterocysts perhaps also develop sometimes from the cells adjoining intercalary ones. The heterocysts are but little wider than the vegetative cells.

Akinetes (*a*) develop both in the middle of a thread, and then not next to a heterocyst (figs. 5, 6, 13, 14), as well as adjacent to a terminal heterocyst (figs. 4, 7, 9, 10). The akinetes arising in the latter position appear always to occur singly and are rather exceptional. Those arising elsewhere in the trichomes are far more abundant and may occur singly (figs. 4, 7) or in pairs (fig. 6) or in chains of 6 to 7 or even more (figs. 12, 14). In longer threads one often finds a solitary akinete, then a stretch of one or more vegetative cells, then another akinete or a pair of them, a further stretch of vegetative cells, and so on. Most of the akinetes are slightly longer than broad (fig. 12), although quite a number are spherical (figs. 7, 13, 16); oblong akinetes (fig. 15) are rare. The thick exospore is yellowish-brown according to my earlier notes. The young akinetes have granular contents, but those of the mature ones are often almost homogeneous. Even prolonged immersion in 0·2% ruthenium red, which stains the contents of the vegetative cells deeply, has no effect on those of the akinetes.

The special features of *A. Oryzæ* are the narrow trichomes, the elongate slightly barrel-shaped cells with little constriction between them, the terminal conical heterocysts and the formation of akinetes, both contiguous to (singly) and remote from (commonly in series) the heterocysts.

A. sphærica Born. et Flah. has somewhat similar akinetes, but these are much larger (even in var. *microsperma* Schmidle) and are next to the heterocysts ; moreover, the vegetative cells are considerably broader (5-6 μ) and spherical, as also are the heterocysts which appear to be only intercalary. *A. thermalis* Vouk (1916, p. 106) resembles *A. Oryzæ* in the width and general shape of the cells, in the development of akinetes in series away from the heterocysts, but the akinetes are appreciably bigger and there are no terminal heterocysts. These appear also to be

lacking in *A. propinqua* Setchell & Gardner (1919, p. 90), which has similar narrow threads, although the cells are described as " almost quadratic " and judging by the figure (pl. 8, fig. 9) are cylindrical, without much constriction between them. The akinetes are remote from the heterocysts, spherical or broadly ellipsoidal, and only slightly larger than those of *A. Oryzæ*. As Geitler (1932, p. 875) points out, *A. propinqua* and *A. thermalis* are closely related and differ only in features which do not warrant specific separation. Comparison may also be made with *A. nodularioides* Geitler & Ruttner (1935, p. 459), a planktonic species distinguished by its more robust dimensions, its short cells, and the occasional presence of pseudo-vacuoles within the latter.

It is the terminal heterocysts and the development of certain akinetes adjacent to them that distinguishes *A. Oryzæ*. In this respect there is resemblance to *Cylindrospermum*, as also in the frequent short trichomes and the usual elongate form of the cells. It must be realised, however, that there are important differences from *Cylindrospermum* in the presence of a number of intercalary heterocysts in the longer trichomes and in the customary production of akinetes from parts of the threads, not contiguous to heterocysts and commonly arranged in series of 6 or more. As compared with most species of *Cylindrospermum*, moreover, the akinetes are far smaller and lack the elongate form which is characteristic of that genus. An analogous condition has been recorded by Cannabæus (1929, p. 42) for an *Anabæna* which she, with some justification, refers to *A. hyalina* Schmidle (1902, p. 61). Here the resemblance to *Cylindrospermum* is greater inasmuch as the akinetes, formed singly adjacent to the terminal heterocysts, possess an elongate barrel-shaped form. *A. Oryzæ* and *A. hyalina* clearly constitute connecting links between *Anabæna* and *Cylindrospermum*.

The terminal heterocysts also recall the genus *Anabænopsis*, which is only doubtfully distinct from *Anabæna* and where the akinetes, which are spherical or oblong, never arise in a position contiguous to the heterocysts. The species of *Anabænopsis* are planktonic forms with circular or spirally coiled trichomes and can have little affinity with the species above described. Although very occasional spirally coiled trichomes occurred in the strata of *A. Oryzæ*, they were quite exceptional.

Anabæna naviculoides n. sp. (figs. 17-39)

Strato tenui, explanato, valde gelatinoso, ærugineo. Trichomatibus elongatis, plus minus contortis, moniliformibus, finibus interdum acuminatis. Cellulis 3·5-5 μ latis, vulgo tam longis quam latis vel etiam brevioribus quam latis, raro ad duplo longioribus quam latis (akinetis juvenalibus ?), cellula terminali conica apice obtuso vel acuto marginibus lateralibus interdum retusis. Heterocystis rarissimis, intercalaribus, semper singulis, doliiformibus, 5-6 μ latis, tam longis vel paullo longioribus quam latis. Akinetis in catenis longis irregularibus dispositis, mox disjunctis et tum dense aggregatis et interdum cum heterocystis intercalaribus et terminalibus intermixtis ; akinetis ellipsoideis, finibus plerumque acutis et interdum protractis, exosporio tenui hyalino, vagina hyalina mucosa plus minus lata in superficiem interdum granulata circumdato. Sporis (akinetis) 11-12·5 μ longis × 6-7 μ latis, vel 8·5-9 μ longis × 5·5 μ latis.

The material of this species shows a number of striking features. The kinetes are ellipsoidal, usually with rather pointed ends (figs. 23, 29) which not uncommonly are even slightly protruded so that the akinetes have an altogether naviculoid shape (figs. 29, 33). The numerous

few-celled germlings present in the culture taper at either end (figs. 18, 21), the end-cells (*t*) being conical with rounded or somewhat pointed apices and not uncommonly with slightly retuse lateral margins (figs. 19, 22). The germlings thus preserve in their end-cells the original shape of the spore-extremities. The end-cells, and commonly also one or two of the underlying cells, are narrower than the other cells of the thread which may therefore definitely taper, though not pronouncedly so, at either end (figs. 18, 21). Longer threads only exceptionally have pointed end-cells at either end ; as a general rule one extremity is altogether rounded (figs. 17, 24). It is therefore probable that the germling threads fragment into two pieces at an early stage. Many of the elongate trichomes are rounded at both extremities and have no doubt originated by further fragmentation. It seems that, in this species, the pointed end-cells are developed only by germinating akinetes. They, as well as sometimes the narrower adjoining cells, are distinguished from other cells of the trichomes by having scanty non-granular contents which, unlike those of the ordinary cells, are not stained or less markedly stained by ruthenium red.

The longer trichomes are generally markedly moniliform, with cells that are 4·5-5 μ wide and as long or even shorter than their width (fig. 17). There is, however, a second rarer type of thread, sometimes only 3·5 μ wide and somewhat less markedly constricted between the cells, which are often in large part elongate, up to twice as long as broad (fig. 25). The two types of threads grade over into one another and no sharp demarcation can be made between them; both possess the tapering end-cells above described. Many of the longer trichomes of both kinds, with upwards of 100 cells, are completely devoid of heterocysts (fig. 17) which is one of the distinctive features of the species; even where heterocysts could be found in such threads, there was never more than one, usually situated approximately in the middle, at a considerable distance from either extremity (fig. 27). The heterocysts are barrel-shaped, slightly wider than the vegetative cells (5-6 μ broad) and about as long or slightly longer than broad (fig. 26); they are invariably of the intercalary type. No mucilage-sheath is recognisable around the majority of the trichomes, even in material stained for several hours in ruthenium red, although very occasional threads show a close-fitting envelope.

Akinetes arise from a large proportion of the cells and are evidently formed in long series, not contiguous to the heterocyst when this is present (figs. 27, 32). The cells that are developing into akinetes (*a*) are invariably elongate and ellipsoidal and have clearly ceased to divide for some little time (fig. 32) ; the second type of thread with elongate cells referred to above is probably one in a condition of incipient akinete-formation. The contents of such developing akinetes usually contain a number of conspicuous granules (fig. 27), few of which commonly remain in the ripe akinetes which sometimes have almost homogeneous contents. There is probably some lengthening during differentiation of the akinete, and this results in displacements so that the series of akinetes form irregular chains or zigzag groups (fig. 29). Development seems to proceed in a rather haphazard manner, as practically mature akinetes may be interspersed with others which are not yet fully differentiated (fig. 32).

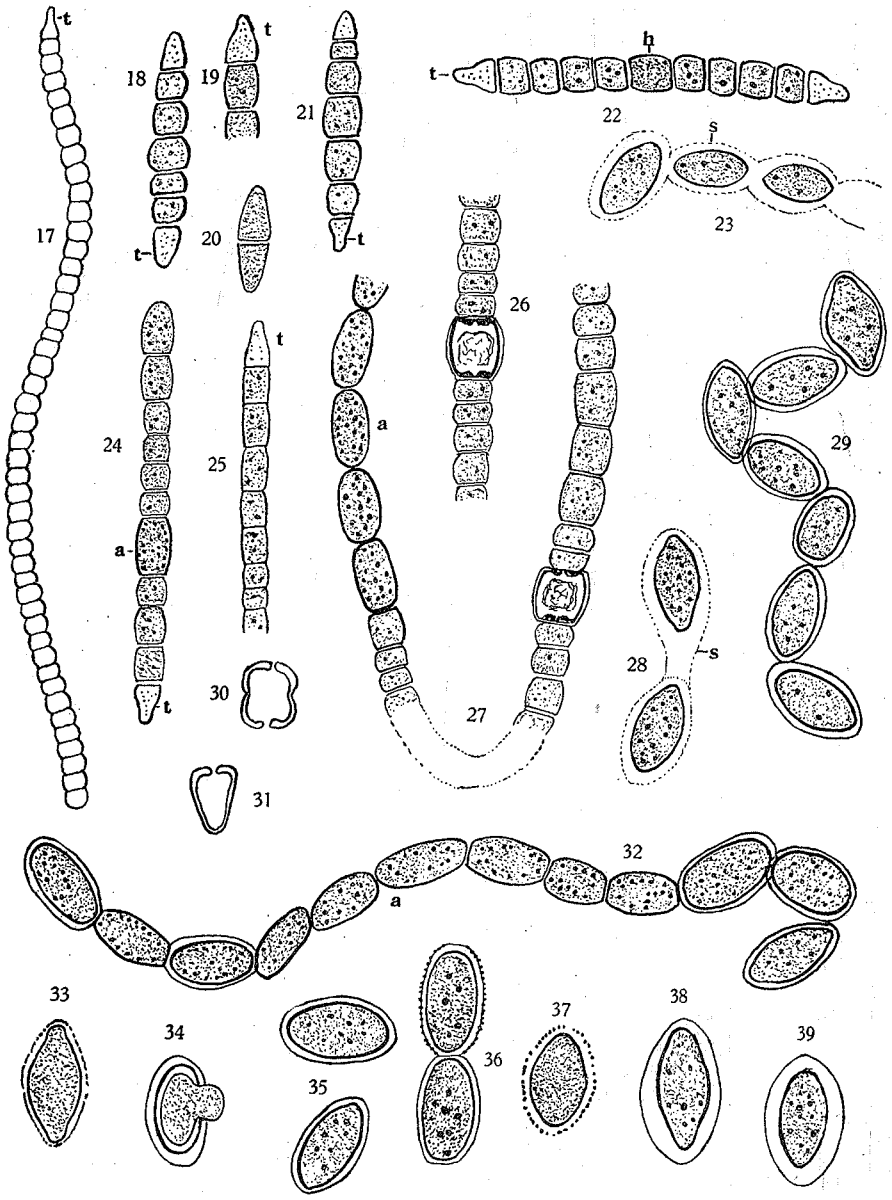

Fig. 17-39.—*Anabæna naviculoides* n. sp. **17,** elongate thread without heterocysts. **18-21,** diverse germlings. **22,** somewhat older germling, with a developing intercalary heterocyst. **23, 28,** young akinetes, still enclosed in a continuous mucilage-envelope. **24,** short thread with developing akinetes (*a*). **25,** thread with more elongate cells. **26, 27,** parts of threads with intercalary heterocysts, in

27 with a chain of young akinetes (*a*). **29**, group of mature akinetes. **30** intercalary heterocyst formed from a dividing cell. **31**, terminal heterocyst. **32**, chain of mature and immature akinetes. **33**, **35** various shapes of mature akinetes. **34**, unusual stage in germination (?). **36**, **37**, akinetes with granular mucilage-envelope. **38**, **39**, the same with exceptionally wide mucilage-envelopes. *a*, akinetes ; *h*, heterocyst ; *s*, mucilage-envelope ; *t*, end-cells. (**17** × 563 ; **18-22**, **24**, **25** × 750 ; **26**, **27** × 837 ; the rest × 903).

In conformity with the two sizes of vegetative threads, there are two sizes of akinetes, the one 11-12·5 μ long and 6-7 μ wide, the other 8·5-9 μ long and 5·5 μ wide. Both possess a pronounced, but usually rather narrow mucilage-envelope, 0·5-0·75 μ wide, which sometimes appears more or less truncate at the ends (fig. 36). It stains deeply with ruthenium red and is probably a specially differentiated part of the mucilage-sheaths which can be recognised in later stages around akinete-forming trichomes (figs. 23, 28). In some, but by no means in all, of the akinetes the surface of this envelope is granulate (figs. 36, 37) ; this may be an artefact. Some of the akinetes (figs. 38, 39) possess an appreciably wider (smooth) envelope, and it is possible that the latter contracts considerably during maturation. Series of as many as 30 akinetes were present. There were no indications of remnants of membranes near the numerous short germlings present, and it seems probable that the envelopes become completely diffluent during germination. The exceptional instance shown in fig. 34 may be abnormal.

The cultures, upon which this description is based, contained numerous clumps of isolated akinetes, in part embedded in yellowish diffuse mucilage. In these aggregates an occasional intercalary heterocyst could be found. The threads, from which such clumps had arisen, had clearly consisted in the main only of vegetative cells. Other clumps of akinetes, however, and especially those of the smaller type, included more plentiful heterocysts, some of which moreover were conical and of the terminal type (fig. 31). Terminal heterocysts were never seen *in situ* in the threads. The facts would seem to indicate that conversion of vegetative cells into heterocysts normally only takes place after large numbers of the cells have differentiated into akinetes, that the extent of heterocyst-development is variable, and that the end-cells can under certain circumstances develop into terminal heterocysts. In this connection it is noteworthy that the intercalary heterocysts observed *in situ* in the trichomes still possessed contents (figs. 26, 27).

The most striking feature of the culture, upon which the description of this species is based, is the extreme rarity of heterocysts in the vegetative threads. The majority of the trichomes are devoid of heterocysts and would be referred to the doubtful genus *Isocystis*. It is not possible to say whether the paucity of heterocysts in the vegetative condition is a specific feature or whether it is a result of the special method of culture. If the latter proved to be the case, it would go far to render probable that the species of *Isocystis* are but *Anabænas* in which the special circumstances of the environment do not call forth the production of heterocysts. Cannabæus (1929, p. 7) established that the numbers of heterocysts in *A. variabilis* varied considerably in cultures with and without sodium chloride, but there is at present no evidence that environmental

factors can bring about a complete absence of heterocysts (cf. also Fogg, 1944, p. 173). In *A. constricta* (Szafer) Geitl. (*Pseudanabæna constricta* (Szafer) Lauterborn, 1916, p. 437), a species inhabiting putrefying lacustrine bottom-deposits, the great scarcity of heterocysts appears to be a specific feature, since heterocysts have only rarely been encountered (Koppe, 1924, p. 642).

There is a good deal of resemblance between *Anabæna naviculoides* and *A. doliolum* Bharadwaja (1935, p. 105), which apparently has similar moniliform trichomes and produces chains of ellipsoidal akinetes with pointed ends (cf. figs. 85, 86). It is possible that *A. naviculoides* should be regarded only as a variety of *A. doliolum*, but for the present I have preferred to maintain it as a separate species because of (a) the great rarity of heterocysts in the vegetative threads, (b) the rather wider cells, (c) the frequent protrusion of the poles of the akinetes, (d) the presence of a special mucilage-envelope around each akinete. In certain respects both species show resemblances to *A. variabilis* Kütz. in which, however, the akinetes are stated to be barrel-shaped with flattened ends.

Anabæna variabilis Kütz. var. *ellipsospora* n. var. (figs. 40–50)

Strato tenui, valde gelatinoso, ærugineo. Trichomatibus leviter flexuosis, sine vaginis propriis, laxe aggregatis, cellula terminali rotundata, interdum conica apice valde obtuso. Cellulis 4-4·5 μ latis, plerumque elongatis, 5·5-9 μ longis, fere cylindricis vel leviter doliiformibus, inter cellulas constrictis, interdum etiam isodiametricis et moniliformibus. Heterocystis intercalaribus, fere semper solitariis, sphæricis vel doliiformibus, 5·5-6 μ latis et 5-8 μ longis ; heterocystis terminalibus hemisphæricis raris. Akinetis in catenis, heterocystis remotis, ellipsoideis, polis plus minus obtuse rotundatis, 5-7 μ latis, 7·5-12 μ longis, endosporio tenui, exosporio solum pro parte indurato.

The usually more or less flexuous and frequently elongate trichomes are to a large extent composed of elongate cells (4–4·5 μ broad), about 1½ times as long as broad and often almost cylindrical or only slightly barrel-shaped, the lateral margins being in part barely curved, although there is usually distinct constriction between the cells (fig. 40). In some of the trichomes there are stretches of shorter, almost moniliform cells, with more marked constrictions between them (figs. 42, 50). Cannabæus (1929, p. 37, fig. 14, 3, 4) figures the two kinds of cells for the type, but in the Faridpur material rather short moniliform stretches usually alternate with others in which the cells are elongate and subcylindrical. The end-cells of the trichomes are rounded or sometimes faintly conical, with a bluntly rounded apex (fig. 41 e). The plentiful intercalary heterocysts, always appreciably wider than the vegetative cells and nearly always solitary, are spherical (fig. 43) or barrel-shaped (fig. 45, 50) and often slightly longer than broad (5·5–6 μ wide and 5–8 μ long). Many of the longer heterocysts are peculiar in that the longitudinal walls are only very feebly indurated (fig. 49). Terminal heterocysts (*t*) are very rare and always only present at one end of a trichome (fig. 42) ; they are usually hemispherical in shape. They were never seen on the many few-celled germlings present, but only on trichomes with upwards of 15 cells.

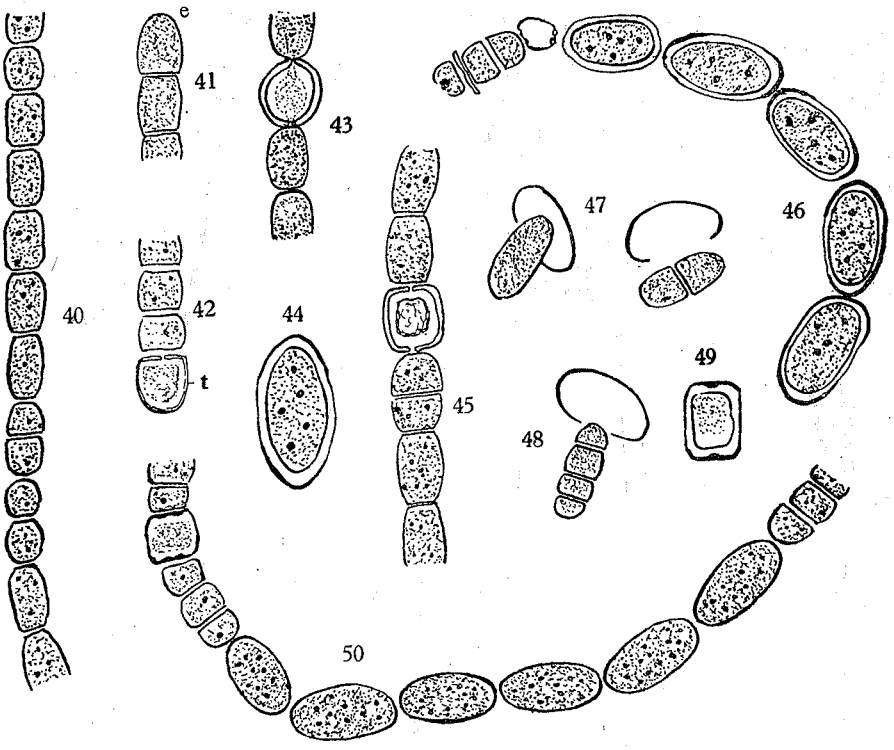

Fig. 40-50.—*Anabæna variabilis* Kütz. var. *ellipsospora* n. var. **40,** short length of trichome showing varying shapes of cells. **41,** end of a thread. **42,** part of a young thread with a terminal heterocyst (*t*). **43, 45,** parts of threads with intercalary heterocysts. **44,** mature akinete. **46,** chain of akinetes. **47, 48,** germination. **49,** intercalary heterocyst with little-thickened lateral margins. **50,** young akinetes. (×1038).

The akinetes are clearly formed in long series (fig. 46, 50) and never arise contiguous to the heterocysts. They are usually ellipsoidal with rounded poles (fig. 46), although a certain number are somewhat pointed at the ends (fig. 44) ; they are not much wider than the vegetative cells (5–7μ wide) and 7·5–12μ long. They are provided with a delicate endospore and a somewhat offstanding exospore, which was only indurated over part of its surface (fig. 46) ; this is likely to be a special cultural effect and is no doubt related to the copious germination of recently formed akinetes that was taking place. During such germination the thin part of the exospore seemingly becomes dissolved and the contents escape surrounded by the endospore (fig. 47, 48).

It is open to doubt whether most of the published figures of *A. variabilis* show really mature akinetes. That of Frémy (1930, fig. 294), which is reproduced by Geitler (1932, p. 876), certainly does not give that impression, and that of Hansgirg (1892, p. 67, fig. 22) is not much

more convincing. The akinetes depicted in the small figure of Hansgirg seem to be ellipsoidal, while those shown by Frémy are barrel-shaped. Tilden (1910, pl. 9, fig, 9) reproduces two larger figures after Hansgirg, in which the (seemingly unripe) akinetes are definitely barrel-shaped. Bornet and Flahault (1888, p. 226) give "sporis ovalibus, apicibus truncatis" which is tantamount to barrel-shaped. If this is the normal shape of the akinetes of the type, then the form above discussed is distinguished by its ellipsoidal (and rather smaller) akinetes. Setchell and Gardner (1919, p. 91) record this species from brackish water. The akinetes in their figure (pl. 8, fig. 8) appear to be mature, but are rather more of the ellipsoidal type ; most of them certainly do not show the truncate ends mentioned in the diagnosis. The form described and figured by Ghose (1927, p. 241) from Rangoon differs from all others in the very short akinetes and can scarcely belong to *A. variabilis.*

Apart from the special shape of the akinetes, this variety is distinguished by the usual absence of distinctive end-cells and the elongate shape of the majority of the cells. It shows distinct resemblances to *A. doliolum* Bharadwaja (cf. fig. 85, 86), although the akinetes are never as pointed as shown in Bharadwaja's figure ; *A. doliolum*, moreover, seems to lack the elongate form of vegetative cell and the end-cells are definitely pointed.

Anabæna torulosa (Carm.) Lagerh., forma (fig. 51-59).

Differt a typo heterocystis vulgo doliiformibus, cellulis terminalibus sæpe valde elongatis et attenuatis, akinetis cylindricis, exosporio bene evoluto. Diam. cell. veg., 3·5-4 μ ; diam. akinet. 7-8·5 μ, long., 11-14 μ.

The stratum is thin, rather gelatinous, and bright blue-green. The trichomes are markedly constricted between the cells (fig. 51) and are commonly straight and arranged in parallel groups, although some of them are flexuous or even spirally wound, exhibiting a number of coils. The end-cells (*e*) are usually appreciably longer than the others (fig. 51, 52, 54), with paler, non-granular contents ; they are distinctly attenuated, the margins being often somewhat retuse and the apex bluntly rounded. The vegetative cells are 3·5-4 μ (usually 4 μ) broad, for the most part shorter than broad (fig. 51, 52), with rather delicate septa and with marked constrictions between them. The heterocysts are only slightly wider (diam., 5 μ) than the vegetative cells and are usually barrel-shaped (fig. 58, 59), rarely spherical. No terminal heterocysts were observed, although numerous germlings were present. Some of them, sometimes comprising as many as 50 cells, still terminated at both extremities in the characteristic attenuated end-cells. Certain of these longer germlings had produced an intercalary heterocyst, approximately in the middle of the thread (fig. 51). The first step in the formation of the heterocyst is the cessation of cell-division in an intercalary cell, while the adjacent cells continue to divide (fig. 52, *h*) ; the initial of the heterocyst has dense, non-granular contents. Longer trichomes possess a number of intercalary heterocysts, usually occurring singly.

The akinetes are generally formed singly on either side of the heterocyst (fig. 58), but there may be two (fig. 59) (or more?). They are shortly cylindrical, 7-8·5 μ broad, 11-14 μ long, with broadly rounded (fig. 59)

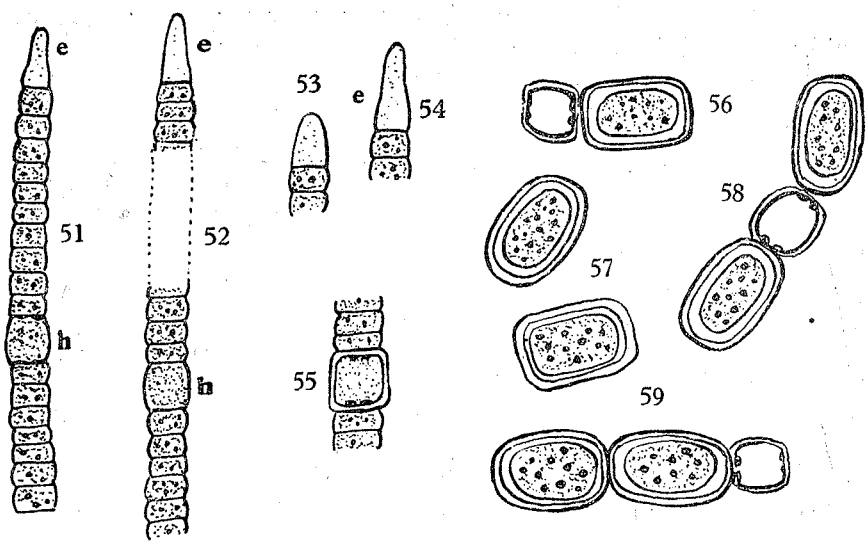

Fig. 51-59.—*Anabæna torulosa* (Carm.) Lagerh., forma. **51, 52,** threads with developing heterocysts (*h*). **53, 54,** types of end-cells. **55,** intercalary heterocyst. **56-59,** heterocysts and mature akinetes. *e*, end-cells ; *h*, heterocysts. (×1300).

or even almost flattened ends (fig. 56, 57) and subparallel lateral margins ; at the best they only showed the barest indications of a median waist (fig. 57). There is a thick firm exospore and a delicate endospore ; the contents of most of the akinetes had contracted markedly in the formalin preservative.

Most of the published figures of *A. torulosa* show akinetes with a marked median waist (Frémy, 1930, fig. 306 ; Biswas, 1932, tab. 28, fig. 8 ; Carter, 1933, p. 167, fig. 14), a feature also occasionally seen in those of *A. catenula* (fig. 100). Geitler (1932, p. 887), on the basis of certain observations of Cannabæus (1929, p. 36), suggests that this feature is worthless as a characteristic of *A. torulosa* and draws attention to the close resemblance between *A. torulosa* and *A. oscillarioides* in other respects. Lemmermann (1910, p. 190) had already suggested that the former might be a salt-water form of the latter. All the forms depicted in the above-cited figures come from brackish waters, and the species is no doubt widely distributed in such habitats.[1] Harvey's figure (1846, pl. 113 A) of *Sphærozyga Carmichælii* Harv., which is synonymous with *Anabæna torulosa*, however, shows quite unconstricted akinetes. It would nevertheless be well to keep in mind the possibility that akinetes with a waist might be specially characteristic of a race inhabiting salt water.

[1] The record from Kentani, Cape Colony (Fritsch, 1921, p. 67) likewise comes from a probable brackish habitat.

If we ignore this character, *A. torulosa* is distinguished from *A. oscillarioides* by its distinctive end-cells, by its usually shorter vegetative cells, and by akinetes which do not seemingly ever reach the length recorded for *A. oscillarioides* and have broad and flat, instead of rounded, ends. It is on the basis of these characters that I have referred the Faridpur form to *A. torulosa*. Bornet and Flahault (1888, p. 237) say for *A. torulosa* " sporis brevibus, subcylindraceis, 7–12 μ crassis, diametro sæpius duplo longioribus, apicibus depressis, in media parte sæpius leviter constrictis ", a description which tallies better with the above-cited figures than that given by Geitler. Even if the median waist of the akinetes is only an occasional character, *A. torulosa* and *A. oscillarioides* appear readily distinguishable.

The Faridpur form differs from the type in the usually barrel-shaped heterocysts, the often marked elongation of the attenuated end-cells, and the cylindrical form of the akinetes which have a well-developed exospore.

Anabæna anomala n. sp. (fig. 60-73).

(Syn. : *A. thermalis* Vouk var. *indica* Fritsch in De, 1939, p. 125).

Strato tenui gelatinoso ærugineo. Trichomatibus vulgo elongatis, dense et irregulariter aggregatis, plus minus contortis, sæpe moniliformibus, cellula terminali rotundata vel subconica apice obtuso. Cellulis plerumque 2-3 μ latis, fere tam longis quam latis, sphæricis vel doliiformibus, interdum 1½ plo longioribus quam latis et usque ad 3·5 μ latis (akinetis juvenalibus ?). Heterocystis (?) raris, parvis, vulgo singulis, intercalaribus, sphæricis, 2 μ latis, vel absentibus (?). Akinetis primum sæpe doliiformibus et paullo longis quam latis ; akinetis maturis sphæricis vel subsphæricis, 3·5-5·5 μ latis, vulgo disjunctis, exosporio solido, endosporio tenui.

The material occurred as a thin blue-green gelatinous stratum in which the commonly elongate trichomes were rather densely crowded and usually more or less contorted, without any definite arrangement. The bulk of the vegetative cells are spherical or barrel-shaped, 2-3 μ broad and about as long as broad so that the trichomes often present a definitely moniliform appearance (fig. 60, 61). In many of the trichomes, however, one finds a more elongate type of cell, up to 1½ times as long as broad (fig. 62, 70) ; these cells may occur singly, but are usually found in short series, are often wider than the others (up to 3·5 μ broad), and are probably incipient akinetes. Only rarely are long stretches composed of such cells. The variability, both in length and width of cell, in different parts of many of the trichomes (cf. fig. 62, 63) is a striking feature of the material and suggests that akinete-development commences at sundry places and is perhaps a rather slow process. The end-cells are rounded (fig. 61, 68) or slightly conical (fig. 64) with an obtuse apex.

I have been unable definitely to establish the presence of heterocysts in the preserved material. In the notes made in 1939, when I examined the living culture, I remarked that heterocysts were rare, spherical, about the same size as the vegetative cells and disorganising early. In some of the trichomes of the preserved material there are small (diam. about 2 μ) spherical cells (fig. 60, 67, 68, 70*h*), with scanty contents, usually solitary, sometimes in pairs (fig. 73); these may be heterocysts. They show up very clearly in material stained with cotton blue in lactophenol.

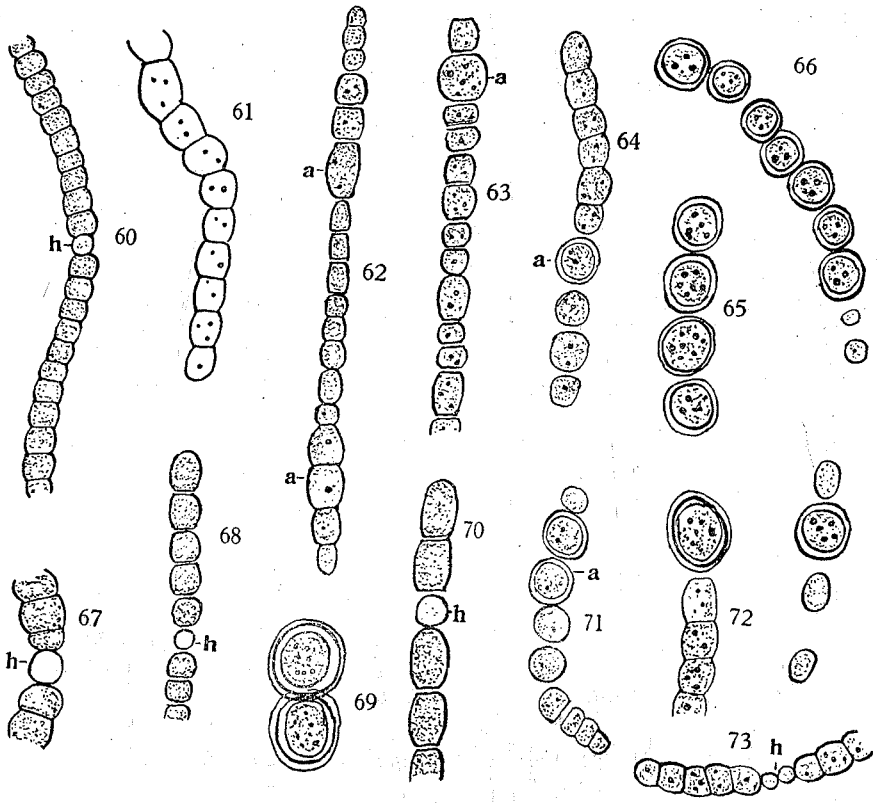

Fig. 60-73.—*Anabæna anomala* n. sp. **60, 67, 73,** moniliform trichomes. **61, 68, 70,** ends of trichomes. **62, 63,** older trichomes showing varying shapes and widths of cells. **64, 71,** parts of trichomes with mature and immature akinetes. **65, 66,** chains of akinetes. **69, 72,** subspherical akinetes. *a*, akinetes; *h*, possible heterocysts (?). (**69, 72** × 1606 ; the rest × 1425).

Such cells are always intercalary and contrast very markedly with the adjoining ones in their small size and pale colouration, but I have been unable to recognise in any of them the pores which are characteristic of true heterocysts, nor could I obtain any evidence of a cellulose stain with chlor-zinc-iodide. These cells are lacking in the majority of the trichomes, and I have not found any heterocysts among the clumps of detached akinetes. If the small colourless cells are heterocysts, they must disorganise rapidly.

The akinetes, as already mentioned, develop at several points in the course of the longer trichomes and are mostly formed in series, commonly of 4 or 5 (fig. 66, 71). At first they may be barrel-shaped (fig. 62, 63) and slightly longer than broad, but as they enlarge they become rounded. Akinetes can also arise by direct enlargement of the spherical vegetative cells (fig. 71). The mature akinetes are spherical (fig. 65, 66, 69) or

sub-spherical (fig. 72), 3·5-5·5 μ in diameter. During development the akinetes separate from the neighbouring cells (fig. 66, 71), and it is unusual to find mature akinetes *in situ* in the trichomes. Their abundant formation is shown by the extensive clumps present in the material. There is a firm exospore and a delicate endospore.

This species resembles *A. thermalis* Vouk, to which I originally referred it as a variety, in the narrow width of the vegetative cells, but it differs from Vouk's species (cf. Vouk, 1916, p. 106, Geitler, 1932, p. 875), in the fact that the vegetative cells are usually about as long as broad, in the lack of clearly differentiated end-cells and of heterocysts, and in the spherical shape of the akinetes. In the first and last of these respects there is more resemblance to *A. propinqua* Setch. & Gardn. (cf. p. 3). The most distinctive feature of *A. anomala*, apart from the apparent absence of heterocysts, is the considerable inequality, both in length and breadth of cell, which is commonly observable in one and the same trichome (fig. 62, 63) and which seems to be related to slow and promiscuous development of akinetes. Since the narrower cells in such trichomes are always about as long as broad, and only the wider ones commonly longer than broad, the latter are regarded as incipient akinetes which by further widening assume a spherical shape.

A comparison can also be made with the species of *Isocystis* described by Borzi (1878, p. 264), both of which (cf. Geitler, 1932, p. 913) show appreciable resemblances to the alga above described, though differing in dimensions. Only further investigation can enable one to evaluate the degree of resemblance and difference.

II. Specific Characters within the Genus Anabæna.

Size and shape of cell. The ratio of length to breadth of the cells is probably in general a feature of importance, but under certain circumstances may be affected by frequency of cell-division. Trichomes composed of elongate cells (*i.e.* such as are 1½ times or more as long as broad) nearly always display stretches in which the cells are short and where cell-division has proceeded more actively (cf. fig. 9, 40); on the other hand, trichomes in which the cells tend to be short (*i.e.* as long as or somewhat shorter than their breadth) rarely show any marked deviation from that condition (cf. fig. 17, 77-79). In general therefore the presence of elongate cells in considerable stretches of the trichomes may be regarded as a specific characteristic, even though some of the cells be short. It might be more useful in a diagnosis to state the approximate percentage of elongate cells than to give as is done at present the range of length as compared with breadth. There are far more short-celled than long-celled species of *Anabæna*.

The data provided by Cannabæus (1929, p. 37) merely serve to show that, under certain cultural conditions, the cells of trichomes with elongate cells may divide more frequently so that such trichomes become short-celled over parts of their length. This is, however, no proof that cell-length is of no taxonomic value.

The shape of the cells is related to their length-breadth ratio. Elongate cells are usually either barrel-shaped (cf. fig. 2, 3, 13), or cylindrical (fig. 82, 83, 92), according to the degree of convexity of their sides ; when the shape is cylindrical, as in *A. aphanizomenoides* Forti (1911, p. 126) or *A. cylindrica* Lemmermann (1896, p. 188) and especially marked in *A. Levanderi* Lemm. (1906a, p. 536), there is little constriction between the cells. The elongate cells of *A. elliptica* Lemm. (1904, p. 104) have an unusual ellipsoidal shape. Short cells may be barrel-shaped (fig. 17, 86), although there are generally deeper constrictions between them than in trichomes with elongate cells, and such barrel-shaped cells grade over imperceptibly into the almost spherical cell which is characteristic of the moniliform trichome (fig. 98). Another feature, the taxonomic value of which is as yet uncertain, is the thickness of the septa between contiguous cells. It would seem, however, that certain species are characterised by appreciable thickness of the septa so that the cells appear spatially separated (e.g. *A. constricta* (Szafer) Geitl.).

End-cells. In diverse species of *Anabæna* the end-cells of the trichomes are specially differentiated. Such cells are usually pointed (fig. 3, 4, *e* ; 81, 86, 88), more or less attenuated, in short-celled species commonly longer than the ordinary vegetative cells (fig. 17, 51), and generally with homogeneous contents which probably for the most part disappear at an early stage. These end-cells, both in *Anabæna* and in related genera, would merit a fuller investigation than has so far been undertaken and a comparison with the terminal heterocysts found in some species might be instructive. Where they occur, they seem to develop already at the two ends of the germlings (fig. 18, 21, 22, *t*) and, when these fragment, the special end-cell is found only at one end of the two resulting trichomes (fig. 17, 24), the other end being rounded. There does not seem to be any evidence that these rounded end-cells can subsequently change their form and differentiate into an end-cell of the elongate pointed type, although such a development might take place. In *A. naviculoides* (p. 138), however, all the longer trichomes terminate in rounded end-cells at both extremities. The presence of specially differentiated end-cells is a character of taxonomic importance, but cannot be expected to occur on all, or necessarily even on the majority, of the trichomes of a given population.

Heterocysts. The statement of Cannabæus (1929, p. 14), that one of the end-cells of the germlings of *Anabæna* becomes transformed into a terminal heterocyst at quite an early stage, is by no means universally true, as shown by the descriptions of *A. naviculoides* (p. 138) and *A. torulosa* (p. 144). In *A. Oryzæ*, on the other hand, it is not unusual for a heterocyst to develop at both ends of the germling (fig. 1, 2). The shape of the terminal heterocysts depends on that of the end-cells ; where these are rounded, the heterocysts are hemispherical (*A. variabilis* var. *ellipsospora*, fig. 42) ; where they are pointed, the heterocysts are approximately conical (*A. Oryzæ*, fig. 2, 3).

The usual type of heterocyst in *Anabæna* is intercalary, and its width relative to that of the vegetative cells, depending on the degree of broadening during differentiation, is probably of some taxonomic

importance. The shape is often variable, especially where there is variability in this respect in the vegetative cells. The commonest shapes are barrel-shaped (fig. 26, 27, 86, 87) and spherical (fig. 43, 78, 79, 84), both often occurring in the same material, although one or other type frequently predominates. The occurrence of barrel-shaped heterocysts, longer than they are broad, as the principal type in short-celled trichomes (*A. doliolum*, fig. 85, 86 ; *A. torulosa*, fig. 55, 59 ; *A. batophora* Frémy, 1930, p. 369), indicates a cessation of division on the part of the parent-cell of the heterocyst some little time before further differentiation sets in. In such instances one may find heterocysts constricted in the middle (fig. 8, 30) and clearly developed from cells which had begun to divide. On the other hand, the presence of spherical heterocysts in long-celled species (*A. aphanizomenoides*) may indicate development from recently divided cells.

On present information it is impossible to say whether these features could be of value in classification, but a comparison of the existing diagnoses of a considerable number of species of *Anabæna* leaves one with the impression that the shape of the heterocyst is not of much taxonomic importance. On the other hand the presence of appreciable numbers of terminal heterocysts may prove to be a character of some value (cf. p. 138). The importance of great scarcity of heterocysts has already been discussed on p. 141.

Akinetes. These afford by far the most useful taxonomic characters. Their position, whether contiguous to or remote from the heterocysts, although subject to some variation (especially in such a species as *A. catenula* (Kütz.) Born. & Flah.), still remains a valuable systematic feature (Cannabæus, 1929, p. 28). Most of the species, which normally form their akinetes from cells contiguous to heterocysts, only rarely depart from this habit. On the other hand, species forming series of akinetes from cells not adjoining heterocysts, do occasionally form one next to a heterocyst. Geitler (1932, p. 869), citing Cannabæus, states that in such species akinetes are not rarely found contiguous to a heterocyst. Cannabæus (1929, p. 36), however, scarcely gives the impression that this is anything but exceptional.

Greater suspicion attaches to the use of the number of akinetes adjoining a heterocyst as a specific character. In *A. Volzii* Lemmermann (1906, p. 153), with which *A. unispora* Gardner (1927, p. 59) is doubtless identical (cf. also Drouet, 1937, p. 601), the akinetes occur singly on one side of a heterocyst, although one of the two akinetes in Lemmermann's figure 5 (t. XI) does not appear to be next to a heterocyst. *A. mediocris* Gardner (loc. cit., p. 61) differs essentially only from *A. Volzii* in the presence of akinetes in pairs (cf. fig. 99) and their occurrence on both sides of the heterocysts, although the end-cell seems more pointed and there are some differences in dimensions. It seems highly probable that this is at best but a variety of *A. Volzii* and that all three " species " (*A. Volzii*, *A. unispora*, *A. mediocris*) are but habitat-variants of a common type (cf. also p. 156).

There are three principal shapes of akinetes, the spherical (fig. 65, 66, 80), the ellipsoidal (fig. 23, 46, 85), and the cylindrical (fig. 56-59,

93, 98); the last type may have rounded or almost flat ends. Species usually producing spherical akinetes not uncommonly possess some which are shortly ellipsoidal (e.g. *A. sphærica*, *A. Oryzæ*, fig. 12; cf. also fig. 77-79). It seems that in most, if not in all, species of *Anabæna* the akinetes are capable of immediate germination ; this is at least a common experience in laboratory-cultures and no doubt is also not infrequent in nature during part of the season of occurrence. In such instances the akinetes probably fail to develop their full characteristics. In particular the envelopes may not be typically differentiated and may not show those features (colour, thickness, etc.) associated with the true resting state, which is produced at the end of the season of occurrence of the species. For this reason features like colour and even sculpturing of the akinete-membrane must be employed with caution as a means for systematic discrimination, except in species which have been repeatedly recorded from various localities.

Mucilaginous envelopes. The threads of *Anabæna* are no doubt usually surrounded by mucilage, which in non-planktonic species forms the basis of the soft gelatinous strata within which numerous trichomes are often embedded. Their arrangement, and especially the density of their aggregation, within such strata is certainly to a large degree dependent on environmental conditions, and the only distinction likely to be of taxonomic importance is that between straight and parallel or markedly contorted and interwoven trichomes.

A clearly defined mucilage-envelope is only occasionally detectable around the individual trichomes (cf. fig. 84) and then often only after staining (fig. 2, 6) and usually only around some of them. It is still more unusual to find a number of trichomes included within a common sheath, as is distinctive (fig. 74, 75) for the South African *A. vaginicola* Fritsch & Rich (1929, p. 87), a species allied to *A. cylindrica* Lemm., but distinguished from it by this characteristic, as well as by the possession of ellipsoidal akinetes formed in series adjacent to the heterocysts. Randhawa's statement (1936, p. 407) that the only vital difference between the two species is the occurrence of a number of trichomes within a single sheath is erroneous. In *A. inæqualis* (Kütz.) Born. & Flah. several filaments are commonly, but by no means always enclosed in a common sheath (cf. Fritsch, 1918, p. 578) ; 1921, p. 367 ; Rich, 1933, p. 34).

Randhawa (loc. cit.) advocates the reference of *Anabænas* with this habit to a separate genus *Anabænothrix*, in which he includes *A. vaginicola*, as well as two other Indian species, *A. cylindrica* Randhawa and *A. epiphytica* Randhawa. The accompanying illustrations of the habits of these two species are not clear, but one obtains the impression of rather wide and ill-defined envelopes containing a considerable number of trichomes. The " spores " of *Anabænothrix cylindrica* are stated to be 4-5 μ broad [1] and 18-20 μ long, *i.e.* at least four times as long as broad, but those shown on Pl. XX, fig. 2 in Randhawa's paper (cf. fig. 76) are

[1] The dimensions are certainly incorrect, since the heterocysts are given as 9-10 μ in diameter ; yet fig. 2 on pl. XX, reproduced in fig. 76 shows them to be of about the same width as the akinetes.

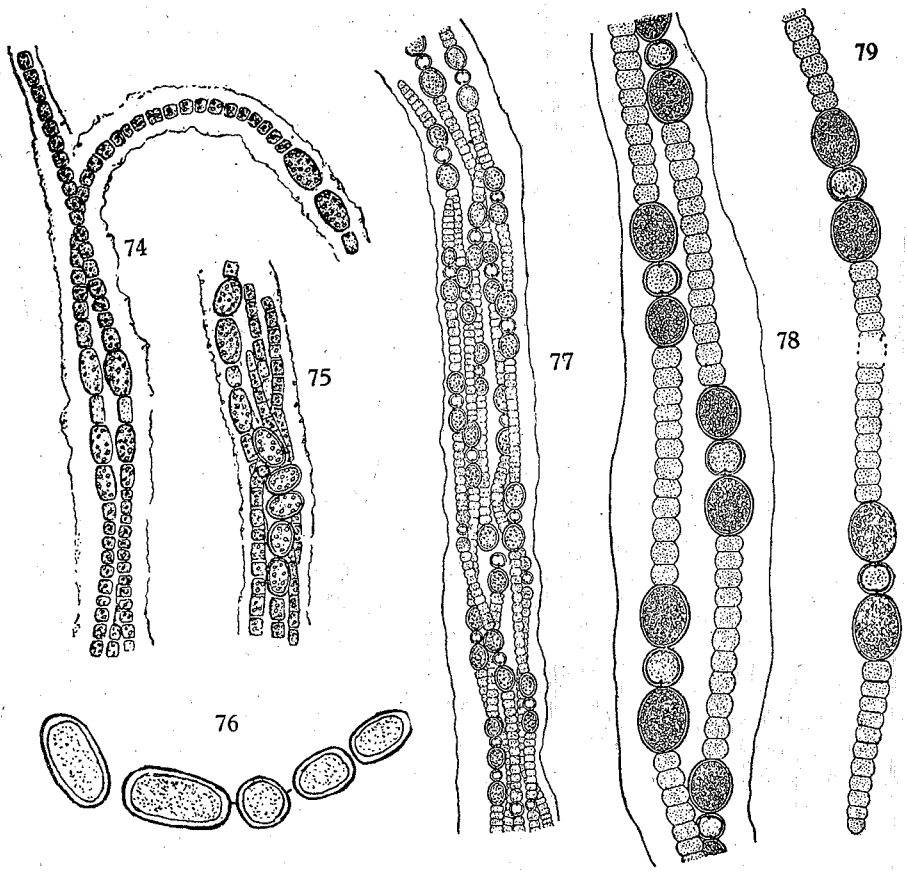

Fig. 74-79.—**74, 75,** *Anabæna vaginicola* Fritsch & Rich (after Fritsch & Rich). **76,** heterocyst and akinetes of "*Anabænothrix cylindrica*" (after Randhawa). **77-79,** *Anabæna ambigua* Rao (after Rao); **79,** thread without a mucilage-envelope. (**74, 75** × 420; **76** × 900; **77** × 250; **78, 79** × 515).

only about twice as long as broad. They do not differ very materially in form, or even in the ratio of length to breadth, from those of *A. vaginicola* and, if Randhawa's figures are correct, *A. cylindrica* Randhawa is probably an Indian form of *A. vaginicola*. *A. epiphytica* differs in the fact that the akinetes are not contiguous to the heterocysts and that the vegetative threads are narrower. This species is too imperfectly described to admit of an adequate assessment of its characteristics, but the akinetes are practically identical in shape and dimensions with those of *A. cylindrica* Randhawa, and *A. epiphytica* may be a variety in which the akinetes are not formed next to the heterocysts. There are certainly at present no clear grounds for keeping these three forms of *Anabænothrix* as distinct species.

Rao's (1937) *Anabæna ambigua*, in which the trichomes occur singly (fig. 84) or in groups (figs. 77, 78) within a well-defined mucilage-sheath or may lack the latter altogether (fig. 79), would be another species of *Anabænothrix*. Except in the special habit, it does not differ fundamentally from *Anabæna sphærica* in which the akinetes may be shortly ellipsoidal.

It may be doubted whether there is any real justification for reference of these diverse forms to a separate genus. Randhawa seeks a parallel for his new genus in *Schizothrix* among Oscillatoriaceæ, but this genus is distinguished by a number of features (branching, tapering of the mucilage-sheath), apart from the usual presence of several trichomes within a common sheath, and a better analogy could be found in *Microcoleus*. In the latter, however, the mucilage envelope invariably contains several, and frequently numerous, trichomes and the aggregates are clearly defined. The " species " of *Anabænothrix* may include one or several trichomes within the sheath and, when only one is present there is no difference from the ordinary *Anabænas*, except that the mucilage is sometimes more clearly defined. The absence of any distinct contrast, such as exists between *Microcoleus* and *Oscillatoria*, does not justify the maintenance of *Anabænothrix* as a genus distinct from *Anabæna* (cf. also Rao, 1937, p. 106 ; Geitler, 1942, p. 184 ; Fritsch, 1945, p. 835).

III. The Species of Anabæna Recorded from India and Burma

I. Species with spherical or subspherical akinetes.

(a) Akinetes contiguous to the heterocysts.

1. *A. sphærica* Born. & Flah. (recorded by Schmidle, 1900, p. 161). The f. *tenuis* G. S. West is recorded by Bharadwaja (1935, p. 103) and was also found by R. Senior White in a tank at Delhi. Both it and var. *attenuata* Bharadwaja (1935, p. 103 ; Rao, 1939, p. 147 ; Rao, 1940, p. 128) do not differ appreciably from the type.

2. *A. spiroides* Klebahn is recorded by Crow (1923, p. 143) from Ceylon and the var. *contracta* Klebh. from the Colombo lake by Lemmermann (1907, p. 267). Ghose (1923, p. 341), who lists this variety, did not observe akinetes so his record is doubtful.

(b) Akinetes remote from the heterocysts.

3. *A. Oryzæ* n. sp. (p. 136), but occasional akinetes next to terminal heterocysts (figs. 1-16).

4. *A. fertilissima* Rao (1937a, p. 363) (fig. 80).

5. *A. anomala* n. sp. (p. 147) (figs. 60-73).

6. *A. gelatinicola* Ghose (1923, p. 341). This species is not very fully described, and its relation to the two preceding species is not clear. Rao's species has smaller dimensions, but is very similar in other respects. Geitler (1932, p. 900) suggests that *A. gelatinicola* is a form of *A. variabilis*, but the spherical akinetes render this improbable.

II. Species with ellipsoidal akinetes.

(a) Akinetes contiguous to the heterocysts.

7. *A. ambigua* Rao (1937) (figs. 77-79, 84). The relation of this species to *A. sphærica* is open to question. A figure of *A. sphærica* f. *tenuis* West, drawn from the Delhi material mentioned above by Miss F. Rich and included in my figure collection, shows the single trichome within a rather wide offstanding sheath.

8. *A. aphanizomenoides* Forti var. *ellipsospora* Rao (1937a, p. 362). This variety might perhaps more appropriately be referred to *A. orientalis* Dixit (cf. 12 below).

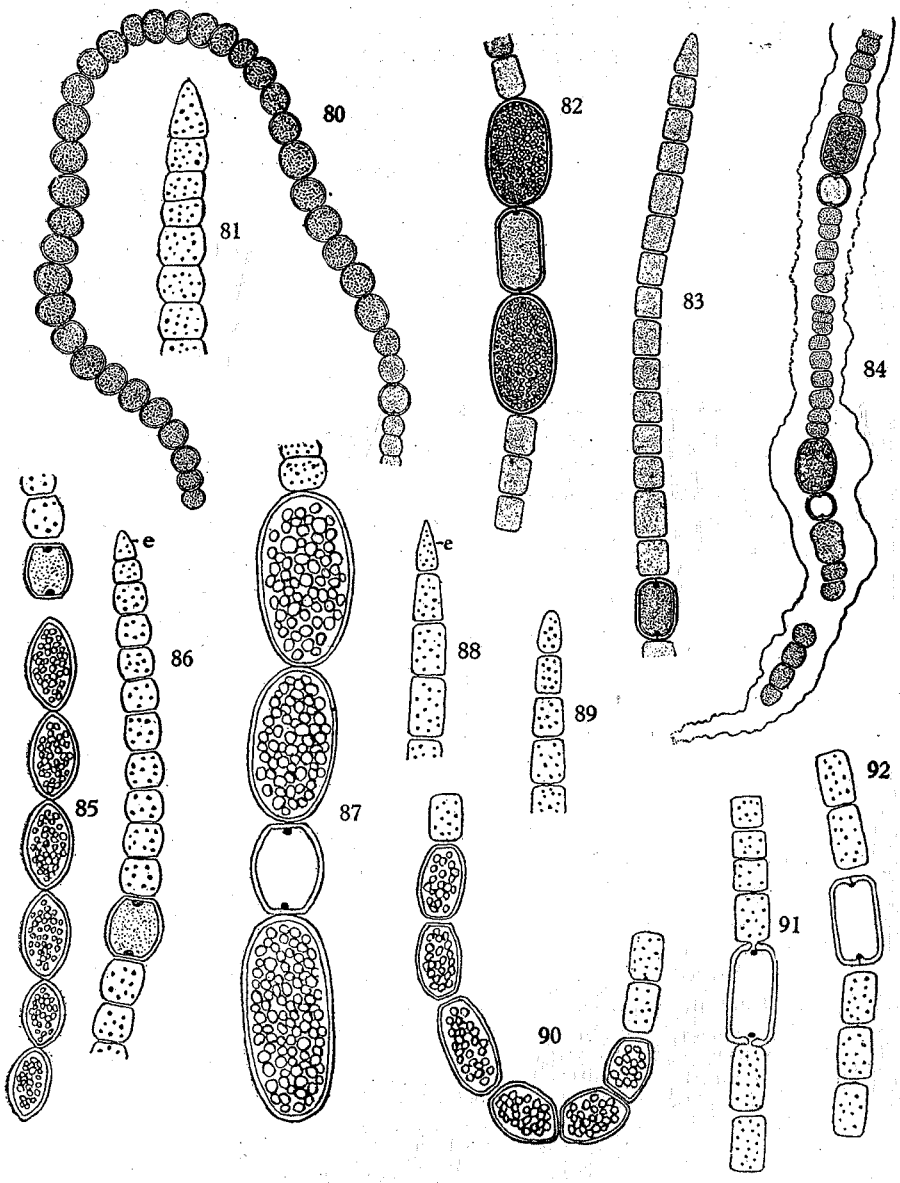

Fig. 80-92.—**80**, *Anabæna fertilissima* Rao. **81**, **87**, *A. Iyengari* Bharadwaja. **82**, **83**, *A. orientalis* Dixit. **84**, *A. ambigua* Rao. **85**, **86**, *A. doliolum* Bharadwaja. **88-92**, *A. kashiensis* Bharadwaja (=*A. variabilis* Kütz. var. *kashiensis*). *e*, end-cells. (**80**, **84** after Rao; **82**, **83** after Dixit; the remainder after Bharadwaja). (**80**× 707 ; **81-83** **85-92**×1094; **84**×465).

9. *A. Beckii* De Toni (1935) (Syn. ; *A. indica* Beck, non Zeller). Collected from marshes near Bombay by Hansgirg (cf. Forti, 1907, p. 441).

10. *Anabænothrix cylindrica* Randhawa (fig. 76)=*Anabæna vaginicola* Fritsch & Rich, forma (p. 152).

11. *A. Iyengari* Bharadwaja (1935, p. 105) (fig. 81, 87). Rao (1939, p. 148) records a form with smaller heterocysts and narrower akinetes from the Bihar Province. Singh's (1939, p. 66) var. *unispora*, although different in certain respects, has marked points of contact with *A. ambigua* Rao. The var. *tenuis* Rao (1937a, p. 361 ; 1940, p. 127) does not differ appreciably from the type.

12. *A. orientalis* Dixit (1936, p. 101) (figs. 82, 83).

13. *A. Volzii* Lemm. (Syn. : *A. unispora* Gardn., cf. p. 150). Rao (1937a, p. 362) records a var. *crassa* which only differs in slight respects from the type.

(b) Akinetes remote from the heterocysts.

14. *A. doliolum* Bharadwaja (1935, p. 105)[1], cf. p. 150 (figs. 85, 86).

15. *A. naviculoides* n. sp. (p. 140, figs. 17-39).

These two species have akinetes of a special shape.

16. *Anabænothrix epiphytica* Randhawa=*Anabæna vaginicola* Fritsch & Rich, var. ? (p. 152).

17. *A. kashiensis* Bharadwaja (1935, p. 105) (figs. 88-92). This comes very close to *A. variabilis* Kütz., which it resembles in its barrel-shaped akinetes (p. 154), although it is distinguished by its pointed end-cells and cylindrical heterocysts.

18. *A. variabilis* Kütz. (recorded by Ghose, 1923, p. 341 ; Dixit, 1936, p. 101 ; and from China by Li, 1938, p. 75). The akinetes of this species are probably typically barrel-shaped with flattened ends (cf. p. 143). Rao (1936, p. 171) describes a form with " occasionally cylindrical spores ", but judging by the dimensions given, they cannot be very different from those of the type. *A. kashiensis* Bharadwaja is best regarded as a variety of this species. Re var. *ellipsospora* nov. var. see p. 143 (figs. 40-50).

III. Species with cylindrical akinetes.

(a) Akinetes contiguous to the heterocysts.

19. *A. oscillarioides* Bory (recorded by Carter, 1926, p. 268). Bharadwaja (1935, p. 103) describes a var. *angustus*, with somewhat narrower filaments and akinetes, which is probably not distinct from the type. The latter is also recorded by Ostenfeld (1907, p. 395) from Mongolia.

20. *A. torulosa* (Carm.) Lagerh. (recorded by Biswas, 1932, p. 172). Regarding this species and the form found in the Faridpur soils, see p. 145 (figs. 51-59).

(b) Akinetes remote from the heterocysts.

21. *A. circinalis* (Kütz.) Hansg. Ghose (1925, p. 249) records a var. *crassa* from Rangoon which is probably not distinct from the type. Akinetes were not observed.

22. *A. inæqualis* (Kütz.) Born. & Flah. (recorded from Rangoon by Ghose, 1925, p. 249 under the name of *A. oblonga* De Wildem.). As Ghose did not see any akinetes, the record is uncertain. The species is also recorded by Jao (1939, p. 197) from China. *A. laxa* A. Br., which is probably synonymous with *A. inæqualis*, is recorded by Crow (1923, p. 143) from Ceylon and by Li (1938, p. 75) from Kiangsi, China.

Two other species recorded from India, viz. *A. Hansgirgii* Schmidle (1900, p. 185) and *A.* (*Sphærozyga*) *Nordstedtii* Turner (1892, p. 13), are excluded. The first of these is probably not an *Anabæna* at all, but is suggestive of a *Scytonema* in the unbranched condition, which species

[1] Bharadwaja says of the akinetes " in short or long chains adjoining the heterocysts but developed centrifugally ". I take this to mean that their formation commences away from the heterocysts, but may extend up to them.

of this genus sometimes assume, probably when the conditions of the environment are unfavourable. Turner's species is so imperfectly described that it could never be recognised.

A number of further species of *Anabæna*, in part new, which have been recorded from China in recent years, may be briefly considered, as one may expect their discovery in India or Pakistan.

1. *A. hunanensis* Jao (1939, p. 197, cf. fig. 93) can scarcely be distinguished from *A. oscillarioides* Bory. The dimensions are practically the same, except that Jao evidently found akinetes of exceptional length. As regards the rectangular heterocysts on

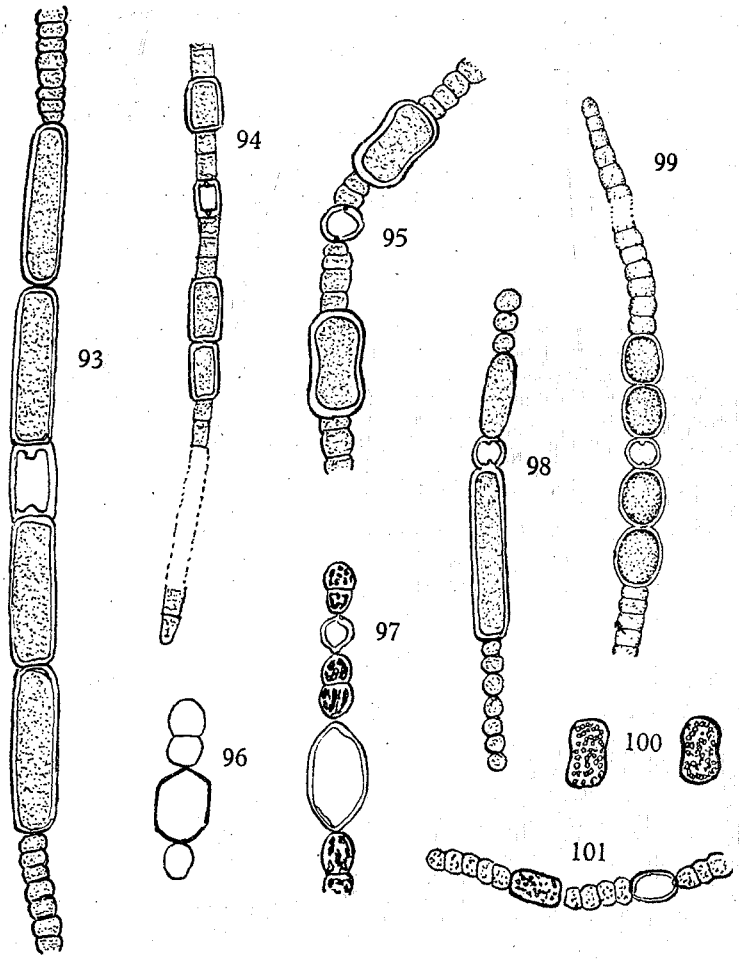

Fig. 93-101.—**93,** *Anabæna hunanensis* Jao (=*A. oscillarioides* Bory, forma). **94,** *A. subdelicatula* Jao. **95.** *A. kwangtungensis* Ley. **96, 97,** *A. macrospora* Klebahn. **98,** *A. lapponica* Borge. **99,** *A. mediocris* Gardn. var. *minor Ley* (=*A. ambigua* Rao var.?). **100, 101,** *A. catenula* (Kütz.) Born. & Flah. (**93, 94** after Jao; **95, 99** after Ley; **96, 97** after Klebahn; **98** after Borge; **100, 101** after Tilden). (**93, 94** × 550; **95, 99** × 840; **96, 97** × 420; **98** × 390; **100, 101** × about 600).

which stress is laid, Bornet and Flahault's diagnosis (1888, p. 233) already states for them : "in proximitate sporarum usque ad 10 μ longis". Jao's species can only be regarded as a form of *A. oscillarioides*.

2. *A. subdelicatula* Jao (1939, p. 196, cf. fig. 94) is certainly closely related to *A. delicatula* Lemm., a little known species. The principal differences lie in the occurrence of the trichomes in a stratum and in the shorter akinetes of the former ; in both species the akinetes are formed from cells remote from the heterocysts. Whether the two forms really belong to distinct species, only further investigation can show.

3. *A. lapponica* Borge (fig. 98), recorded by the same author, is a species distinguished by its spherical cells and elongate cylindrical akinetes. According to Skuja (1926, p. 168) the akinetes may develop a very thick stratified membrane.

4. *A. kwangtungensis* Ley (1947, p. 79, cf. fig. 95), is distinguished by the shape of the mature akinetes which recall those of some forms of *A. torulosa* (cf. p.144) and of *A. catenula*. There is considerable similarity to the latter species. Ley does not describe the end-cells.

5. *A. mediocris* Gardner var. *minor* Ley (1947a, p. 272, cf. fig. 99). I have already (p.150) drawn attention to the close resemblance between *A. mediocris* Gardn. and *A. unispora* Gardn. (=*A. Volzii* Lemm.) and suggested that the former should at best be regarded as a variety of *A. Volzii*. Ley's form shows many resemblances to *A. ambigua* Rao (p.152) and might be regarded as a variety of it.

6. *A. catenula* (Kütz.) Born. & Flah. (figs. 100, 101), This species is recorded by Ostenfeld (1907, p. 395) from Mongolia and a form by Skuja (1937, p. 33) from the Szechwan Province, China.

7. *A. flos-aquæ* (Lyngb.) Bréb. is recorded by Skuja (loc, cit.) from the plankton of a lake at Yungning, Szechwan Province, China.

8. *A. macrospora* Klebahn (figs. 96, 97, cf. Ostenfeld, 1907, p. 395). Gardner (1926, p. 2) records a var. *distorta* nov. var. of this species, floating in great abundance along the margin of a pool, Amoy Island, Fukien Province, China. In the absence of a figure the nature of this form is uncertain.

In the following key only the species recognised in the above survey are included.

I. Akinetes spherical or subspherical.
  A. Akinetes usually contiguous to intercalary heterocysts, sometimes shortly ellipsoidal.
    (*a*) Trichomes straight, cells without pseudovacuoles, akinetes 8-12 μ broad .. .. *A. sphærica*
    (*b*) Trichomes spirally coiled, cells with pseudovacuoles, akinetes 14 μ or more broad .. .. *A. spiroides*
  B. Akinetes not contiguous to intercalary heterocysts, but occasionally next to terminal heterocysts, sometimes shortly ellipsoidal .. *A. Oryzæ*
  C. Akinetes remote from the heterocysts, usually spherical.
    (*a*) Trichomes 5-7·5 μ wide, heterocysts wider than the vegetative cells.
      1. Vegetative cells 5-5·6 μ wide, end-cell rounded, akinetes 4·8-8 μ wide, in long chains.. .. *A. fertilissima*
      2. Vegetative cells 6-7·5 μ wide, end-cell pointed, akinetes 14 μ wide, in short chains .. .. *A. gelatinicola*
    (*b*) Trichomes 2-3·5 μ wide, heterocysts (?) narrower than the vegetative cells, akinetes 3·5-5·5 μ wide .. .. .. *A. anomala*

II. Akinetes ellipsoidal.
  A. Akinetes usually contiguous to the heterocysts.
    (*a*) Several trichomes commonly within a well-defined mucilage-sheath, akinetes shortly ellipsoidal.
      1. Akinetes single, on either side of the spherical heterocysts .. .. *A. ambigua*

2. Akinetes in series of 4-5, heterocysts cylindrical or barrel-shaped.. .. .. .. *A. vaginicola*

(*b*) Trichomes not so arranged.

1. Akinetes 12·3-13·5 μ broad, up to 17 μ long .. *A. Beckii.*
2. Akinetes 8-21 μ broad, mostly twice as long as broad, usually with broadly rounded ends.
   i. Akinetes 8-10·5 μ wide.
      a. Cells 2·5-4 μ broad, up to twice as long, akinetes singly on either side of the heterocysts .. .. *A. orientalis*
      b. Cells 5·2-6·3 μ broad, about as long as broad, akinetes usually in chains.. .. *A. Iyengari*
   ii. Akinetes 15-21 μ broad, heterocysts elongate cylindrical .. .. *A. Volzii*

B. Akinetes singly or in pairs, mostly remote from the heterocysts, 17 μ broad, rounded-hexagonal in optical section, with pointed ends .. .. *A. macrospora*

C. Akinetes in series, remote from the heterocysts, usually about twice as long as broad.

(*a*) Cells about as long as broad, markedly constricted at the septa, end-cells pointed.

1. Akinetes with pointed and commonly protruded ends surrounded by a special mucilage-sheath, heterocysts rare .. .. *A. naviculoides*
2. Akinetes with pointed ends, devoid of such a sheath heterocysts normally developed .. .. *A. doliolum*

(*b*). Cells usually longer than broad, not pronouncedly constricted at the septa, end-cells bluntly conical or rounded.

1. Akinetes barrel-shaped, with flattened ends .. .. *A. variabilis.*
2. Akinetes barrel-shaped, with flattened ends, heterocysts cylindrical, end-cells pointed .. .. *A. variabilis* var. *kashiensis.*
3. Akinetes ellipsoidal, with rounded ends .. .. *A. variabilis* var. *ellipsospora.*

III. Akinetes cylindrical.

A. Akinetes usually contiguous to the heterocysts.

(*a*). Cells 4-6 μ broad, barrel-shaped, about as long as broad.

1. End-cells conical, akinetes about twice as long as broad, with flattened ends, sometimes with a median waist.. .. .. *A. torulosa*
2. End-cells rounded, akinetes up to 3-4 times as long as broad, with rounded ends .. .. *A. oscillarioides*

(*b*) Cells 4-8 μ broad, ellipsoidal, usually with pseudovacuoles, akinetes elongate with rounded ends .. .. *A. flos-aquæ*

(*c*) Cells 7·5-9 μ broad, spherical, akinetes up to 6 times as long as broad, with flattened ends .. .. *A. lapponica*

B. Akinetes mostly (cf. *A. catenula*) remote from the heterocysts, cells about as long as broad.

(*a*) Trichomes tending to be straight and parallel, 3-6 μ broad, akinetes 6-10 μ broad.

1. End-cells rounded, akinetes cylindrical, up to 2½ times as long as broad (6-8 μ), with flattened ends .. *A. inæqualis*

2. End-cells conical, akinetes up to 1½ times as long as broad.
   i. Akinetes cylindrical, single or in series of 2-3, ends truncate.. .. .. .. *A. subdelicatula*
   ii. Akinetes hourglass-shaped, with retuse lateral margins, usually single, ends truncately rounded, cells 3-3·5 μ broad .. .. ..*A. kwangtungensis*

(*b*) Trichomes spirally coiled, cells 8-10 μ broad, with pseudovacuoles, akinetes 16-18 μ broad, up to 34 μ long, ends truncately rounded .. .. *A. circinalis*

(*c*) Trichomes variously contorted, cells 5-8 μ broad, end-cells rounded, akinetes in series contiguous to or remote from the heterocysts, cylindrical or with a median waist, 7-10 μ broad, up to 3 times as long .. .. *A. catenula*

Summary

This paper contains the descriptions of five different kinds of *Anabæna* which were isolated by De (1939) from Faridpur soils. Three of these, viz. *A. Oryzæ* (=*A. gelatinosa* Fritsch in De, 1939), *A. naviculoides*, and *A. anomala* (=*A. thermalis* Vouk var. *indica* Fritsch in De, 1939), are new species, while a fourth is a new variety (var. *ellipsospora*) of *A. variabilis* Kütz. Their description is followed by a discussion of the value of the taxonomic features used in the diagnoses of species of *Anabæna*, and by a consideration of the species of the genus recorded from the Indian Peninsula and the adjacent parts of the Asiatic mainland. A key for the determination of the species is added.

Most of the investigations forming the subject-matter of this paper were carried out in the Botany School, Cambridge, and I am glad to have the opportunity to thank the authorities of the School for the facilities afforded me.

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