THE NATURAL VEGETATION OF OHIO.

III. PLANT SUCCESSION.

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PRELIMINARY STATEMENT.

In the preceding papers of this series (1) it has been shown that within the glaciated area the physiographic results of glaciation offer the best general key to the pattern of natural vegetation. The results of glaciation, in turn, have been largely influenced by preglacial conditions.

In analyzing the composition of the natural vegetation of Ohio certain groups of associations were distinguished, to wit, Prairie, Ash, Oak, and Beech. Each group includes several related classical associations as described by Cowles (2) and others.

Geographical influence is very marked in the detailed composition of these association groups. Plants whose centers of distribution—in the sense that Waller has employed the term (3)—lie outside of Ohio, occur under proper ecological conditions in those parts of the state most accessible to them. The southeasterly (xerophytic), southern and southwestern (generally mesophytic) elements in these admixtures are most widespread and the boreal least so. Northeastern and western elements are of intermediate importance.

The task of the present, concluding, paper of the series is to develop salient facts with regard to the natural plant succession, particularly in the glaciated Erie Basin. Since the aim is essentially historical, no space will be given to discussion of the excellent detailed modern work of Jennings, Dachnowski, Schaffner, and others, further than to state that their results seem to be entirely consistent with those obtained from a study of early sources.

It will be recalled (1) that Riddell’s Western Flora contains considerable habitat data, especially with reference to prairie and related associations. Fig. 1 represents a tabulation of all species listed by him according to habitat. Apart from the very large group which must be classed as miscellaneous in
Succession diagram obtained by statistical analysis of habitat notes in Riddell's Western Flora, 1835. The number of species peculiar to each distinctive habitat was obtained, also the number of species occurring in more than one habitat. The resulting sequence is perfectly definite.
habitat, it will be seen that certain very distinct habitat groups appear. Moreover, if these groups be arranged so that those having large numbers of species in common are in juxtaposition, a very definite sequence develops for the whole series. This sequence, beginning with open water (Pool), runs into Marsh, Wet Meadow, Dry Meadow, Open Woods, and culminates with Shady Woods. Swamp, Bog, and Barren form offshoots of the main series. It is a curious fact that only the hydrarch succession can be developed from these habitat notes, data on the “miscellaneous” species being so vague ecologically that it cannot be analyzed. However, we know that Riddell’s peculiar interest lay in the prairie, nor did he seemingly appreciate the problems suggested by great areas of swamp forest (“Ash”) in northwestern Ohio, although he visited this district in 1836 (4). Neither is it surprising that, living as he did in southwestern glaciated Ohio, the xerarch series of the unglaciated region failed to resolve themselves clearly in his mind. Botanists more recent than Riddell have had their troubles with these series.

Something of the inherent difficulty of analyzing the xerarch series becomes evident by inspection of our next line of historical evidence, to wit, a tabulation of notes made by the first geologists, (5).

These notes have been arranged below in order of the age of the rock strata examined as nearly as the same can be identified. Only the unglaciated region is here considered.

2nd Report: “Blue Limestone” (Ordovician).

p. 207. Trees even on wet upland flats, which, however, dry early.
p. 216. Wet bottoms, drying early, very fertile—gigantic sugar maple, oak, black walnut, elm, sycamore, hickory, honey-locust, ash, etc.

“Great Marl Stratum” (Upper Silurian).

“Cliff Limestone” (Upper Silurian).
p. 266. oak forest.
p. 252. Hillside showing huckleberry and chestnut which are scarce on limestone—but this hill was capped with sandstone).
p. 260. Slope—fine oak forest with service tree and shrubby Hypericum.
p. 242. Level, loam-covered, fertile—hickory, oak, black walnut, sugar-maple, dogwood, sassafras, and gigantic poplar—the characteristic tree.

“Slate” (Upper Devonian).
p. 270. Disintegrating slate—almost barren, a few pines.
p. 262. Hillside, abundant sweet gum; slopes, sugar maple, etc.
p. 254. Hillside showing huckleberry and chestnut “the signs of slate” (this hill was capped with loose sandstone, rolling down).
p. 260. Broad slate bottoms—heavy growth beech, sugar-maple and tulip tree.
"Sandstone" (Lower Carboniferous).


p. 262. Id. covered with stoneless clay—andromeda, huckleberry, scattered hickory and oak.

p. 290. Hill—plants of sandstone formation, as huckleberry and chestnut.

p. 259. Sandy gravels along sluggish streams—_Nymphaea odorata_ which seems not to thrive on limestone.

p. 269. Ascent, mixed with slate—two species of huckleberry.


Scioto valley sides—general mixture of "western" trees, including locust and paw-paw.

"Conglomerate" (Lower Carboniferous).

2nd Report: p. 131. Topped by oaks or evergreens.

p. 130. Declivities—often covered by evergreens.

(Id., Pottsville and Alleghany Series).

1st Report: p. 102. (Sand) rock knobs—pine on n. and w. slopes, oak elsewhere.

p. 36. Calcareo-siliceous region—heavy forest of largest trees, esp. chestnut and tulip tree.

(Id., Monongahela & Dunkard Series).

p. 50. Thin, fissile, slaty hard sandstone—only stunted scrub oaks and vines.

p. 49. Sandy loam on coarse sand rock above limestone and marls—yellow oak, chestnut and tulip tree.

p. 45. Sandy Pomeroy Series, lime, shale, sand mixture—very fertile, heavy forest, sugar maple and beech to tops of hills.

p. 49. Calcareo-argillaceous chocolate colored soils on red shales—present limits yellow pine.

p. 49. Non-fossiliferous limestones and marls—uplands heavy forest, chiefly oaks and hickories containing abundant remains of yellow pine, but only occasional living specimens of same.

p. 50. Limestone residual soil—fertile, alluvial type of forest to tops of hills.

Two facts at least emerge from a study of the above somewhat confusing list of observations. In the first place there appear to have been selective effects exerted by some of the residual soils, which tended to disappear on weathering and in mixtures. In the second place, so far as our evidence goes, the progress of physiographic development was accompanied by a marked trend toward mesophytism upon all of the rocks.

Our next line of evidence is derived from contemporary description of actual successional phenomena upon glaciated country, principally within the Erie Basin. From among a great many observations the following are selected as most illuminating.

In Stark County, near Waynesburg, in Sandy Township, the first settlers saw young oaks coming up everywhere amongst
rank prairie grass (6, a). Read (7, a) in discussing the physiography of Huron County, describes a primitive forest mainly of large oaks growing upon an old swamp consisting of several feet of black mold. He also describes the physiographic history of a filled swamp which he found largely occupied by yellow and swamp oaks. Parts of Tiverton Township, Coshocton County, (6, b) were covered when first settled with a low underbrush of oak over which a wagon could be driven. White oak, accompanied by elm, ash, white thorn, elder and plum, composed the scattering trees of a grassy intervale on the 6th meridian (8, a) between Ashtabula and Geauga counties. The succession on the poorly drained flat between the Miami and Stillwater rivers in Miami County, is described by John Hussey (9) as beginning with sedges, "mosses," etc., followed by elms, soft-maple, buttonbush, etc., leading on to burr oak and ash. The oak openings of Fulton County (6, c) were stabilized dunes, with lagoons occupied by marsh and prairie and the rounded hills showing no tree but oak, and this only in the flatter portions. It is to be noted, however, that with settlement and the discontinuance of Indian fires, the growth of oak became very dense in parts of the oak openings, instead of sparse as theretofore, while aspen appeared in some of the drier prairies, (10, b).

The first surveyors of Mahoning County encountered, 3rd Merid., 10th Mi., (8, b) a soil "of a hard pale coloured marle or clay & * * smart to taste * * the Timber * * White Oak, Hickory & * * various kinds of Whortles." Oak-chestnut covered the hills of Portage (11) and Coshocton (6, b) counties, while on the clay uplands of Greene County (12, a) and the cold, poorly drained till of Madison County (12, b), there was little timber beside oak. In the latter county this consisted of Quercus palustris, Q. obtusiloba and Q. alba; on somewhat better land—clay over gravel—bur oak was found, while the upland gravel "points" of Greene County bore black walnut, sugar, blue ash, and hickory in contrast to the oak of the surrounding clay. The heavy clay moraine near Defiance (13) was covered by oak woods with hazel undergrowth. Adjacent was a French and Indian cornfield of over 1,000 acres. This field is called a prairie by Spencer, who was a captive among the Indians, but elsewhere is spoken of as a clearing. In the first survey of Trumbull County, (8, b) 3rd Merid., 13th Mi., the following notes were recorded "water, but does not run * * thicket of vines & briers & willows, small popples, thorns, crabtree,
cherry, oak * * spots of grass, Angelica & Golden Rod] soil excellent * * some Hazle bushes * * also now and then a stately White Oak which escaped the fire, the cause of the thicket * * to a ridge of White Oak."

Turning next to stages of succession beyond the oak, the first reconnaissance of Medina County (8, c) noted as remarkable the absence of beech in the eastern half of Tp. No. 4 N., R. 13 W. The other timber here was linden, hickory, black oak, chestnut, and cucumber. The western half of this township, which even on modern maps is clearly more mature physiographically than the eastern, contained beech, sugar-maple, chestnut, and hickory. Fulton Township, Fulton County, (6, c) in its primitive state was covered with a heavy growth of timber consisting of white oak, some red oak, elm, ash, and a large amount of cottonwood, interspersed with tulip tree and some linden. Beyond the grassy intervale between Trumbull and Geauga counties, already referred to in the preceding paragraph, lay gently rising land with many small white pines growing amongst oak and ironwood. In Portage County (11) when the white man came the juvenile topography of the hills was occupied by oak-chestnut and that of the depressions by ponds and bogs, while the relatively more mature topography of the level lands was covered by beech-sugar maple forest. The whole tract now covered by Cleveland (6, d) was a sandy loam, covered with a mixture of chestnuts, oaks, elms, maples, and beeches with large trunks. In Lorain County, Tp. 2 N., R. 18 W. on soil of good quality T. Kirtland (8, c) and his associates found in the eastern part "large Oak and small Timber Beech Sugar tree and here it is apparent that the kinds of Timber have been shifting for considerable time."

Having thus some contemporary evidence that oak forest, xerarch or hydrarch was eventually being succeeded by beech-sugar maple mesophytic, it is interesting to examine some records which throw light on the purely hydrarch forest succession. In Tp. 4 N., R. 18 W., Lorain County, (8, c) the forest was beech-sugar maple, mixed with ash, elm, and linden, but on the so-called "scalded" patches of land the trees were sycamore, black ash, and white ash. In the same county and township but in R. 16, (8, c) the forest was scalded beech-sugar maple, with black and white ash "remarkably straight and tall." In Portage County, 7th Merid., Tp. 4 N. (8, d) was found a willow swamp, adjoined by ash land, cold, wet, and plain.
The timber here was black ash, birch, maple, beech, and some swamp oak. Howe (13) in giving an account of the Black Swamp as found in Henry County, describes the dense and uniform growth of forest-trees, "among which beech, ash, elm, and oak, cotton-wood and poplar most abound." He also states that the limestone ridges running through the swamp were covered with black walnut, butternut, red elm, and maple, while flood plain species occupied the gravel ridge at Van Wert. Riddell (4) in his brief mention of the Black Swamp as he saw it in Wood, Lucas, and Ottawa counties, notes the fine black soil, underlain by limestone, and describes the forest vegetation as very similar to that on the level tracts of the Scioto and Miami rivers. Oaks, hickories, black walnut, and cottonwood seemed to him especially abundant.

In the 22nd Mi. of the 6th Merid., between Trumbull and Portage Counties (8, a) was a swamp of willow, alder, maple, ash, and gray birch, with low beech ridges. Read (7, b) in discussing the filled valleys of Knox County states that they had so much gravel that walnut and maple was the usual growth instead of [oak and prairie] as in the clay-filled valleys. The surface soil of Wayne County, (6, c) was pronounced friable, except in the beech and marshy districts. Where the 6th Merid. was run between what are now Ashtabula and Geauga Counties (38th Mi. N.) Pease (8, a) observes "besides Alders and swampy shrubs there is Elm, Butternut, and Ash Staddles and they appear to be the first of the kind ever produced here. The Alders are the largest I ever saw and are by far the biggest Timber in the Swamp it is not a miry place the horses passed it loaded * * * [beyond] is grass and Solandine * * * the upland is gently rising good land * * * Timber, Maple, Beech, Oak, Cherry, Bass, Elm, and Ironwood." Read (7, c) in his geological report on Lake County, states that the dense forests of elm and black ash found in places in the northern part of Willoughby and Mentor Townships indicate areas long occupied by shore swamps.

There is little doubt that wooded swamps, even those containing alder and birch, were passing through a succession involving ash, or at times, oak, as prominent genera. The latter stages in turn were succeeded by a mesophytic forest in which beech and sugar maple were conspicuous. Such seems to have been the genesis of the wet beech flats in northeastern Ohio and the general tendency of the more fertile Black
Swamp of the northwestern region. What factors favored oak swamp forest as against ash is not clear. There is some reason to regard water relations as the key, the oak swamp being, perhaps, more resistant to summer drought. Species of oak

\[ \begin{align*}
\text{Rosa} & \quad \text{Prunus} & \quad \text{Crataegus} & \quad \text{Populus} & \quad \text{Quercus} & \quad \text{Carya} \\
\text{Salix} & \quad \text{Fraxinus} & \quad \text{Ulmus} & \quad \text{Celtis} & \quad \text{Platanus} & \quad \text{Aesculus} & \quad \text{Liriodendron} \\
\text{Fagus} & \quad \text{Acer} & \quad \text{Carpinus} & \quad \text{Cornus} & \quad \text{Liquidambar} & \quad \text{Tilia} & \quad \text{Juglans} \\
\text{Alnus} & \quad \text{Sassafras} & \quad \text{Hamamelis} & \quad \text{Robinia} & \quad \text{Betula} & \quad \text{Magnolia} & \quad \text{Castanea} \\
\text{Juniperus} & \quad \text{Larix} & \quad \text{Thuja} & \quad \text{Pinus} & \quad \text{Abies} & \quad \text{Picea} & \quad \text{Tsuga} \\
\end{align*} \]

\( \text{\*} \quad \text{P. virginiana}, \quad \text{\*} \quad \text{Q. alba}, \quad \text{\*} \quad \text{Q. falcata}, \quad \text{\*} \quad \text{Q. macrocarpa} \)

\( \text{\*} \quad \text{Q. marilandica}, \quad \text{\*} \quad \text{Q. palustris}, \quad \text{\*} \quad \text{Q. rubra}. \quad \text{\*} \quad \text{swamp oak?} \)

\( \text{\*} \quad \text{F. americana}, \quad \text{\*} \quad \text{F. nigra}, \quad \text{\*} \quad \text{U. americana}, \quad \text{\*} \quad \text{U. fulva}. \)

\( \text{\*} \quad \text{A. saccharum}, \quad \text{\*} \quad \text{A. rubrum}, \quad \text{\*} \quad \text{Ostrya virginiana}, \quad \text{\*} \quad \text{J. nigra}. \)

\( \text{\*} \quad \text{J. cinnerea}, \quad \text{\*} \quad \text{Gleditsia sp} \)

\text{Figure 2.}

\text{Key to mapping symbols used. Above, generic symbols; below, species or special genera.}

were numerous and included a fair range of physiological types, but we must agree with Gleason (14, a) that the genus is relatively immobile. Certainly the relation of swamps to adjacent forest, rodent ecology, germination requirements, and rooting habits must all have been elements in the problem.
Mention should be made of an observation recorded by Lesquereux (15) who states that swamp rose and buttonbush require rotten logs for the germination of their seeds in swamps, the roots then penetrating the soil during the dry season and becoming established. This may give a valuable clue to the puzzling fact that some swamps remained herbaceous indefinitely, while others seemingly much like them, became wooded very rapidly.

The early records contain substantial evidence that land subsidence, beavers, and Indian culture all have had marked effect on successional history. One cannot spend many years on the problems of Ohio vegetation without becoming con-
vinced of the profound importance of a better knowledge than we now have concerning ethnological factors and reactions.

Coming now to the detailed forest map of Ohio (1) based upon the bearing trees at one-mile intervals, what information does it supply with respect to natural succession? The general morainal relation of Oak, Beech, and Ash types as pointed out in Part I certainly suggests that the mesophytic Beech occupies the most mature region physiographically of the three.

In Fig. 2 are reproduced as a key to the figures following the mapping symbols used to designate various species of trees transcribed from original survey records. Fig. 3 represents Tp. 4 N. R. 8 E. in Henry County, surveyed in 1821, (16),

Figure 4.
*Present drainage and original forest of Tp. 5 S., R. 15 E., Marion Co. Vegetation white oak-black oak, bur oak, hickory, prairie; topography youthful.*
showing the species of bearing trees at section corners at that time. The drainage is mapped as shown on the McClure Sheet, done in 1906–7 (17). Most of this drainage it will be noted, consists of rectangular ditches made since the region was settled. The forest cover is typical for the Black Swamp region, consisting largely of white and black ash, elm, maple, cottonwood, with some oak and hickory, and even the more mesophytic linden, tulip tree, and beech in places. The extensive ditching indicates clearly enough the youthful physiographic character of this forest association.

The Oak group of associations is represented in two of its phases in Figs. 4 and 5. Fig. 4 records the trees present in
Tp. 5 S., R. 15 E. of Marion County (16) when originally surveyed, (about 1810). Black oak-white oak, bur oak, hickory, and prairie are conspicuous. The drainage was mapped about 95 years later, in 1905 on the Marion Sheet (17). It is known to be much more extensive than formerly (1, II), but is obviously still far from mature. The other area, Tp. 19 N.

Figure 6.

Present drainage and original forest of Tp. 2 S., R. 11 E., Hancock Co. Beech-sugar maple association, drainage pattern fairly uniform and mature.

R. 14 W. of Wayne County (8, b) was predominantly white oak and black oak (16). Seemingly well drained, it is actually quite youthful physiographically, as the diverging stream heads and the ditches at the western and southwestern edge bear witness (West Salem Sheet, 17). The trees were recorded here in 1807, the drainage between 1905 and 1912.
From among a number of typical areas of beech-maple forest two have been selected, quite at random. Fig. 6 represents the virgin forest and the modern drainage of Tp. 2 S. R. 11 E. of Hancock County (16) (Arlington Sheet, 17), and Fig. 7, the same for Tp. 7 N. R. 2 E. of Preble County (16) (Oxford Sheet, 17). In both the trees are predominantly beech and sugar maple, with more or less admixture of oak, ash, hickory, and linden. A glance is sufficient to establish the relative maturity of the physiography of both as indicated by the drainage.

Since there naturally are objections to comparing modern drainage with vegetation of one hundred years ago, Figs. 8
Figure 8.
Original drainage and forest of Tps. 3 S., Rs. 14 and 15 E., Wyandot and Crawford Counties. Organized drainage almost nil in prairie-oak-hickory mixture at bottom and left; better in transition zone of upper center; best in beech-maple at right.
and 9 of Tp. 3 S., Rs. 14 and 15 E. in Wyandot and Crawford counties are of interest. In Fig. 8 is represented not only the forest but also the drainage as mapped in 1819, about 10 years after the original survey (16) (18). The absence of any organized drainage whatsoever in the prairie-oak-hickory area to the south of the Sandusky river is striking, while in the eastern area north of the river, occupied by beech and sugar maple, the drainage is clearly well developed. The triangular patch* in the north center of the map shows drainage somewhat developed and here instead of prairie and oak is elm, maple, and

*Riddell, entering this patch from the west in 1836, describes it as follows (4):

"After crossing the Sandusky, we traversed two miles of plain, where the prairie and woodland vegetation contend for mastery. The trees then began to occur more closely together, and we soon had a dense, unbroken forest."
CLIMATIC CONTROL.

In constructing the trend of succession in a given region the broad climatic tendencies are of first importance. What evidence is afforded by the natural vegetation on this point?

1. J. G. Kirtland, a most excellent naturalist, who knew the native fauna and flora of Ohio well (19) pronounced the flora of the southern shore of Lake Erie mainly southern, but with some hyperborean elements. Certainly boreal associations, in the form of bogs, while frequent, were not extensive nor aggressive. For example, none were found within the great hydrarch area last vacated by Lake Erie and enclosed within the ancient shore lines of Lake Whittlesey. This means apparently that such boreal associations have not been initiated within more recent postglacial times. What is more, in a great number of former bog habitats, which give every evidence of having been occupied by boreal subclimax the present vegetation consists of non-boreal successors, e. g., beech and sugar maple.

2. Plants whose centers are westerly, such as *Andropogon furcatus*, *Tilia americana*, *Ostrya virginiana*, *Quercus macrocarpa*, etc., although numerous in northwestern Ohio, are all clearly members of subclimax associations. In this region the bulk of space has for a long time been occupied by subclimax plants and the most active, hence most significant phase of succession climatically is that which leads on to climax associations. As will be seen later, the climax here includes beech and sugar maple, with other forms decidedly more southern than western.

3. In the nonglaciated region of deep relief the most active changes are due to erosion. Aggressive associations would be expected then in the uplands, xerophytic, and predominantly southeastern in their forest cover. Mesophytes of north-easterly origin such as *Tsuga* were largely confined to isolated ravines, long stabilized, and were certainly not as abundant in the natural climax as *Fagus*, *Acer saccharum*, *Magnolia acuminata*, *Liriodendron tulipifera*, etc.

4. Much of central and southwestern glaciated Ohio has been long since covered by subclimax vegetation. Here again the most active phase of succession is from subclimax on.
There is no question that apart from *Acer* and *Fagus* the predominant mesophytes in this portion of Ohio, e. g., *Aesculus, Juglans, Liriodendron*, etc., have southern and southwestern centers of optimum growth.

5. The behavior above described for western as well as boreal forms suggests a retreat from Ohio—more recent for the western than the boreal. This accords with the general theory of postglacial northward movement of boreal vegetation and with the hypothesis of an ensuing period of continental climate (14, b). If one postulates an Arctic-Labrador-Manitoban sequence of climate for Ohio this does not seem unreasonable. But a xerothermic hypothesis which assumes Arctic-Labrador-Coloradoan climates in sequence is harder to follow.

6. Reviewing these five propositions we arrive at a definite suggestion with reference to climatic trend as expressed in natural vegetation between 1798 and 1835. The aggressive phases of natural vegetation in Ohio were southerly in their general character and indicated a continuing northerly trend of southern climate.

**SUMMARY.**

1. In this third and concluding paper of the series on Natural Vegetation of Ohio the historical method has been extended to an attempt to reconstruct the natural plant successions.

2. Since the data available for this purpose consist largely of the observations of men who perceived the process of succession incompletely or not at all, only the broadest general outlines can be derived.

3. By analyzing and plotting the habitat data of Riddell's Synopsis of the Western Flora the hydrarch sequence of much of glaciated Ohio was found to consist of the following series: Water, Marsh, Wet Meadow, Dry Meadow, Open Woods, and Shady Woods. Bog and Swamp seem to represent restricted offshoots from the main course of succession, at least in Riddell's experience. His data fail to shed light on either the xerarch series or the series involving swamp forest.

4. Tabulation of observations published by the Geological Survey in 1838 confirms the findings of Part I regarding the selective influence of rock beneath residual soils in unglaciated
Ohio. This tabulation also shows progressive mesophytism accompanying physiographic development in unglaciated Ohio.

5. Field observations of the first surveyors and of early naturalists have been studied. They indicate clearly the existence of a trend toward mesophytism in all parts of the state that have been glaciated. In xerarch successions the oaks were conspicuous, accompanied by chestnut on silicious soils. In hydrarch successions, following the wet meadow, ash was conspicuous along with elm and soft maple. Oak frequently played a part in the hydrarch series, but was often lacking. The oak stage in any series yielded to hickory, red oak, linden, sugar maple, and finally beech, to which was added white ash, tulip, and other mesophytes. (In mellower soils, however, such as rich sandy alluvium, or gravelly upland clay, the final mesophytic stage containing beech seems to have been preceded by one in which hickory, sugar maple, black walnut, and tulip tree were prominent). On stiff, wet clay flats, ash swamps were succeeded directly by beech, often in fairly pure stands. Here the other mesophytes made but slow progress, but were not altogether absent.

6. Maps of the original section corner trees showing the present drainage indicate clearly, in spite of the lapse of time, that beech-sugar maple mesophytic forest occupied the most mature ground physiographically, while the subclimax and pioneer associations, such as oak-prairie, black oak-white oak, ash-elm-maple, etc., were found on relatively youthful topography.

7. The climatic trend, as judged by the character of associations actively developing in the native forest, seems to have been in favor of southerly forms.

8. The climax forest seems to have been a modification of beech-sugar maple in the direction of mixed mesophytic forest.
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