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THE MUTUAL AFFINITIES OF THE SPECIES OF THE GENUS CAMBARUS, AND THEIR DISPERSAL OVER THE UNITED STATES.

(PLATE III.)

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In a previous study of the geographical distribution of the crayfishes of the United States (see *Proc. Amer. Phil. Soc.*, xli, 1902, pp. 277–285), the present writer took it for granted that the division of the genus *Cambarus*, into five groups, as introduced by Faxon (*Mem. Mus. Harvard*, 10, 1885), and the arrangement of the species within each group adopted by him, would correspond, as far as one might expect, to the natural affinities.

This, however, is true only to a certain degree. There is no doubt that Faxon correctly recognized the chief systematic groups within the genus, and that he also had, in most cases, appropriate views as to the relationship of smaller groups of species. But accepting his system as a whole, and trying to correlate it with the peculiarities shown by the geographical distribution, a number of cases are revealed, where such a correlation is not very apparent, and attempts to give a reasonable theoretical explanation prove to be more or less unsatisfactory. I shall mention here a few instances.

1. The fifth group of the genus follows, in Faxon's system, after

the fourth, and he apparently believes, that it is connected genetically with the latter. The geographical distribution, however, is opposed to this assumption, and a closer study has led me to think that there is no such affinity between these two groups, and that the fifth is more closely allied to the first and second. (Compare Ortmann, *l. c.*, 1902, p. 283.)

2. Faxon believes (*l. c.*, 1885, p. 19) that the first group contains the most primitive forms. This is not probable when we consider the very highly specialized character of most of the species. Indeed, there are rather primitive forms among them, but they are clearly not as primitive as certain species of the second group (Ortmann, 1903, p. 283), and further, the main range of the first group occupies a territory that is, geologically, comparatively young, namely, the lowlands of the southern states (Mississippi, Alabama, Georgia, Florida), of which we know that they became land by degrees during the Tertiary period, the more southern parts in very recent times. It is not very likely that this recent land is occupied by an ancient group of animals.

3. I strongly object to placing *Cambarus pellucidus*, the blind cave-species of Kentucky and Indiana, with the first group, where it stands entirely isolated, morphologically as well as geographically. If we place this species at the beginning of the fourth group, it comes into an assemblage, from which it is not so strongly different. It will always remain a remarkable, and, as Faxon believes, a primitive type, but it is not *the most primitive* type of the genus in all respects. In the shape of the male organs it certainly points rather to the fourth group than to the first.

4. Faxon places *C. blandingi* at the head of the genus: this is apparently due to the desire to let the type-species of the genus stand first. This, however, may convey the wrong impression, that *C. blandingi* is the lowest (or else the highest) form of the whole genus. But I do not think that it is either, and regard it as a highly specialized (but not *the most highly* specialized) form of a branch of the genus that is rather ancient. The distribution of *C. blandingi* has all the characters of a comparatively modern encroachment upon foreign territory.

5. I believe that the second group of Faxon contains the most primitive types of the genus. But this is to be understood "cum grano salis." There are, in this group also some very highly

specialized types (*C. gracilis* and allies), and even some of the primitive forms (*C. cubensis*) possess some peculiar and apparently advanced characters. I think we can express it this way: among the second group, there are species that approach most closely the original stock of the genus, but they themselves are modified to a degree. If I am to single out a species that possibly is *the* most primitive, I should name *C. digueti* Bouvier (*Bull. Mus. Paris*, 1897, p. 224), which is identical with *C. carinatus* Faxon (*Pr. U. S. Mus.*, 20, 1898, p. 648). It is remarkable that the most primitive forms are found in Mexico (and Cuba), which agrees well with the theory of the origin of the genus in these parts (see Ortmann, *l. c.*, 1902, p. 283).

CHARACTERS OF THE GENUS CAMBARUS THAT SERVE TO DISTINGUISH GROUPS AND SPECIES.

Sexual Organs. — Already the earlier writers (Girard, Hagen) have pointed out the importance of the anterior pair of abdominal appendages of the male (copulatory organs) for systematic purposes. Faxon made large use of them in defining his five groups, but within the groups he rarely tried to avail himself of these limbs to reveal the mutual affinities of the different species. It is now generally known that these organs furnish not only the best specific characters, but that their similarity in certain assemblages of species clearly indicates genetic relationship. In close connection with the shape of this organ is that of the female "annulus ventralis," as we now know, the receptaculum seminis. There is, however, not so much variety in the shape of the latter organ, it is not so polymorphous, and the main types occur in different groups, which is apparently due to the more simple structure of this organ. Nevertheless, the annulus — in connection with the male organ — is rather important. We may add that in a number of species the annulus is not very well known.

As regards the male organs, their shape is very complex and much varied. Several main types may be distinguished, and these again show much diversity. It is hardly likely that in so complex an organ the identical form has developed several times, that is to say that there are cases of parallelism; where there is identity or similarity of these organs in different species, this is generally and surely a sign of close affinity. Only one or two exceptions in the first and second group are known to me, where the question is admissible, whether convergency plays a part. There are rarely two species known, where the shape of the male organs is absolutely identical (except in the third group of Faxon, where they are remarkably uniform), and since they have developed from the beginning in three or four different main lines, it is easily understood why they furnish the best specific characters as well as the best criteria for judging the affinities. Thus the danger of being misled by convergency of structure, which is the chief impediment of properly recognizing natural affinities in any group of animals, is here reduced to a minimum. We shall see below that by the actual use of this principle we arrive at conclusions that render the investigation of the development of the genus *Cambarus* a comparatively easy task, furnishing a clue to the explanation of the geographical distribution; further, the study of the male organs gives us a standard by which to judge the other characters that are of systematic value, and as we shall presently see, there is hardly another structure that has the same value for revealing the affinities within the genus, that is to say, the same characters generally develop independently in different groups, being clearly subject to parallelism, presumably under the influence of similar external conditions. In a few cases the latter is very evident.

Copulatory Hooks of the Male.—Faxon lays much stress upon the number of hooks present in the male on the ischiopodite of the second, third, or fourth pereiopods, which are used to take hold of the female in copulation. The third pereiopods always possess these hooks, and in many cases only this pair is present. But sometimes there is an additional pair on the second, or on the fourth pereiopods. The number of pairs of hooks is very constant in the single species (except for occasional abnormities), and it is remarkable that certain types of male sexual organs are generally connected with certain type of hooks; this is chiefly the case in the third, fourth and fifth group of Faxon, while it is not in the first or second, where similar types of sexual organs may be connected with different types of hooks.

If we consider that the presence of two pairs of hooks is certainly a more highly advanced stage than that of only one pair, that is to say, that the difference of the number of hooks is only a difference in the degree of development of one and the same feature, it is easily conceivable that the increase of the number of hooks may have taken place independently in different groups, and we shall see below that there is at least one case (*C. pellucidus*), where we are to assume an independent origin of an additional pair of hooks on the fourth pereiopods; this is also rendered probable by the variability of this character seen in this species. That Faxon's fifth group has developed an additional pair of hooks independently is clearly shown by the fact that here it is the second pair of pereiopods that carries the additional hooks.

Indications of a more general tendency to increase the number of hooks are found in occasional freaks in other groups (*C. propinquus*, *C. virilis*).

General Shape of Carapace.—The primitive type of the carapace seems to be more or less ovate, generally depressed. It assumes, however, sometimes a more cylindrical form (in some cave-species), and in some cases it is rather compressed. The latter character is most remarkable in all burrowing species, and has developed independently at least in two groups (second and third of Faxon, *gracilis*- and *diogenes*-groups).

The *Areola* seems to be originally rather broad and short. But there is a general tendency of it to become narrower, and at the same time to increase its relative length. This is evidenced in almost all groups, and a narrow, sometimes partly obliterated areola is found in species that have nothing whatever to do with each other. In fact, it is only the fifth group of Faxon where this tendency is not manifested. Generally, the length of the areola is correlated to the width, but there are exceptions.

Rostrum.—The shape of the rostrum is characteristic for most species, but it is available only as a specific character. The original type seems to be a rather long rostrum, with more or less parallel margins, with a marginal spine on each side, and a rather long acumen. The chief tendency in further development is for the marginal spines to disappear, and for the whole rostrum to become shorter. This, however, is found in all five groups of Faxon in species which are not at all allied to one another. Even certain peculiar types of rostrum may reappear in a widely divergent group. Thus the *blandingi*-type is imitated, if the expression is permitted, by *C. immunis*, and the burrowing species possess all a rostrum of similar shape.

[It is very remarkable, that burrowing crayfishes of the southern hemisphere (*Parastacus defossus* Fax. from southern Brazil is at hand) resemble the North American burrowing species in a remarkable degree externally, chiefly so in the shape of carapace, rostrum, chelæ, length of abdomen, etc.]

The *Chelæ* are very variable in shape: they are fully developed only in old males, but generally quite characteristic for the species. One and the same type is often common to large groups of species, and thus they are often a good help in the investigation of the natural affinities. But in other cases a similar form of chelæ is found in different groups which is most striking again in the burrowing species.

Among the more primitive species the shape of the chelæ seems to be more or less subcylindrical, and rather elongated. This shape is found in Faxon's first, second, third, and fifth groups, but only in the first, second and fifth it is frequent. Removing *C. pellucidus* to the fourth group, also in the latter this type of chelæ is represented. In part of the second group, and in the third and fourth, a more or less ovate, broad, and depressed chela becomes common, but there is not much uniformity in detail, each group generally developing its own type.

The above are the more important characters. We see that all of them must be dealt with cautiously, if they are to be used for the investigation of affinities of species. Indeed, in many cases, they support the conclusions arrived at by the examination of the the sexual organs, but very frequently similarities of the above characters are due to convergency. The same is true of all other characters, such as armature of carapace, chelæ, shape of epistoma, antennal scales, of abdomen, telson, etc.

SUBGENERA OF CAMBARUS, ACCORDING TO THE CHIEF TYPES OF THE SEXUAL ORGANS OF MALE.

There are three chief types of the male sexual organs (first pair of abdominal appendages), the last of which is easily divided into two subtypes. According to these, I should like to distinguish four subgenera, as follows:

1. Subgenus: CAMBARUS (sens. strict.).

Sexual organs of male *stout*, more or less straight, and comparatively short, *truncated or blunt at the tip, the outer part ending in 1–3* *horny teeth,* which are sometimes recurved, or compressed, or platelike, and are *always sharply distinguishable from the blunt end.* Inner part terminated by a shorter or longer, acute spine, which is sometimes distinct from the tip of this part, so that it appears two-pointed. In the male the third or the third and fourth pereiopods have hooks.

2. Subgenus: CAMBARELLUS nov. subgen.

Sexual organs of male *stout,* straight, or slightly curved at the tips. *Outer part ending in two horny teeth,* which are rather long, taper rapidly, and are *not sharply distinguishable from the end, which is not truncated.* Inner part terminated by a rather long, acute spine. In the male, the second and third pereiopods have hooks.

[The two following subgenera represent the third type of male sexual organs, in which both parts, outer and inner, each terminate in *only one* tooth, which is rather slender, and *not sharply distinguishable* from the end, which is never truncated.]

3. Subgenus: FAXONIUS nov. subgen.

Sexual organs of male shorter or longer, *not very stout, generally slender,* or with slightly curved tips. *Tips never truncated, ending always in two more or less elongated spines,* the one formed by the outer part, and horny, the other formed by the inner part and softer. There is *never more than one tip to the outer part,* and there is no terminal tooth distinguishable, but the tip tapers gradually, or the whole outer part is setiform. In the male generally the third pereiopods only have hooks, very rarely (in *C. pellucidus*) hooks are found on third and fourth pereipods.

4. Subgenus: BARTONIUS nov. subgen.

Sexual organs of male very uniform throughout the subgenus. They are *short and thick,* inner and outer part each terminating in *only one short and thick spine,* tapering to a point. Both terminal spines are *strongly recurved,* forming with the basal part about a right angle. In the male, only the third pereiopods possess hooks.

Subgenus: CAMBARUS. (Type: *C. blandingi.*)

This subgenus comprises Faxon's first and second group, excluding the species *C. pellucidus.* Both groups are rather heterogeneous, and so is this subgenus, and there are considerable variations in the male sexual organs. The chief feature of the latter is their blunt ending, a character that possibly points to the condition seen in the genus *Potamobius;* for the rest, the terminal teeth are quite variable, but always very characteristic for the species.

It is advisable to distinguish groups within this subgenus, not only with reference to the sexual organs, but also with reference to the hooks of the male, for the presence of one or two pairs of hooks seems to constitute, as already Faxon recognized, important differences, the presence of two pairs, on third and fourth pereiopods, being evidently a more advanced stage. Using in addition some other differences of the areola and the chelæ, we obtain the following three sections.

1. Section: C. digueti.

Sexual organs of male with one to two teeth at the tip of the outer part. Male with hooks on third pereiopods. Areola wide or narrow, but never obliterated, about half as long as the anterior section of the carapace (incl. rostrum), or shorter. Chelæ elongated and subcylindrical.

2. Section: C. gracilis.

Sexual organs of male with one to two teeth at the tip of the outer part. Male with hooks on third pereiopods. Areola obliterated in the middle, considerably longer than half of the anterior section of the carapace. Chelæ short, broad, ovate.

3. Section: C. blandingi.

Sexual organs of male with one to three teeth at the tip of the outer part. Male with hooks on third and fourth pereiopods. Areola wide or narrow, rarely obliterated in the middle, shorter or longer. Chelæ generally elongated, narrow, and subcylindrical.

The most primitive sexual organs are found in species of the first section, where there is only one tooth at the end of the outer part. Similar sexual organs are found in the second (*C. advena*) and in the third section (*C. evermanni*): in the latter cases, however, I think we have to deal with parallelism, the single tooth in both cases being due possibly to reduction. Since these two species are very rare and poorly known, and since *C. evermanni* belongs to a group that offers other difficulties, further investigations are needed.

A closer examination may reveal the fact, that the sexual organs of the *digueti-group* are more sharply distinguished from those of *C. advena* and *evermanni.* Through the courtesy of Professor E. Bouvier of Paris, I have received two cotypes (male and female) of his *C. digueti*, which show, on the one hand, that *C. carinatus* Fax. is a synonym of this species, and on the other hand, that the sexual organs have a rather peculiar shape. The figures of these organs, given by Faxon (*Pr. U. S. Mus.*, 20, 1898, pl. 63, f. 2 and 3) are absolutely correct, but the description (p. 648) is rather short and unsatisfactory. Faxon says: "Inner and outer parts ending in a small horny tooth, anterior margin furnished with a small tooth near the tip." Fig. 2 represents this organ of the right side, seen from the outside: the outer part ends bluntly, without a distinct tooth, while the inner part ends in a rather pointed tooth, outside of which is a sharp spine that is longer than the outer part. Faxon's Fig. 3 represents the identical part seen from the inside: only the two tips of the inner part are seen here, and the tip of the outer part is hidden behind the end of the inner; the inner part is flattened and hairy on the inside, and the "shoulder" ("small tooth near tip") is distinctly developed. My male specimen of *C. digueti* agrees in every detail with the figures of Faxon.

A very similar structure is seen in *C. cubensis* (Faxon, 1885, pl. 7, f. 5), only here the flattened face of the inside is dilated, and the shoulder is more prominent. In both cases, there are practically three tips to this appendage, *two* of which belong to the *inner* part.

The description of this organ in *C. mexicanus* (Faxon, *l. c.*, p. 50) agrees closely, but possibly the "small, procurved spine" attributed to the external part belongs to the internal, and then there would be complete agreement.

The double tip to the inner part, and the shoulder, which has a very peculiar position, possibly give to these three species a more isolated position within this subgenus, and might possibly justify the creation of a separate subgenus, which then should stand at the head of the genus. This would also agree well with the geographical distribution.

Aside from these more primitive species (*C. digueti*, *cubensis*, *mexicanus*), the first section contains two others (*C. simulans* and *gallinas*), which mark the transition to the third section, from which they differ only by the number of hooks of the male; the third section contains more advanced forms of the *simulans*-type. The second section is a peculiar side branch going off from the first section, which has acquired burrowing habits; this is known positively of *C. gracilis* and of *C. advena* (Hyeme vitam degit subterraneam. Aestate in fossis invenitur. Leconte).

The large number of species known in the third section makes a further division desirable, which is easily made according to the following characters:

1. Group: (spiculifer).

Outer part of sexual organs with two or three recurved teeth, without prominent angle (shoulder) on anterior margin. Rostrum with marginal teeth, acumen rather long. Areola wide, rarely narrow, distinctly shorter than half of the anterior section of the carapace.

2. Group: (blandingi).

Outer part of sexual organs with three (rarely two) recurved teeth, inner part with terminal spine directed obliquely outward. No shoulder on anterior margin. Rostrum with marginal teeth, acumem rather short. Areola narrow, generally distinctly longer than half of the anterior section of the carapace.

3. Group: (clarki).

Outer part of sexual organs with two compressed tubercles, inner part straight, directed forwards. Anterior margin with a distinct shoulder. Rostrum with marginal teeth, acumen rather short. Areola very narrow, often obliterated in the middle, about half as long as anterior section of carapace.

4. Group: (alleni).

Outer part of sexual organs with one or two teeth, often peculiarly formed (compressed and plate-like), inner part straight or oblique. No shoulder on anterior margin. Rostrum without marginal teeth (at least in the adult stage). Areola moderately wide, about half as long as anterior section of carapace.

There is no doubt, that the *spiculifer-group* is the most primitive of these, and that the others represent special modifications, each developed in a different direction.

The following key for the identification of the species of the subgenus *Cambarus* is submitted; it is claimed that this key represents — as far as is possible in a "key" — the natural affinities. If adult males of the first form are at hand, it should be possible, in every case, to correctly identify the species.

1. *Section of C. digueti* (see p. 98).

a_1 Sexual organs of male with only one terminal tooth on outer part, inner part with two tips; anterior margin with an angular projection (shoulder) near the tip (*digueti-group*).

b_1 Rostrum with marginal teeth.

c_1 Sexual organs of male with inner part not broadly dilated on inner side, curved forward at apex ; shoulder small. Rostrum carinated above. Carapace with lateral spines.
C. (*Cambarus*) *digueti* Bouv.

c_2 Sexual organs of male with inner part greatly dilated, forming a broad, flat, setose plate on inner side ; shoulder strongly developed. Rostrum not carinated. Carapace without lateral spines.
C. (*Cambarus*) *cubensis* Er.

b_2 Rostrum without marginal teeth, subplane above. Carapace without lateral teeth. Inner part of sexual organs flattened within, but not greatly dilated. C. (*Cambarus*) *mexicanus* Er.

a_2 Sexual organs of male with two terminal teeth on outer part, one of which is flat and disk-shaped, inner part with one terminal spine ; without shoulder on anterior margin. Rostrum without marginal teeth (*simulans-group*).

b_1 Terminal teeth of sexual organs oblique, both of about the same length Acumen of rostrum longer. C. (*Cambarus*) *simulans* Fax.

b_2 Terminal teeth of sexual organs straight, one much longer than the other. Acumen of rostrum shorter. C. (*Cambarus*) *gallinas* Cock. and Port.

2. *Section of C. gracilis* (see p. 98).

a_1 Rostrum suddenly contracted into a short acumen. Sexual organs with two teeth at end of outer part. Terminal spine of inner part straight, longer than outer part.

b_1 Anterior margin of carapace forming a blunt suborbital angle.
C. (*Cambarus*) *gracilis* Bund.

b_2 Anterior margin of carapace not forming a suborbital angle.
C. (*Cambarus*) *hagenianus* Fax.

a_2 Rostrum triangular, margins not suddenly contracted to form an acumen. Sexual organs with only one compressed, triangular tooth at the end of outer part. Inner part straight, not longer than outer.
C. (*Cambarus*) *advena* (Lec.).

3. *Section of C. blandingi* (see p. 98).

1. *Group of C. spiculifer* (see p. 100).

a_1 Areola wide. Chelæ rather broad. Two lateral spines on each side of the carapace.

b_1 Chelæ with large, remote tubercles. Margin of rostrum converging. Outer part of sexual organs with two terminal teeth.
C. (*Cambarus*) *spiculifer* (Lec.).

b_2 Chelæ with small, crowded tubercles. Margins of rostrum subparallel· Outer part of sexual organs with three terminal teeth.
C. (*Cambarus*) *versutus* Hag.

a_2 Areola wide or narrow. Chelæ generally narrower. One lateral spine on each side of the carapace.

b_1 Rostrum subplane above, ciliated. Areola wide. Outer part of sexual organs with two terminal teeth, the inner part with terminal spine directed outward. C. (*Cambarus*) *pubescens* Fax.

b_2 Rostrum concave above, smooth. Areola narrower.
  c_1 Margins of rostrum subparallel. Outer part of sexual organs with two terminal teeth, the inner part straight.
    C. (*Cambarus*) *angustatus* (Lec.).
  c_2 Margins of rostrum convergent. Outer part of sexual organs with three terminal teeth, the inner part directed outward.
    C. (*Cambarus*) *lecontei* Hag.

2. *Group of C. blandingi* (see p. 100).

a_1 Eyes rudimentary. Outer part of sexual organs with two terminal teeth.
  C. (*Cambarus*) *acherontis* Loennb.
a_2 Eyes well developed. Outer part of sexual organs with three terminal teeth.
  b_1 Sexual organs straight, terminal teeth well developed.
    c_1 Sexual organs not excavated on outer side near distal end.
      C. (*Cambarus*) *blandingi* (Harl.)
    c_2 Sexual organs excavated on outer side near distal end.
      C. (*Cambarus*) *hayi* Fax.
  b_2 Sexual organs curved back distally, terminal teeth minute.
    C. (*Cambarus*) *fallax* Hag.

3. *Group of C. clarki* (see p. 100).

a_1 Rostrum concave above, acumen slightly longer. Shoulder of sexual organs slightly developed. *C.* (*Cambarus*) *clarki* Gir.
a_2 Rostrum plane above, acumen shorter. Shoulder of sexual organs very prominent. *C.* (*Cambarus*) *troglodytes* (Lec.).

4. *Group of C. alleni* (see p. 100).

a_1 Outer part of sexual organs with one or two terminal teeth; inner part not longer than the outer. Hooks of fourth pereiopods of male not bituberculate.
  b_1 Rostrum concave above. Outer part of sexual organs with one recurved terminal tooth; inner part with the terminal spine placed obliquely.
    C. (*Cambarus*) *evermanni* Fax.
  b_2 Rostrum plane above. Outer part of sexual organs with terminal part plate-like, covering the inner part, and with two very small teeth.
    c_1 Chelæ bearded on inner margin. *C.* (*Cambarus*) *barbatus* Fax.
    c_2 Chelæ not bearded on inner margin.
      C. (*Cambarus*) *wiegmanni* Er. (?).
a_2 Outer part of sexual organs forming at apex a broad, flattened plate, whose anterior margin is furnished with hairs and one strong seta, the posterior margin of the plate produced anteriorly into a blunt process. Inner part produced into an erect spine, which is much longer than the outer part. Hooks of fourth pereiopods of male bituberculate.
  C. (*Cambarus*) *alleni* Fax.

Note: The position of *C. wiegmanni* is very doubtful, since the male sexual organs are unknown. It has been placed with *C. barbatus* by Hagen and Faxon, but only the external resemblance to this species speaks for its position here. The geographical distribution, however, is entirely opposed to it, and I very strongly suspect that it belongs somewhere else.

GEOGRAPHICAL DISTRIBUTION OF THE SUBGENUS CAMBARUS.

Taken as a whole, the subgenus *Cambarus* occupies a rather continuous area, with a possible interruption in northern Mexico: this gap, however, may be due only to the incompleteness of our knowledge. It covers Mexico, and a large part of the southern, central and eastern United States, but leaves unoccupied the mountainous region of the East; it is lacking in the larger part of Tennessee, in Kentucky, West Virginia, Pennsylvania, and northward. The largest number of species is found in the southeastern states: Mississippi, Alabama, Georgia, and this region represents at present the center of frequency of the subgenus. From here it extends, gradually declining, westward into Texas, northward up the Mississippi valley, becoming quite scarce north of the State of Missouri (only two species), and further it has populated the Atlantic coast plain as far north as New Jersey (only one species north of South Carolina).

Regarding the single sections, the distribution shows rather peculiar features. The *digueti-section* is characterized by a marked discontinuity: two species are found in Mexico, one in Cuba, and two in New Mexico, Texas and Kansas. Since I consider this section the most primitive of the genus, this discontinuity is highly interesting, and tends to confirm this view. And further, this peculiar distribution probably indicates the direction of the immigration into the United States. The most primitive forms (*C. digueti* and *mexicanus*) are still preserved in the original home of the genus, in Mexico, while two other, somewhat more advanced species (*C. simulans* and *gallinas*) occupy the higher plains lying to the east of the Rocky Mountains in the southwestern United States. These parts are largely formed by Cretaceous deposits, and represent the first land-connection between western and eastern North America after the Upper-Cretaceous separation. It is very significant, that just these parts contain the most primitive forms of the United States, and thus the distribution of the *digueti-section* clearly indicates this old condition prevailing at the end of the

Cretaceous and the beginning of the Tertiary time, and also gives a clue as to the direction of the migration: it did not go over the lowlands of Texas, which are geologically younger, but over the higher plains of the interior. (See Ortmann, 1902, pp. 282–285, p. 388.)

The *gracilis-section*, which is a specialized type, arising from the more primitive forms of the subgenus, forms in the distribution of the species *C. gracilis* a direct continuation of this southwestern range of the *digueti-section: C. gracilis* is found from eastern Kansas through Missouri, to Illinois, Iowa, and southern Wisconsin. This is in the same line of the migration marked by the distribution of the species of the *digueti-section*, and plainly its continuation in a northeastern direction. However, the two other species of the *gracilis-section*, *C. hagenianus* and *advena*, are entirely isolated, being found only far in the east, in the lowlands of Georgia and South Carolina. Here again we have discontinuity, indicating old age. I have no doubt, that these separated localities once were connected, namely from Kansas and northern Texas over Arkansas and across the Mississippi valley into Mississippi, and the northern, higher parts of Alabama and Georgia, including probably Tennessee.

Thus I think that the most primitive forms of *Cambarus* occupied, in the United States, first the Cretaceous plains of the southwest, necessarily reaching in very early times the Ozark Mountains, following the Ozark uplift into Illinois and beyond, and, on the other hand, crossing the present Mississippi valley, and reaching the southern end of the Appalachian system, and finally the sea coast in Georgia and South Carolina. Representatives of the primitive sections of the subgenus have now disappeared in the Appalachian region, and this is very likely due to the fact, that, as we shall see below, just in this region some other very vigorous groups developed, which apparently suppressed those earlier forms. In the southwestern extremity, where these new groups are rather scarce or entirely lacking, there was a chance for the old types to survive, and this may account for the presence of *C. simulans* and *gallinas* in this region, while *C. gracilis*, which is found right in the chief domain of the subgenus *Faxonius*, survived possibly on account of its different habits. For similar reasons *C. hagenianus* and *advena* may have survived at the extreme eastern seashore.

The *third* section of the subgenus *Cambarus* represents typically the distribution of the whole subgenus, with the exception that it is not found in the extreme west and in Mexico. (I disregard *C. wiegmani*, since I do not believe that its position with this section is correct.)

Here again we have peculiar facts of distribution. The more primitive forms (*spiculifer-group*) are restricted to the states Georgia, Alabama, and northwestern Florida. Thus they come into close contact with the hypothetical old range of the more ancient types of the subgenus in the southern Appalachians, and I believe that they originated from an original stock of the *digueti-section*, that immigrated into the lowlands south of the mountains, which became dry land by degrees during Tertiary times. Here in these lowlands, chiefly in Alabama and Georgia, is the center of origin of the *blandingi-section*, which represents a secondary center for the subgenus. The more primitive forms (*spiculifer-group*) still stick to this center, while the more advanced forms have spread out from here as follows.

The *blandingi-group* invaded (*C. fallax*) northern Florida, and spread out northeastwardly along the Atlantic coast plain (*C. blandingi-typicus*), and also it migrated westward aud northward, up the Mississippi valley (*C. hayi* and *blandingi acutus*). The *clarki-group* extended chiefly westward from northern Florida far into Texas (*C. clarki*), and slightly eastward into South Carolina (*C. troglodytes*, in South Carolina and Georgia). Finally, the *alleni-group* occupied Florida: *C. alleni*, the most aberrant form, goes farthest south here (Caloosahatchee River, Lee Co.). (The other species, *C. evermanni* and *barbatus*, are known from scattered localities in Georgia, western Florida, and Mississippi, and their distribution needs further investigation; *C. wiegmanni* from Mexico possibly does not belong here.)

Thus the distribution of the subgenus *Cambarus* illustrates the early history of the immigration of the genus into the United States, and it also illustrates the later population of the southern parts of the United States during Tertiary times by forms of the *blandingi-section*. The latter prevail here, and hardly ever had any competitors, and thus the southern states are at the present time the center of the frequency of the whole subgenus. They are, however, the center of origin only for the *blandingi-section*, while the center of origin of the subgenus is to be sought in Mexico.

The more advanced forms of the subgenus *Cambarus* generally seem to prefer the ponds, lakes, and sluggish streams of the lowlands.

Subgenus: CAMBARELLUS (Type: *C. montezumæ*).

This subgenus corresponds to the fifth group of Faxon.

Faxon compares the male sexual organs with those of his fourth group (= *Faxonius*), but I rather think that they are more closely allied to those of his first and second group (= subgenus *Cambarus*). This latter relation, with the more primitive forms of the subgenus *Cambarus*, is confirmed by other characters: carapace and areola which are rather primitive, at least not very highly advanced; the rostrum has lateral teeth, which show a tendency to disappear; the chelæ are very simple, more or less elongated and subcylindrical, which is distinctly a primitive feature. The annulus ventralis of the female seems to be very remarkable in *C. montezumæ* (movable, fixed only at the posterior end), and also in *C. shufeldti* (a transverse curved ridge, the hind side of the ridge concave).

The three species of the subgenus may be distinguished as follows:

a_1 Sexual organs of male with straight terminal teeth. Carapace with lateral spines. Rostrum with distinct marginal spines.
C. (*Cambarellus*) *shufeldti* Fax.

a_2 Sexual organs of male with curved terminal teeth. Carapace without lateral spines. Rostrum with or without marginal spines.
  b_1 Carapace slender and subcylindrical. Rostrum longer and narrower, with sharp marginal spines, and long, spiniform acumen.
  C. (*Cambarellus*) *chapalanus* Fax.
  b_2 Carapace ovate. Rostrum shorter and wider, with or without marginal spines, in the first case, the acumen is much shorter.
  C. (*Cambarellus*) *montezumæ* Sauss.

C. shufeldti is apparently more primitive than the other two species. I have no doubt that *Cambarellus* took its origin from the most primitive species of the subgenus *Cambarus* (*digueti-group*), but developed in a peculiar direction, which is chiefly characterized by the male sexual organs, and by the presence of hooks on the second pereiopods, a condition that is found nowhere else in the genus.

The *distribution* of this subgenus also suggests its antiquity, for it is characterized by a strong discontinuity, *C. shufeldti* being found in Louisiana, the other two species in Mexico. This geographical discontinuity is accompanied by morphological discontinuity, the former species differing very strongly from the two latter. While

C. chapalanus and *montezumæ* still remain in the original home of the genus, although they have changed a good deal, *C. shufeldti* seems to be an early emigrant, which, however, has not much changed. Further investigations in this subgenus are much needed.

Subgenus: FAXONIUS (Type: *C. limosus*).[1]

This subgenus corresponds to Faxon's fourth group, with the addition of *C. pellucidus*. As regards the latter species, which Faxon places with his first group, apparently chiefly on account of the presence of hooks on the third and fourth pereiopods in the male, it is easy to see that the sexual organs do not agree with the *blandingi-type*. Faxon himself says (1885, p. 42), that they are very simple, and generally admits that this species unites characters of different groups. Looking at the figures of the sexual organs given by Hagen (Ill. Cat. Mus. Harvard, 3, 1870, pl. 1, f. 68–71), and Hay (*P. U. S. Mus.*, 16, 1893, pl. 45, f. 11–14), I fail to see any similarity to any of the species of the subgenus *Cambarus*, but their shape approaches rather closely that of some species of Faxon's fourth group, namely: *C. limosus*, *indianansis* and *sloanei*. Indeed, in *C. pellucidus* this organ is different from any one of these, but it agrees with them in the more or less straight and simple form, with the outer and inner parts separated at the tips for a short distance; there is also no trace of a terminal truncation. The rostrum and the chelæ are rather primitive in *C. pellucidus*, while carapace and areola are peculiar, which is possibly a character due to the subterranean life (see Faxon).

If we place *C. pellucidus* with the species of the fourth group named above, it loses its isolated position also with reference to the geographical distribution: it is found in a region (Kentucky and southern Indiana), where at least two of the above species are also found: *C. indianansis* and *sloanei*.

I think, that *C. pellucidus* is a rather primitive form, connecting the subgenus *Faxonius* with the more primitive forms of *Cambarus*

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[1] *Astacus limosus* of Rafinesque has been considered by all authors (Girard, Hagen, Faxon) as very probably identical with *A. affinis* of Say. Although Rafinesque's description is very poor, the locality given ("muddy banks of the Delaware near Philadelphia") renders it absolutely certain that *C. affinis* was intended. There is no other species on the banks of the Delaware but this, and it is so abundant there, that it even attracts the attention of the casual observer. Thus I do not see why the older name of Rafinesque should not be restored.

(*digueti-group*), and that the development of an additional pair of hooks on the fourth pereiopods is a parallelism to the similar tendency in the more highly advanced forms of the subgenus *Cambarus* (*blandingi group*) : to the latter, *C. pellucidus* has no direct relation at all.

With regard to all the rest of the species of this subgenus, I agree with Faxon in thinking them to form a natural, genetically connected group. Nevertheless there is much diversity within this subgenus, and is chiefly indicated by the shape of the male sexual organs. Faxon did not use the latter in arranging the species of his fourth group, and thus his key (1885, p. 86) is, as he admits himself, artificial to a degree. But I shall show here, that according to the sexual organs we can divide the subgenus in groups, which seem to be quite natural.

1. *Section : C. limosus.*

Sexual organs short, rather thick up to near the tips, reaching to the base of the third pair of pereiopods. Tips split for a short distance, each tapering to a point. Hooks on third, or on third and fourth pereiopods.

This is the most primitive section of the subgenus, and it is also in other characters quite indifferent, and not highly specialized; and further, it appears a little heterogeneous. The rostrum is quite uniform in shape, generally with marginal spines (except in certain varieties of *C. pellucidus*), with a rather long or a moderate acumen. The areola is wide and of medium length (except *C. pellucidus*); the chelæ are comparatively narrow and without remarkable features (except in *C. harrisoni*).

The annulus of the female shows the tendency to develop tubercles upon its face; these tubercles have a more or less central position (*limosus*, *indianensis*), or a posterior (*sloanei*), or have the shape of a transverse ridge (*harrisoni*), or form a "median keel" (*pellucidus*).

2. *Section : C. propinquus.*

Sexual organs shorter or longer, not thick, deeply split at the tips, tips slender, more or less straight, sometimes the outer one slightly curved, but never both tips curved in the same direction. Always only third pereiopods with hooks (*barring freaks*).

The other characters are very uniform in this section. The rostrum possesses with one exception (*C. medius*), marginal spines, and a rather long or moderate acumen. The carapace is of normal shape, oval and depressed; the areola uniformly rather wide, and there is no tendency to become narrow. There are, however, some differences in length: generally, the areola is about half as long as the anterior section of the carapace (incl. rostrum); but in certain species (*erichsoni* and *forceps*) it is slightly, and in one species (*spinosus*) decidedly shorter, and in two others (*rusticus* and *medius*) it is decidedly longer. The chelæ in this section are also rather uniform, but not very primitive: they are more or less broad and ovate. The fingers (in old males) generally are gaping at the base, and in contact distally, and the movable finger possesses a peculiar S-shaped curve. The immovable finger is generally not bearded at the base (a slight indication of a beard is seen in: *C. propinquus, obscurus, neglectus*). In *C. forceps*, the fingers are unusually and widely gaping, up to the tips. In *C. medius* the chelæ are unusually broadly ovate, and the movable finger has no S-curve.

The annulus of the female is flat, with a median depression and raised margins. Very often the anterior margin is elevated into tubercles, and in *C. hylas* the posterior margin is very prominent, which is rather unusual in this section, and ought to be confirmed by additional investigations.

This section contains ten species, which may be divided into two groups.

1. *Group: (propinquus).*

Tips of sexual organs comparatively short, reaching only to the third rarely (in erichsonianus) to the second pereiopods, without or with (obscurus) a shoulder on the anterior margin. Outer tip regularly tapering from base to end.

2. *Group: (rusticus).*

Tips of sexual organs long, reaching rarely only to the second, generally to the first pereiopods, mostly with a shoulder on the anterior margin. Outer tip not regularly tapering, but thin (setiform) from base to end.

C. erichsonianus forms a transition between the two groups: the sexual organs are rather long, but they lack a shoulder, and in shape they resemble those of *C. propinquus.*

3. *Section: C. virilis.*

Sexual organs generally quite long (rarely rather stout), reaching about to the second pereiopods, deeply split at the tips, tips slender *(rarely shorter) and more or less strongly curved backward, both in the same direction. Always only the third pereiopods with hooks (barring freaks).*

The shape of the sexual organs is quite uniform in this section, and they do not vary much in the different species, with one exception: *C. difficilis.* Here they are remarkably short and stout, reaching only to the third pereiopods. But we cannot separate this species on this account from the section, since in other characters it is closely allied to *C. palmeri.*

This section closely approaches the *propinquus* type, especially that represented by *C. rusticus,* in fact, the curvature of the tips of the sexual organs is the only important differential character. Besides, however, there is in no case a shoulder developed here, which is so frequently seen in the *propinquus-section.*

In other characters this section is more variable than the *propinquus-section,* and this is most evident in the width and length of the areola. The chelæ are built according to the type of the *propinquus-section,* but a remarkable character is the presence of a dense tuft of hairs (*beard*) at the base of the immovable finger. This beard is absent in *C. compressus* only. In two species, *C. alabamensis* and *compressus,* the chelæ are very broad, and exceptionally smooth.

The annulus of the female is depressed in the middle, with raised margins, similar to that of some species of the *propinquus-section* (*virilis, longidigitus*). In other cases it is elevated posteriorly, and the anterior part is depressed; it is never elevated anteriorly, as is generally the case in the *propinquus-section.* (In some species, *alabamensis* and *mississippiensis,* the description of the annulus is inadequate).

The eleven species of this section are easily arranged into three groups according to the areola.

1. *Group*: (*alabamensis*).
Areola wide and short.

2. *Group*: (*virilis*).
Areola narrow, of medium length.

3. *Group*: (*palmeri*).
Areola obliterated in the middle, of medium length.

4. *Section*: *C. lancifer.*
Sexual organs very peculiar; short, and with slightly curved tips, the outer tip remarkably compressed.

This section is formed to receive an isolated species, the position of which seems quite uncertain. There is a remote resemblance of the sexual organs to those of *C. difficilis* of the third section of this subgenus, and in other characters there are resemblances to *C. mississippiensis,* namely in the lack of marginal spines of the rostrum, and in the obliteration of the areola. The annulus of the female agrees with *C. palmeri* in being depressed in front, and prominent and tuberculated behind: but a similar shape is found in the subgenus *Bartonius.* On the other hand, also the male sexual organs can be compared with *Bartonius,* although they are by no means identical with the very uniform type seen in the latter subgenus. The chelæ, according to the description, are very peculiar, namely long and subcylindrical, the palm with subparallel margins: this is entirely unlike anything that is seen in the *virilis-section* of the present subgenus, and rather stamps this species a primitive one. Then, again, this species presents in the elongate rostrum and antennal scale very unusual features.

Thus it is hard to form a positive opinion about its position. I should not hesitate to place it with the *palmeri-group* of the *virilis-section,* if it was not for the primitive character of the chelæ. According to the latter, and possibly also according to the sexual organs, we might place it at the beginning of the subgenus, as a peculiarly developed primitive form, but it also may be the most highly specialized form of the subgenus. The distribution (Mississippi and northeastern Arkansas) would fit either assumption.

KEY TO THE SPECIES OF THE SUBGENUS FAXONIUS.

1. *Section of C. limosus* (see p. 108).

a_1 Generally third and fourth pereiopods with hooks in the male. Carapace subcylindrical. Areola wide and long. Chelæ subcylindrical. Eyes rudimentary. *C.* (*Faxonius*) *pellucidus* (Tellk.).

a_2 Only third pereiopods with hooks in the male. Carapace ovate, depressed. Areola rather wide, of medium length (about half as long as anterior section of carapace). Chelæ not subcylindrical, compressed, and more or less ovate. Eyes well developed.

  b_1 Sexual organs thick, swollen in the middle, tips short and stout, both slightly curved in the same direction. *C.* (*Faxonius*) *harrisoni* Fax.

  b_2 Sexual organs short, thick, but not swollen, straight. Tips divergent.

    c_1 Sides of carapace with one spine behind the cervical groove.

      d_1 Sexual organs with tips not crossed, the outer directed outward, the inner inward. *C.* (*Faxonius*) *sloanei* Bund.

d_2 Sexual organs with tips crossed, the outer directed inward, the inner outward. *C.* (*Faxonius*) *indianensis* Hay.

c_2 Sides of carapace spinose, several spines behind cervical groove, and spines on the hepatical region. Tips of sexual organs crossed. *C.* (*Faxonius*) *limosus* (Raf.).

2. *Section of C. propinquus* (see p. 108).

1. *Group of C. propinquus* (see p. 109).

a_1 Sexual organs reaching to the third pereiopods, with or without shoulder.

b_1 Rostrum with or without median keel. Sexual organs without shoulder on anterior margin. *C.* (*Faxonius*) *propinquus* Gir.

b_2 Rostrum without median keel. Sexual organs with shoulder on anterior margin. *C.* (*Faxonius*) *obscurus* Hag.

a_2 Sexual organs reaching to the second pereiopods, without shoulder. *C.* (*Faxonius*) *erichsonianus* Fax.

2. *Group of C. rusticus* (see p. 109).

a_1 Rostrum with marginal spines. Carapace with a lateral spine.

b_1 Margins of rostrum concave. Sexual organs reaching to the second pereiopods

c_1 Tip and marginal spines of rostrum bent upward. Fingers of chela gaping only at base. *C.* (*Faxonius*) *rusticus* Gir.

c_2 Tip and marginal spines of rostrum not bent upward. Fingers of chela gaping to the tips. *C.* (*Faxonius*) *forceps* Fax.

b_2 Margins of rostrum straight, generally subparallel. Sexual organs reaching to the first pereiopods.

c_1 Rostrum with distinct median keel. Sexual organs without shoulder. *C.* (*Faxonius*) *neglectus* Fax.

c_2 Rostrum without median keel. Sexual organs with more or less distinct shoulder.

d_1 Areola shorter than half of the anterior section of carapace. *C.* (*Faxonius*) *spinosus* Bund.

d_2 Areola half as long as the anterior section of carapace.

e_1 Margins of rostrum almost parallel, *C.* (*Faxonius*) *putnami* Fax.

e_2 Margins of rostrum distinctly convergent. *C.* (*Faxonius*) *hylas* Fax.

a_2 Rostrum without marginal spines. Carapace without lateral spines. *C.* (*Faxonius*) *medius* Fax.

3. *Section of C. virilis* (see p. 109).

1. *Group of C. alabamensis* (see p. 110).

a_1 Areola very short. Carapace not compressed. *C.* (*Faxonius*) *alabamensis* Fax.

a_2 Areola a little longer. Carapace compressed. *C.* (*Faxonius*) *compressus* Fax.

2. *Group of C. virilis* (see p. 110).

a_1 Margins of rostrum concave, acumen moderately long, together with marginal spines bent upward. *G.* (*Faxonius*) *meeki* Fax.

a_2 Margins of rostrum straight, parallel or convergent. Marginal spines and acumen not bent upward.
  b_1 Acumen of rostrum long, marginal spines sharp, margins parallel. Fingers of chela long. C. (*Faxonius*) *longidigitus* Fax.
  b_2 Acumen of rostrum short, marginal spines small or absent, margins more or less convergent.
    c_1 Acumen of rostrum not considerably shorter than width of rostrum at base; marginal spines small, but present; margins slightly convergent; upper surface slightly concave. Fingers of chelæ not remarkably long and not emarginate at base.
      d_1 Sexual organs longer, slightly curved. C. (*Faxonius*) *virilis* Hag.
      d_2 Sexual organs shorter, more strongly curved.
        e_1 Immovable finger bearded at base, chela for the rest without hairs. C. (*Faxonius*) *nais* Fax.
        e_2 Immovable finger bearded at base, chela pilose. C. (*Faxonius*) *pilosus* Hay.
    c_2 Acumen of rostrum considerably shorter than width of rostrum at base; marginal spines generally wanting (rarely present and small); upper surface deeply concave; margins strongly convergent. Movable finger of chela with a deep emargination at base of inner margin. C. (*Faxonius*) *immunis* Hag.

3. *Group of C. palmeri* (see p. 110).

a_1 Rostrum with marginal spines.
  b_1 Sexual organs long. C. (*Faxonius*) *palmeri* Fax.
  b_2 Sexual organs remarkably short. C. (*Faxonius*) *difficilis* Fax.
a_2 Rostrum without marginal spines. C. (*Faxonius*) *mississippiensis* Fax.

4. *Section of C. lancifer* (see p. 110).

Rostrum very long, without marginal spines. Antennal scale very long. Areola obliterated in the middle. Chelæ long, subcylindrical. C. (*Faxonius*) *lancifer* Hag.

GEOGRAPHICAL DISTRIBUTION OF THE SUBGENUS FAXONIUS.

The area occupied by this subgenus is almost entirely continuous; it extends over all of the central parts of the United States, from northern Texas to Lake Winnipeg in Canada, and from Kansas to the Appalachian Mountains. To the south, it hardly encroaches upon the domain of the subgenus *Cambarus*, being found only in the northern parts of Alabama and Georgia. To the North, it reaches the Great Lakes, and follows down the St. Lawrence valley. Eastward, the Allegheny Mountains apparently form a boundary, but at two places it has crossed these mountains, namely in the north, where *C. limosus* is found in the lowlands and rivers of

Virginia, Maryland, Pennsylvania and New Jersey; and in the south, where *C. spinosus* and *erichsonianus* cross over from the Tennessee River drainage into that of the gulf and the Atlantic Ocean in Alabama, Georgia, South and North Carolina. These latter cases are continuous, the same species being found in both drainages, while in the former case discontinuity is implied, *C. limosus* being cut off and isolated from the rest of the range of the subgenus.

Generally speaking, this subgenus seems to belong to the great rivers of the interior basin, its center lying about in the region where the rivers Missouri, Mississippi, and Ohio come together, that is to say, in the states of Mississippi, Kentucky, southern Illinois, and southern Indiana. From this center it spreads out in the directions of these rivers and tributaries, chiefly toward the North and Northeast. However, the area remained not restricted to the Mississippi drainage, but crossed the divides into other systems in the following cases: From the Tennessee River two species (*spinosus, erichsonianus*) have crossed over into the Gulf and Atlantic drainages, and from the upper Ohio drainage another species (*limosus*) has crossed over into the Chesapeake and Delaware Bay drainage. Another species (*mississippiensis*) is found in the Gulf drainage (outside of that of the Mississippi River) in the state of Mississippi. In the North the area largely extends into the drainages of the great lakes, and even into that of Hudson Bay (through the Red River of the North and Winnipeg Lake).

Studying the distribution of the single sections, the following is to be remarked. The most primitive *section* (that of *C. limosus*) is marked by discontinuity: *C. limosus* being found on the Atlantic coast plain, *C. pellucidus, indianensis, sloanei* in Kentucky and southern Indiana, *C. harrisoni* in Missouri. This discontinuity, chiefly the isolation of *C. limosus*, is accompanied by morphological isolation, the latter species possessing in its spinosity a character, that only recurs in the allied, but otherwise peculiar species, *C. pellucidus*. This latter species, as well as *C. sloanei, indianensis* and *harrisoni*, undoubtedly are the last remnants of the primitive stock of the subgenus in its original home, *i. e.*, in the central basin formed by the three great rivers. Thus the geographical distribution of the *limosus-section* confirms the character of antiquity: most of the species remain in the original home, while *C. limosus* apparently is an early emigrant that has crossed over into the Atlantic drainage, and has been entirely cut off from the connection with the original stock. At present, I am not prepared to say which was the way by which *C. limosus* reached its present habitat.

The *section of C. propinquus* contains quite a number of species: studying their distribution, we see that the distributional areas of the two groups into which this section is divided correspond to the main ranges of two species, while the other species seem to be rather local forms of these. The typical form of the *propinquus-group*, *C. propinquus*, occupies a continuous range that belongs in part to the Mississippi drainage (Iowa, Illinois, Minnesota), in another part to the Ohio drainage (in Indiana), and for the rest to the Lakes and St. Lawrence drainage (in Michigan, Ohio, Pennsylvania, New York and Canada). Compared with *C. rusticus*, this range is more northern and northeastern, and it is remarkable, that there is hardly a locality known for the typical *C. propinquus*, that lies south of the Terminal Moraine of the Wisconsin ice sheet. *C. obscurus* is found at the eastern edge of the range of *C. propinquus*, namely in the upper Ohio drainage in western Pennsylvania and western New York (See Ortmann, *Ann. Carnegie Mus.*, v. 3, 1905, p. 387–406), and seems to be the representative form of *C. propinquus*, in this region.

C. rusticus, the typical species of the *other group* of this section, has a wide range over the central basin, from Ohio, Indiana, and Kentucky to Iowa, Missouri, and Tennessee. With reference to *C. propinquus* it is more southern and western, although it extends, in Ohio, far northward, and is found in the lake drainage in Michigan and Wisconsin. (The investigation of the distribution of these two species, *rusticus* and *propinquus*, in Ohio, Indiana, Illinois, Michigan, and Wisconsin will certainly be very interesting.) Associated with *C. rusticus* in the same group are six other species: all of these are rather local, and all are found at or near the edge of the range of *C. rusticus*. *C. forceps*, *spinosus*, and *putnami* are found at the southeastern edge, namely in the Cumberland and Tennessee river drainages in Kentucky, Tennessee, and northern Alabama. One of these species (*spinosus*) has crossed over into the Gulf and Atlantic drainages in northern Georgia, South and North Carolina. (This is an additional case throwing light upon the changes of the drainage systems in the southern Appalachians, see: Simpson, *Science*, 12, 1890, p. 133, and chiefly Adams, *Americ. Natural.*, 35, 1901, p. 844 ff.; where on p. 849 three species of Cambarus are mentioned (*C. spinosus*, *extraneus*, and *erichsonianus*) that belong into this category). The species *C. neglectus*, *hylas*, and *medius* belong to the southwestern and western edge of the range of *rusticus*, and are found in Missouri, Arkansas, Texas, Kansas, and Iowa. Thus it is evident, that the six species morphologically allied with *C. rusticus* in the same group, express this relation also in their distribution, being apparently locally modified forms of the *rusticus*-type, and being naturally found just where we ought to expect them, namely at the edge of the range of this *rusticus*-type.

C. erichsonianus seems to be abnormal: morphologically we have placed it with *C. propinquus*, but its range is far remote from it in eastern Tennessee and central Alabama (in both the Tennessee and Alabama river drainages). But, as we have seen above, its position is a little uncertain, it resembling *C. rusticus* and its allies to a degree, and the distribution suggests the same: it clearly agrees better in this respect with *C. forceps* and *spinosus*, and it would thus become another local form of the *rusticus*-type. Further investigations on this question should be made.

The *third section*, that of *C. virilis*, has been divided into three groups. The *virilis-group* agrees somewhat with the *rusticus-group* in its range, belonging to the central basin, only being a little more western, and considerably more northern: it is hardly found in the drainage of the Ohio, but it is very abundant in that of the Mississippi and Missouri, and crosses over not only into the lake drainage, but also into that of Hudson Bay (Winnipeg Lake). The typical species of the group (*virilis*) occupies almost all of this range, while four other species associated with it (*meeki*, *longidigitus*, *nais*, *pilosus*) apparently are local forms of it, being found at or near the southwestern extremity of the range of *C. virilis* in Arkansas and Kansas. *C. immunis* is a peculiar type of the *virilis-group*, and its range coincides with the southern part of the range of *C. virilis* (Kansas, Missouri, Iowa, Illinois, Indiana, Ohio): this is interesting in so far as this occupation of the same territory by two closely allied species is rendered possible as it seems in this case, by the different habits: as far as we know, *C.*

immunis inhabits the (often temporary) shallow, stagnant ponds and roadside ditches of the western prairies, and is a burrower, while *C. virilis* prefers rocky places in running streams. (See Harris, *Americ. Natural.*, 35, 1901, f. 187 ff., and *Kansas Univ. Quart.*, 9, 1900, pp. 268 and 270).

Of the other two groups of the third section, that of *C. alabamensis* contains only two species, which are very local, being found only in northern Alabama. Both are rather primitive, and apparently are the last remnants in the Tennessee drainage of a once more widely distributed stock. The *difficilis-group* seems to represent a southern extension of the subgenus *Faxonius*: the species are found in western Tennessee, Missouri, Arkansas, Indian Territory, northeastern Texas and Mississippi, all in the drainage of the lower Mississippi (below Cairo), only *C. mississippiensis* belongs to the Tombigbee river drainage.

C. lancifer would agree in its range (Mississippi and Arkansas) with this latter group.

The species of this subgenus, generally, are river-species, and prefer the large rivers of the great central basin. Some species have become lake-forms (*C. propinquus*, for instance), and others ascend the rivers into the smaller streams (chiefly so in the Tennessee and upper Ohio drainages), but they rarely inhabit true mountain streams.

Further investigation of the distribution of this subgenus should pay particular attention to the ways by which several species have crossed the divides of the Hudson Bay, Great Lakes, and Atlantic coast plain drainage systems. It is very likely that wandering of the divides has played here an important part.

Subgenus: BARTONIUS (Type: *C. bartoni*).

This subgenus, which corresponds to the third group of Faxon, is a very natural one, and, in my opinion, contains the most modern and most highly specialized forms in those that have acquired burrowing habits (*diogenes-section*). There are, however, other species, which are rather primitive, as indicated by certain characters.

The length of the areola, in this subgenus, is rather variable: in the *extraneus-section* it is shortest, about half as long as the anterior section of the carapace, and it is even shorter than that in *C. acuminatus*. In all other species it is considerably longer. The annulus of the female is, corresponding to the uniformity of the male organs, also very uniform, and is characterized by its posterior elevation. Aside from the length and width of the areola, the shape of the chelæ, the presence or absence of marginal spines of the rostrum, and the shape of the carapace serve to distinguish the more primitive forms from the more highly developed, and furnish a division of the subgenus into sections as follows:

1. *Section: C. hamulatus.*

Carapace subcylindrical. Rostrum with or without marginal spines. Chelæ long, subcylindrical. Areola rather long. Eyes rudimentary.

Only two species, *C. hamulatus* and *setosus*, belong here, both blind cave-forms. They do not seem to be closely related to one another, since they differ in very important characters. The subcylindrical shape of the chelæ, however, indicates, that both are rather primitive, and have become separated from the primitive stock of this subgenus very early, and probably independently. The shape of the carapace, the long areola, and the rudimentary eyes are very likely due to parallel development, brought about by the similar conditions under which these species are found. (See Faxon, *Pr. U. S. Mus.*, v. 12, 1890, p. 628).

2. *Section: C. extraneus.*

Carapace more or less ovate, depressed, with lateral spines behind cervical groove. Chelæ not very elongated, depressed, and rather broad, but a little more elongated than in the following sections. Areola more or less wide, of medium length, about half as long as anterior section of carapace, sometimes slightly shorter, rarely, in C. cornutus, the areola is rather long. Eyes well developed.

Two of the species belonging here (*C. extraneus* and *jordani*) are typical, and are unquestionably the most primitive forms of the subgenus, as is shown by the shape of the carapace, the rostrum, and chelæ, at least as compared with the following sections. The third species, *C. cornutus*, stands by itself, and is a rather aberrant form, peculiar on account of its antennæ, which have a large, compressed flagellum, ciliated on inner margin. Also the spines of the rostrum (upturned) are peculiar. In the long areola, it is rather advanced. It seems to be a peculiar local form, developed out of the primitive stock now represented by *C. extraneus* and *jordani*, and we may safely leave it with this section, since the only alternative would be to create for it a separate section.

3. *Section: C. bartoni.*

Carapace ovate, depressed, with or mostly without lateral spines. Rostrum without marginal spines. Chelæ comparatively short and broad, depressed, ovate. Areola wide or narrow, generally distinctly longer than half of the anterior section of the carapace, only in one case (C. acuminatus) slightly shorter than half of the anterior section. Eyes well developed.

The four species belonging here are all closely allied to one another. Their chief differences are furnished by the shape of the rostrum, width and length of areola, and shape of chelæ: but all are built according to the same plan.

4. *Section; C. diogenes.*

Carapace ovate, compressed, without lateral spines. Rostrum without marginal spines. Chelæ short and broad, depressed, ovate. Areola very narrow or obliterated in the middle, always distinctly longer than half of the anterior section of the carapace. Eyes well developed.

The five species belonging into this section also form a very natural group. They are connected with the *bartoni-section* through *C. latimanus* (chiefly its var. *striatus* Hay). The peculiar, compressed shape of the carapace (and possibly other characters, as shape of rostrum, narrow areola, shape of chelæ) seems to be closely connected with the habits: all these species (it has *not* been reported for *C. uhleri* but it is likely also the case with this one) are burrowing species and so-called chimney-builders. This habit begins to appear in the *bartoni-section*: *C. bartoni* often, but not always, makes burrows and chimneys, apparently forced to do so, when the water supply of the small mountain streams, in which it lives, begins to run short in dry seasons. With the species of this group, this habit becomes firmly established, and they never live without making burrows, having abandoned the streams and brooks, and taken to swampy and springy places, generally to the groundwater, where it is found at a short distance below the surface.

The species of this section are distinguishable by the width of the areola, shape of rostrum, shape of the chelæ, and in some cases by peculiar colors. I believe that it is the most highly specialized group of the whole genus, as is indicated partly by the burrowing habits, no doubt an extreme adaptation, and, in one species (*C. uhleri*), by the adaptation to brackish and salt-water, which is found in no other case in the genus.

KEY TO THE SPECIES OF THE SUBGENUS BARTONIUS.

1. *Section of C. hamulatus* (see p. 118).

a_1 Rostrum with marginal spines. Areola wide.
C. (*Bartonius*) *hamulatus* (Cope and Pack.).

a_2 Rostrum without marginal spines (rarely with spines in the young). Areola narrow. *C.* (*Bartonius*) *setosus* Fax.

2. *Section of C. extraneus* (see p. 118).

a_1 Antennæ with normal flagellum.
  b_1 Rostrum concave above. Areola rather wide.
  C. (*Bartonius*) *extraneus* Hag.
  b_2 Rostrum flat above. Areola narrower. *C.* (*Bartonius*) *jordani* Fax.

a_2 Antennæ with very long, compressed flagellum, which is ciliated on the inner side. *C.* (*Bartonius*) *cornutus* Fax.

3. *Section of C. bartoni* (see p. 119).

a_1 Rostrum long, tapering from base to tip. Areola very wide and short, a little shorter than half of the anterior section of carapace. Carapace with lateral spines. *C.* (*Bartonius*) *acuminatus* Fax.

a_2 Rostrum shorter, suddenly contracted to a short acumen. Areola moderately wide or narrow, distinctly longer than half of the anterior section of carapace. Carapace with or without lateral spines.
  b_1 Areola rather wide. Chelæ smooth, punctate, inner margin of palm with one or two rows of tubercles.
    c_1 Fingers of chelæ broad, slightly gaping at base, not bearded.
    C. (*Bartonius*) *bartoni* (F.).
    c_2 Fingers of chelæ subcylindrical, widely gaping at base, the outer one bearded at base. *C.* (*Bartonius*) *longulus* Gir.
  b_2 Areola narrower. Chelæ rough or tuberculated.
  C. (*Bartonius*) *latimanus* (Lec.).

4. *Section of C. diogenes* (see p. 119).

a_1 Areola very narrow, but not obliterated. Color very striking.
  b_1 Rostrum broad. Outer margin of hand serrate. Color red.
  C. (*Bartonius*) *carolinus* Er.
  b_2 Rostrum narrower. Outer margin of hand not serrate. Color blue.
  C. (*Bartonius*) *monongalensis* Ortm.

a_2 Areola obliterated in the middle. Color dull, greenish or brownish.
  b_1 Rostrum concave above.
    c_1 Fingers of chelæ not remarkably flattened, the inner one without distinct excision at base, the outer one not bearded,
    C. (*Bartonius*) *diogenes* Gir.
    c_2 Fingers of chelæ flattened, the inner one with distinct excision at base, the outer one bearded. *C.* (*Bartonius*) *argillicola* Fax.
  b_2 Rostrum flat above. *C.* (*Bartonius*) *uhleri* Fax.

GEOGRAPHICAL DISTRIBUTION OF THE SUBGENUS BARTONIUS.

This subgenus is characteristic for the mountainous regions of the east of the United States, that is to say, for the Appalachian mountains, but the more highly developed, burrowing species have in part descended from the mountains, and spread largely over the central portions of this country. The greatest number of species is found in the southern extremity of the Appalachian system, and there is no question that we have to regard this as the center of origin of the subgenus.

The two cave forms of the *first section* are widely separated from each other. This indicates, on the one hand, that they are not very closely allied, and, on the other hand, the discontinuity thus displayed again indicates antiquity. The one, *C. hamulatus*, is found in a cave in eastern Tennessee, that is to say, right in the center of origin of the subgenus, while the other one, *C. setosus*, comes from a cave in Jasper Co., Missouri (in the Ozark region). This is very remarkable, and very likely indicates, that the center of origin of the subgenus possibly includes the Ozark Mountains, west of the Mississippi: this is further suggested by the reported presence of *C. carolinus* in the northeastern part of Indian Territory, not far from the locality of *C. setosus* (see below). Consequently, we are to regard *C. setosus* as the last remnant of the primitive forms of the subgenus surviving in the western extremity of the original home.

We have regarded, morphologically, the *second section* of the subgenus as the most primitive group of it: this view is supported by the geographical distribution. *C. extraneus* is known from northern Alabama, northern Georgia, Tennessee, and Kentucky (see below, p. 134); *C. jordani* is found in northern Georgia; and *C. cornutus* in Kentucky (locally, only in Edmonson Co.). Thus all the localities are in or near the old center of origin of the subgenus. The presence of *C. extraneus* in the Cumberland and Tennessee river drainages, as well as in the Alabama river drainage indicates an old drainage feature, namely the Appalachian river (see above, p. 116).

The *third section* presents very interesting conditions, such as we have noticed in several groups of the subgenus *Faxonius*. Here we have apparently one widely distributed, typical form, *C. bartoni*: this is found all along the Appalachian mountains and extends very far to the northeast. This species has followed, in its dispersal, chiefly the direction of the strike of this mountain chain, and reaches now from Tennessee to Maine and New Brunswick. Eastward, it hardly decends to the Atlantic plain, at any rate it does not spread over it, and westward it goes as far as Indiana, always preferring smaller streams in mountainous or hilly regions.

C. bartoni possesses several marked varieties, chiefly at the southern and southwestern extremity of its range, in Kentucky, Tennessee and northern Georgia; one variety (*robustus*) seems to follow the northwestern edge of the range of the main species, from Ohio through northwestern Pennsylvania to western New York (and in Canada). This variety has also been reported from Maryland and Virginia, but I doubt that this is actually the same thing (see below, p. 135).

Besides, there are three other species in this section, which are closely allied to *C. bartoni.* One of them, *C. acuminatus*, is found in North and South Carolina, at the southeastern edge of the range of *C. bartoni;* the second, *C. latimanus*, fringes the southern and southwestern extremity of the area of *C. bartoni* in South Carolina, northern Georgia, northern Alabama, and central Tennessee; and the third, *C. longulus*, is apparently a form belonging to the high mountains, being found in the middle of the southern part of the main range of *C. bartoni* along the highest mountain chains of North Carolina, Tennessee, Virginia, and West Virginia. Thus it is beyond question, that we can regard these three species as local forms of *C. bartoni*, the one belonging to the high mountains, another being its southeastern, the third its southern and southwestern representative.

While the *first* and *second sections* characterize the earlier stage of the distribution of the subgenus, the *third section* expresses its advance and dispersal over the eastern mountain system of the United States.

Finally, the *fourth section* (of *C. diogenes*) offers remarkable conditions. Two of the species, belonging here (*C. carolinus* and *monongalensis*) are evidently a little more primitive than the rest. *C. carolinus* seems to possess a wide range within the Appalachian system. It is a true mountain form, and is found from northern South Carolina to southern Pennsylvania, thus representing the same direction of migration as *C. bartoni*, from southwest to northeast, parallel to the strike of the mountains. This species, however, has also been reported from Indian Territory (Ozark region). This locality is very strange, and at present is not connected with the main range, no localities being known in Missouri, Arkansas or the larger part of Tennessee (except the eastern extremity). But it is possible that a connection exists here, and if this should be so, this would indicate, as has been said above (p. 121) that the Ozark region is to be included in the original home of the subgenus. *C. monongalensis* apparently is a representative form of *C. carolinus* in southwestern Pennsylvania.

The most puzzling distribution is offered by the remaining three species, of which *C. diogenes* is the most widely distributed. This species has an eastern and a western range on both sides of the Allegheny Mountains. Apparently it has descended from the mountains, that is to say, represents a more highly specialized branch of the original mountain-loving chimney-builders. It has descended into the Atlantic coast plain on the one side, and is found from New Jersey to North Carolina (Cape Fear). On the other side, it has descended westward, and is found from southwestern Pennsylvania over all the states north of the Ohio (also in Kentucky) as far north as Minnesota and Wisconsin, westward to Iowa (also reported from southwestern Wyoming and Colorado), Kansas, and southward to Louisiana. This immense distribution represents possibly the widest known range of any of the species of crayfishes of the United States. The question remains open, whether the eastern and western range of *C. diogenes* is actually connected across the mountains.

Of the other two species, *C. uhleri* clearly is a local form of *C. diogenes*, inhabiting the sea coast (brackish and salt marshes) in Maryland. *C. argillicola* is morphologically very closely allied to *C. diogenes*, and might be regarded, at least in Ohio, Michigan and Canada, as a local form developed at the northern edge of the range of *C. diogenes*. But the fact that *C. argillicola* is also found in central and southern Indiana, in southern Illinois, and that it has been reported from Mississippi and southern Texas (Victoria and Brazoria), does not render this assumption probable: further investigations of the range of these two species (*diogenes* and *argillicola*) in the south and west are desirable, before their mutual geographic relation can be ascertained.

Thus the burrowing species of the *diogenes-section* of the subgenus, while conforming in part to the original habit of living in the mountains, have in another part abandoned their original mountain home, and largely spread over the plains. That this was possible is no doubt due to their peculiar way of living. Aside from *C. gracilis* of the subgenus *Cambarus*, which is also a burrowing form, and occupies a certain part of the western plains, there are no other forms in the central basin that have acquired this habit, and thus *C. diogenes* did not find any competition, and was able to occupy a large territory. That *C. diogenes* is a very vigorous and flourishing form is also demonstrated by the fact that it attains, chiefly on the western plains, a considerable size.

GENERAL CONSIDERATIONS AND CONCLUSIONS.

We have divided the genus *Cambarus* into four subgenera: *Cambarus*, *Cambarellus*, *Faxonius*, *Bartonius*. *Cambarus* originated in Mexico, and immigrated, probably at the beginning of the Tertiary, into the southwestern and southern United States, originally occupying only the southwestern Cretaceous plain, the Ozark Mountains, and the southern extremity of the Appalachian System. A side branch, *Cambarellus*, has also its center in Mexico, and spread, possibly along the sea coast, to Louisiana. In the central and southeastern parts of the United States three new centers developed. The one is a secondary center for the subgenus *Cambarus*, and lies at the foot of the Appalachian Mountains in the lowlands of Alabama and Georgia. Here the more advanced forms of this subgenus took their origin, and spread all over the Atlantic and Gulf coast plain, and further up the Mississippi valley. These are species inhabiting chiefly ponds, lakes, and sluggish streams of the lowlands. Another subgenus, *Faxonius*, developed in the central basin of the three great rivers, spreading over almost all of the Mississippi drainage, and crossing over into the Hudson Bay, Great Lakes, and even into the Atlantic drainages, probably by the aid of shifting divides. The species belonging to this subgenus are chiefly true river species. Finally, a fourth subgenus, *Bartonius*, developed in the mountainous region of the southern Appalachians, probably including also the Ozark region, and from here it spread chiefly over the Appalachian chain in a northeasterly direction as far as New Brunswick. Most of the species belonging here are inhabitants of smaller mountain streams and brooks. A peculiar group separated from these, the *section of C. diogenes*, which acquired burrowing habits, and is originally also a mountain loving group, but began to descend into the lowlands. Finding no competition here, on account of its peculiar mode of life, it had a chance to spread over a large area.

The centers for the more highly advanced forms of the subgenus *Cambarus*, and for the subgenera *Faxonius* and *Bartonius*, apparently form physiographically differentiated parts of one larger center, situated in the southeast of the United States, clearly corresponding to the southeastern center of dispersal of Adams (*Biological Bulletin*, 3, 1902, p. 115 ff.)[1] Adams discusses this center chiefly with reference to the glacial and postglacial time, but it existed, no doubt, also during the Tertiary, and the development of the different branches of *Cambarus* falls, in my opinion, chiefly into the preglacial time. As Adams maintains, this center is quite distinct from the southwestern center on the arid plateau of Mexico and the adjoining parts of the United States. This latter does not seem to be very important for the later development of the genus, arid regions being generally unfavorable for crayfishes. In older Tertiary times, however, also the southwestern center played a part, in fact it is the original center of the whole genus *Cambarus*.

The different "outlets or highways of dispersal," as Adams (*l. c.*, p. 123) has characterized them, are rather well represented in the distribution of *Cambarus*, and here again I believe, that they were efficient in preglacial times as well as in postglacial times. The Mississippi valley route is represented in the dispersal of the subgenus *Faxonius*, and also by that of the *blandingi-group* of the

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[1] Adams' southeastern center does not include the central basin, and he thinks that the Mississippi river (although it undoubtedly possessed a fauna of its own) was largely populated by way of the Tennessee River, which, after having captured the upper course of the old Appalachian River, opened an outlet to its fauna toward the Mississippi. This is no doubt quite correct with reference to the freshwater shells, and, as has been pointed out already by Adams, finds some support in the distribution of certain crayfishes (*l. c.*, p. 849). But as we have seen in the above pages, the center of *Faxonius* in the central Mississippi valley is very marked, and apparently distinct from the other two centers. It is, however, easy to unite all three of them, and regard them as parts of one larger center of older (old Tertiary?) age, including parts that are differentiated physiographically, as indicated above.

subgenus *Cambarus* (*C. blandingi acutus*). The route along the coastal plain seems to be the least frequented, only *C. blandingi typicus* characterizing it. But then again the Appalachian plateau formed a third outlet to the north; this is clearly indicated by the dispersal of the subgenus *Bartonius*. Adams says very pertinently (p. 129): "dispersal is both forward and backward along these highways," and thus we see that in special cases the direction of the migration may become the opposite. In one case (*C. clarki*) we have a reversed current of migration from the southeastern United States toward the southwest, going in a direction opposite to the general direction of immigration of the whole genus. A direction downward the Mississippi valley (southward) is probable in the *palmeri-group* of *Faxonius*, and *C. diogenes* seems to represent the identical reversed direction, descending the Ohio valley from the Allegheny Mountains. The same species shows indications of a reversed migration on the Atlantic coast plain, from Maryland to Virginia.

That the different centers of origin assumed above are very likely correct, is shown by a two-fold consideration. First, the largest number of species of each subgenus is generally found in or near these centers (Adams, *l. c.*, 1902, p. 128: first criterium), and then the more primitive forms of each subgenus are found there (third criterium of Adams). For the subgenus *Cambarus*, this is not entirely true, Mexico possessing only two species, while Kansas possesses three of the more primitive forms, but this may be due to deficiency of our knowledge, or else it is due to interruption and breaking up of the old southwestern range of the genus; it is apparently not so flourishing any more in these parts as it used to be. Of the more highly advanced forms of the subgenus *Cambarus* (*blandingi-section*), the largest number of species is recorded for Georgia (7), Florida (6), and Alabama and Mississippi (4 each). The most primitive forms (*spiculifer-group*) are found in Georgia, Florida and Alabama.

The subgenus *Cambarellus* also makes an exception, two species being found in Mexico, and only one, but this a more primitive one in Louisiana.

The subgenus *Faxonius* possesses the largest number of species in Arkansas (8), and in Missouri and Indiana (7 each). Illinois has only 4, but this may be due to defective knowledge. The more primitive forms of the *limosus-section* (aside from *C. limosus* itself) are found in Indiana, Kentucky and Missouri, that is to say, in the same general region.

The subgenus *Bartonius* has the largest number of species in Tennessee (6); then follow: Georgia, North Carolina, Virginia and Pennsylvania (with 4 each). The more primitive forms of the *extraneus-section* are found in Georgia, Alabama, Tennessee and Kentucky. In Tennessee is also found one of the blind cave forms (*C. hamulatus*). Thus also here is apparently a mutual relation between center of origin, location of most primitive forms, and center of frequency. This rule, consequently holds good in the section of *C. blandingi* of the subgenus *Cambarus*, and in the subgenera *Faxonius* and *Bartonius*, while it is not very evident in the more primitive forms of the subgenus *Cambarus*, and in the subgenus *Cambarellus*.[1]

A few peculiar and striking facts ought to be mentioned especially.

Discontinuity of distribution proof of antiquity.—We have found this rule substantiated in the following cases: (1) In the distribution of the more primitive forms of the subgenus *Cambarus* (sections of *C. digueti* and *gracilis*); (2) in the subgenus *Cambarellus*; (3) in the *limosus-section* of the subgenus *Faxonius;* (4) in the *hamulatus-section* of the subgenus *Bartonius*. The discontinuity offered by *C. wiegmanni* in the *alleni-group* of the subgenus *Cambarus* needs further investigation, and cannot be regarded as established before the systematic position of this species has been positively ascertained.

Morphologically isolated species occupy isolated stations.—This is illustrated by: (1) *C. cubensis* in Cuba; (2) *C. shufeldti* in Louisiana; (3) *C. limosus* on the Atlantic coast plain from New Jersey to Virginia; (4) *C. harrisoni* in Missouri; (5) *C. alabamensis* and *compressus* in northern Alabama: (6) *C. setosus* in Missouri (cave-form).

Closely allied species occupy neighboring areas. —This is most evi-

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[1] Addition to our knowledge may change this considerably. I only call attention to the fact, that up to very shortly ago only two species of *Bartonius* were known from the state of Pennsylvania. Investigations during the last four years have revealed the presence of two more species, thus doubling the number. This may happen in any other state.

dent in the following cases, where groups of species occupy a certain range, but represent each other in the different parts of this range: (1) in the *spiculifer-group* of the subgenus *Cambarus: spiculifer* in northern and central Georgia, *versutus* in central and southern Alabama, and in northwestern Florida, *pubescens* in eastern Georgia, *angustatus* in southeastern Georgia. (2) In the *clarki-group: clarki*, parallel to the Gulf coast from Texas to Florida, *troglodytes* in corresponding localities in Georgia and South Carolina. (3) *Limosus-section* of *Faxonius: indianensis* in southwestern Indiana, *sloanei* in southeastern Indiana and Kentucky. (4) *Propinquus-group: propinquus* has a western and northern distribution; it is represented in western Pennsylvania by *obscurus*. (Between both possibly is *C. propinquus sanborni*, occupying an intermediate range.) (5) *Rusticus-group: spinosus* is southern and eastern (North and South Carolina, northern Georgia, northern Alabama and eastern Tennessee), while *putnami* is more northern (Kentucky). (6) In the *palmeri-group* the different species occupy different parts of a range that includes Mississippi, western Tennessee, Arkansas, Indian Territory and northeastern Texas.

Groups of allied species are often formed by a typical species, which shows a wide range, while the allied species form a fringe on the edge of this range thus representing local forms. This is shown beautifully in the following natural groups: (1) *Rusticus-group:* the typical form is *rusticus*, the local forms at the edge of its range are: *forceps* (southeast), *neglectus* (west and southwest), *spinosus* and *putnami* (southeast), *hylas* (south), *medius* (south); probably also *erichsonianus* (southeast). (2) *Virilis-group:* the typical form is *virilis*, the local forms are: *meeki*, *longidigitus*, *nais*, *pilosus*, all in the southwest. (3) *Bartoni-section: bartoni* is the typical form, the local forms of it are: *acuminatus* (southeast), *latimanus* (south and southwest); in this section also a mountain form has developed within the range (*longulus*), and varieties are found in the southern section of the range, as well as at its northwestern edge. (4) *C. monongalensis* is a local form developed at the northwestern edge of the range of *C. carolinus*. (5) In the *diogenes-section*, at least one species, *C. uhleri*, seems to be a local form of the widely distributed *C. diogenes*, developed at the eastern extremity of its range.

More or less closely allied species, occupying the same or nearly the same territory, generally possess different habits. In most of the species, we do not know much about their habits, but a few remarkable cases may be mentioned. (1) *C. virilis* and *C. immunis*, although sharply separated, are rather closely allied, and occupy large identical tracts of the central states. We know that *C. virilis* prefers running water with stony bottom, while *C. immunis* is a pond and ditch form (see above, p. 117). (2) *C. monongalensis* inhabits, in western Pennsylvania, almost the same territory that is occupied by *C. diogenes*. The first, however, belongs to the hills, the second to the lowlands (see Ortmann, *Ann. Carnegie Mus.*, v. 3, p. 400).

The various drainage systems have a different effect upon the species of the different subgenera, which is apparently due to fundamental differences in their habits. (1) *Bartonius* is preëminently a mountain-stream group. It goes up into the smallest streams, up to their very sources. In this region, changes of drainage, due to piracy, are common, and rather the rule than the exception, and thus the species quite generally occupy the headwaters of streams running in different directions from the divides. This is exampled by the distribution of the following species: *extraneus*, *bartoni*, *longulus*, *latimanus*, *carolinus*, and probably also by *diogenes*. (See Adams, "Migration of Divides," in *Americ. Natural.*, 35, 1901, p. 844). (2) The *blandingi-section* belongs originally to the lowlands of ths Gulf and Atlantic plain. Here removal of barriers largely has taken place, and thus the species of this group belong to the drainages of different coast rivers, for instance: *lecontei blandingi*, *clarki*, *troglodytes*, *alleni*. (See Adams, *ibid.*, p. 842: "In a country approaching base-level a wide distribution of the fauna will be facilitated.") (3) The subgenus *Faxonius* belongs to the great rivers of the interior basin, and does not ascend far into the headwaters, at least in the mountainous regions, and also does not descend far toward the coastal plain. Consequently, the drainage systems being more permanent, the distribution of these species is more closely connected with the latter. We may, perhaps, compare this — in a very general way — with the period of maximum roughness of Adams (*l. c.*), although this does not hold good for all of this immense region. Indeed, there are important exceptions, and the subgenus has crossed over into the lake-drainage (*C. propinquus*, *obscurus*, *rusticus*, *virilis*, *immunis*), and even into the Hudson Bay drainage (*C. virilis*). This has been brought about, apparently, by extensive shifting of divides, and we know positively, that this has taken place in great style during and after glacial times. The eastern mountains (Appalachian system) have formed a sharper barrier, but also here certain species have been able to cross: in ancient times *C. limosus*, in more recent times *C. obscurus* (see Ortmann, *Ann. Carn. Mus.*, v. 3, p. 406). The most interesting region is at the southern extremity of the Appalachian system, as we shall presently see.

Very important drainage changes, that have taken place in the southern Appalachian system, are clearly indicated by the distribution of crayfishes, and tend to confirm the results obtained by Simpson and Adams for the freshwater mollusks (see above p. 116). In the region of the Alabama River drainage and that of the Tennessee River, we had at a certain time, a large river running to the South, the Appalachian River, the upper course of which was deflected toward the Northwest, forming the present Tennessee River. The former unity of the drainage system is indicated by identical or closely allied species found now in both systems. The following species illustrate this: *C. erichsonianus, extraneus, jordani, latimanus*, and possibly others. Further investigations of the conditions present in these regions are very desirable.

This is, I think, a rather satisfactory outline-sketch of the distribution of the genus *Cambarus* over the United States. But it is only a sketch, and more detailed investigations are much needed. We see that the migrations of the different groups are very complex, the directions of the migrations crossing at various angles, often being directly opposed to each other. (See map, plate III.)

Further, we are to emphasize, that our knowledge is by no means complete with regard to the distributional facts. There is hardly a single case, where the actual boundaries of a species are known. We have a large number of locality-records, and by plotting them on a map, we obtained a general idea of the range of the different species, but rarely we know the exact limits, and nobody has ever tried to ascertain these, except the present writer in a very limited region, in western Pennsylvania (see *Ann. Carnegie Mus.*, v. 3, 1905). But this ought to be done by all means, and there is no doubt, that very interesting results will be obtained.

It may be remarked in conclusion, that I do not think that a number of reported localities for certain species are trustworthy.

It is astonishing how easy records and museums specimens become mixed up, and a number of localities which are given bona fide by various authors are very questionable. In the following, I put together those records, that appear — at least to me — doubtful or in need of confirmation. At the same time, a number of new records is given which have been made use of in the above pages.

C. blandingi (Harl.).

New Localities. — Millpond at Plainsboro, Middlesex Co., New Jersey, coll. by the writer (Carn. Mus.). — This species is further abundant in the millpond of Grover's Mills, Princeton Junction, Mercer Co., N. J. (seen by the writer), and is rare in the Delaware-Raritan Canal, at Aquæduct near Princeton, Mercer Co., N. J. (seen by the writer).

C. clarki Gir.

New locality. —Devils River, Val Verde Co., Texas, coll. by H. A. Pilsbry, 1903 (specimens in Philadelphia Acad. and Carn. Mus.).

C. limosus (Raf.).

New localities. — Stony Brook, Princeton, Mercer Co., N. J., coll. by the writer, May 30 and Sept., 1898 (Carn. Mus.). — Delaware-Raritan Canal, at Aquæduct near Princeton, Mercer Co., N. J., coll. by the writer, Jan., 1899 (Carn. Mus.). — Delaware River, North Cramer Hill, Camden Co., N. J., coll. by the writer, Sept. 18, 1904 (Carn. Mus.). — Collected by the writer at the following new places in Eastern Pennsylvania in September, 1904: Delaware River, Torresdale Fish Hatchery, Torresdale, Philadelphia Co.; Marcus Hook Creek, Marcus Hook, Delaware Co.; Little Neshaminy Creek, Grenoble, Bucks Co.; Delaware River, New Hope, Bucks Co.; Schuylkill River, West Manayunk, Montgomery Co. (Carn. Mus.). — Further: Tributary of Brandywine Creek, Chadds Ford Junction, Chester Co., Pa. (Acad. Philad.). — Delaware River at Holmesburg, Philadelphia Co., Pa. (Acad. Philad. and Carn. Mus.). — Gettysburg, Adams, Co., Pa., coll. by H. A. Pilsbry (Acad. Philad.). — Potomac River, Cherry Run, Morgan Co., W. Va., coll. by the writer, Sept. 23, 1904 (Carn. Mus.).

Doubtful and spurious older records. — Hagen gives, in 1870, Niagara (L. Agassiz); Lake Erie; New York (Mr. Pike); and Pittsburg. Faxon (1885) drops New York and Pittsburg, but again gives Niagara (" there is no doubt of the correctness of the determination "), and Lake Erie (Peabody Ac. Sci.). In 1890, Faxon says of the latter specimens, that they " are too small to determine with certainty." He further gives, in 1885, Lake Superior (Boston Soc. Nat. Hist.). I do not entertain the slightest doubt that all these localities are wrong. As to Niagara, which is founded upon the authority of L. Agassiz, we only have to consider that the same locality upon the same authority is given also for *C. propinquus*, and it is quite probable, that specimens of *C. limosus* were put by mistake into a jar containing *C. propinquus*. As to Lake Erie and Lake Superior, some other species may be intended, or a similar mistake has been made : I do not believe, most emphatically, that this species is found in the lake-region. With regard to the absence of *C. limosus* in the state of New York, we possess the testimony of De Kay (Zoöl. N. Y., 6, 1844, p. 23) : " I have searched for it (*Astacus affinis*) without success in the tributaries of that stream (Delaware) within the limits of this State."

C. propinquus Gir.

New Localities. — Lake Erie, Lorain Co., Ohio, Lorain gill nets. May 1, 1892, coll. by H. Warden (Mus. Oberlin). These specimens from the lake are the true *C. propinquus*, while all other specimens from the tributaries of the lake in Lorain Co., Ohio, belong to *propinquus sanborni*, see below. Crooked Lake, Oden near Petoskey, Emmet Co., Mich., coll. by E. B. Williamson, Sept. 1, 1904 (Carn. Mus.). This is the northernmost exact locality known, and is very near to a locality recorded by Ward (Bull. Mich. Fish Comm., 6, 1896, p. 15), but not recorded by Faxon, namely: Lake Michigan and Pine Lake at Charlevoix, Charlevoix Co., Mich.

Doubtful Locality. — The latter localities in northern Michigan render it possible that the old records of Lake Superior, given by Hagen on the authority of L. Agassiz, may be correct. But since to L. Agassiz also the record of *C. rusticus* and *virilis* for Lake Superior are attributed, we have again several species mixed up, and it is better to wait for a confirmation.

C. propinquus sanborni Fax.

New Localities. — Oberlin, Lorain Co., Ohio, is the type-locality (Faxon) for this form. I have seen it (Mus. Oberlin) from the following localities in this region and the state of Ohio: Waterworks reservoir, Oberlin, and Plum Creek, Oberlin; further: Vermillion River, Beaver Creek, French Creek, all in Lorain Co.; Killbuck Creek, Creston, Wayne Co.; Tuscarawas River, Gnadenhutten, Tuscarawas Co. The latter two localities belong to the Ohio drainage, while the rest is lake drainage. This variety forms a morphological link between *C. propinquus typicus* and *C. obscurus*, and seems to be intermediate also in its range.

C. rusticus Gir.

The locality Lake Superior (L. Agassiz) given by Hagen (1870) needs confirmation. As I have shown elsewhere (Ann. Car. Mus., v. 3, 1905, p. 387), the locality Pittsburgh is wrong.

C. neglectus Fax.

New Locality.—Rogers, Benton Co., Arkansas, coll. by H. A. Pilsbry, March 25, 1903 (Acad. Philad. and Carn. Mus.).

C. putnami Fax.

New Locality.—Rockcastle River, Livingston, Rockcastle Co., Ky., coll. by E. B. Williamson, June 21, 1904 (Carn. Mus.). (See Williamson, Ohio Natural., 5, 1905, p. 311.)

C. virilis Hag.

New Locality.—Sandy Lake, Ontario, Canada, coll. by G. H. Clapp (Carn. Mus.). This species has been reported by Ward (Bull. Mich. Fish Comm., 6, 1896, p. 15) from Lake Michigan and Pine Lake, Charlevoix Co., Mich.

The locality Lake Superior, given on the authority of L. Agassiz by Hagen (1870), has been confirmed by Faxon (1885) on the authority of C. L. Herrick, and falls within the known range of the species.

Doubtful Records.—Lake George, N. Y. (L. Agassiz) has been recorded by Faxon (1885) with a ? . It surely is very doubtful.

Faxon also mentions this species from Laramie City in Wyoming; this may be correct, but needs confirmation. He records it further from near Bridgeport, Jackson Co., in northern Alabama, in the Tennessee drainage (U. S. Mus.); I seriously doubt the correct ness of this locality, since it is the only one east of the line formed by the Mississippi and Ohio rivers, and is far remote from the rest of the range.

C. immunis Hag.

New Localties.—Lamoni, Decatur Co., Iowa, coll. by J. B. Hatcher (Carn. Mus.). This species is also found in northern

Ohio, as first indicated by Osburn and Williamson (6 Ann. Rep. Ohio Ac. Sci., 1898, p. 21), in Sandusky, Erie, and Lorain Cos., and in Lake Erie. I have seen specimens (Mus. Oberlin) from Huron River, Huron, Erie Co., and from Oberlin, Lorain Co. (Waterworks Reservoir and Plum Creek).

Doubtful Records. — Hagen (1870) gives Huntsville, Madison Co., northern Alabama. This is possibly not this species, at any rate it is "not normal" (Faxon, 1885, p. 100). The locality is too far separated from the rest of the range, to be accepted without hesitation.

Faxon (1885) gives: New York (L. A. Lee); Laramie, Wyoming (U. S. Mus.); Orizaba, Mexico (U. S. Mus.), and further in 1898 he adds: small stream flowing into Oneida Lake, N. Y. The locality in Wyoming may be correct, but we have to try to connect it with the rest of the range, before accepting it. Orizaba, Mexico, is no doubt wrong, and I do not hesitate for a moment to drop it. Oneida Lake in New York seems very strange, since there are no connecting localities with northwestern Ohio. I cannot accept this locality unless verified by unequivocal evidence.

C. palmeri longimanus Fax.

New Locality. — Limestone Gap, Choctaw Mt., Indian Terr., coll. by H. A. Pilsbry (Ac. Philad. and Carn. Mus.).

C. extraneus Hag.

New Locality. — Rockcastle River, Livingston, Rockcastle, Ky., coll. by E. B. Williamson, June 21, 1904 (Carn. Mus.). This is in the Cumberland River drainage; previously, this species was known only from Tennessee, Alabama and Georgia. (See Williamson, Ohio Natural., 5, 1905, p. 310.)

C. bartoni (F.).

New Localities. — Small streams, Princeton, Mercer Co., N. J., coll. by the writer (Carn. Mus.); East Canada Creek, Herkimer Co., N. Y., coll. by R. Ruedemann (Carn. Mus.); Selbysport, Garret Co., Md., coll. by the writer (Carn. Mus.); Cherry Run, Morgan Co., W. Va., coll. by the writer (Carn. Mus.); Greenville, New Castle Co., Del. (Ac. Philad.). The following localities in eastern and central Pennsylvania are represented in the Carnegie Museum (coll. by the writer): Driftwood and Sinnamahoning, Cameron Co.; Keating Summit, Potter Co.; Wills Creek, Mance, Somerset Co.; Cush-Cushion Creek, Indiana Co.; Cresson, Cambria Co.; Ashville, Cambria Co.; Hollidaysburg, Blair Co.;

Wissahickon, Philadelphia Co.; Shoemakersville, Berks Co.; Valley Forge, Chester Co.; Grenoble, Bucks Co.; New Hope, Bucks Co.; West Manayunk, Montgomery Co.; Wallingford, Delaware Co. Other new localities in eastern Pennsylvania are: Headwaters of Loyalsock Creek and Ganoga Lake, Sullivan Co. (Ac. Philad.); Pinegrove, Cumberland Co. (Ac. Philad.).

Doubtful Record. — Lake Superior, given by Hagen on the authority of L. Agassiz, is undoubtedly wrong. As to records of this species from Ohio see *C. bartoni robustus.*

C. bartoni robustus (Hag.).

New Localities. — Small stream tributary to Rockcastle River, Livingston, Rockcastle Co., Ky., coll. by E. B. Williamson, June 21, 1904 (Carn. Mus.). These specimens agree well with young individuals of this variety; adult ones are not in the lot. (See Williamson, Ohio Natural., 5, 1905, p. 310.) Oberlin, Lorain Co., Ohio (Mus. Oberlin). This form was doubtfully reported from Knox Co., Ohio, by Osburn and Williamson (1896). All specimens from Oberlin seen by the writer belong to this variety. The typical form seems to prevail in southern Ohio.

Doubtful Records. — Faxon (1885) gives Decatur, Macon Co., Ill., but this needs confirmation. Further it is doubtful, whether the form called by this name in Maryland and Virginia is identical with the true (northern) *robustus.*

C. bartoni longirostris (Fax.).

Doubtful Record. — Pollard, Escambia Co., Alabama, seems doubtful, since it is close to the Gulf coast, and far away from the original mountain home of this form.

C. latimanus (Lec.).

The locality, Ocean Springs, Miss., is doubtful for the same reason.

C. carolinus Er. (= *dubius* Fax.).

The reported occurrence of this species in Indian Territory (Faxon, 1890) seems strange. It must be looked upon as doubtful till the connection with the rest of the range is established.

C. diogenes Gir.

New localities. — Cooper, Greene Co., Iowa, coll. by J. B. Hatcher (Carn. Mus.); Seaford, Sussex Co., Delaware, coll. by S. N. Rhoads, June 18, 1903 (Ac. Philad. and Carn. Mus.). — Oberlin, Lorain Co., Ohio (Mus. Oberlin). — The specimens from this locality have been mentioned by Osburn and Williamson (1898) as *C. dubius ?*, but they are typical *C. diogenes.*

Doubtful records. — Faxon, 1885, gives Deer Park, Garrett Co., Md. This should be confirmed; according to the writer's experience, *C. carolinus* ought to be expected there. If confirmed, this locality will be highly interesting.

Faxon further gives: Cheyenne, Wyoming, and Clear Lake, Colorado; in both cases the most western extremity of the range of the genus is reached. Harris (Kansas Univ. Quart., 9, 1900, p. 267) gives: Boulder, Colorado. This serves to establish the correctness of the above records, but the connection with the rest of the range must be found (I have not been able to locate Clear Lake in Colorado). The southern localities for *C. diogenes* recorded by Faxon, Monticello, Lawrence Co., Miss., and New Orleans, Louisiana, certainly need further support.

C. argillicola Fax.

New locality. — Oberlin, Lorain Co., Ohio (Mus. Oberlin). — I have seen three specimens from Oberlin (adult and young male, adult female), two of which bear the label: Hovey's Ice house, northeast of Oberlin, coll. by Leuthi, Sept. 29, 1892.

Doubtful records. — The localities, Kinston, N. Carolina, and New Orleans, Louisiana, given by Faxon in 1885 are doubtful, as admitted by himself. The localities given in 1898, Victoria and Brazoria, Texas (U. S. Mus.), most emphatically need confirmation.

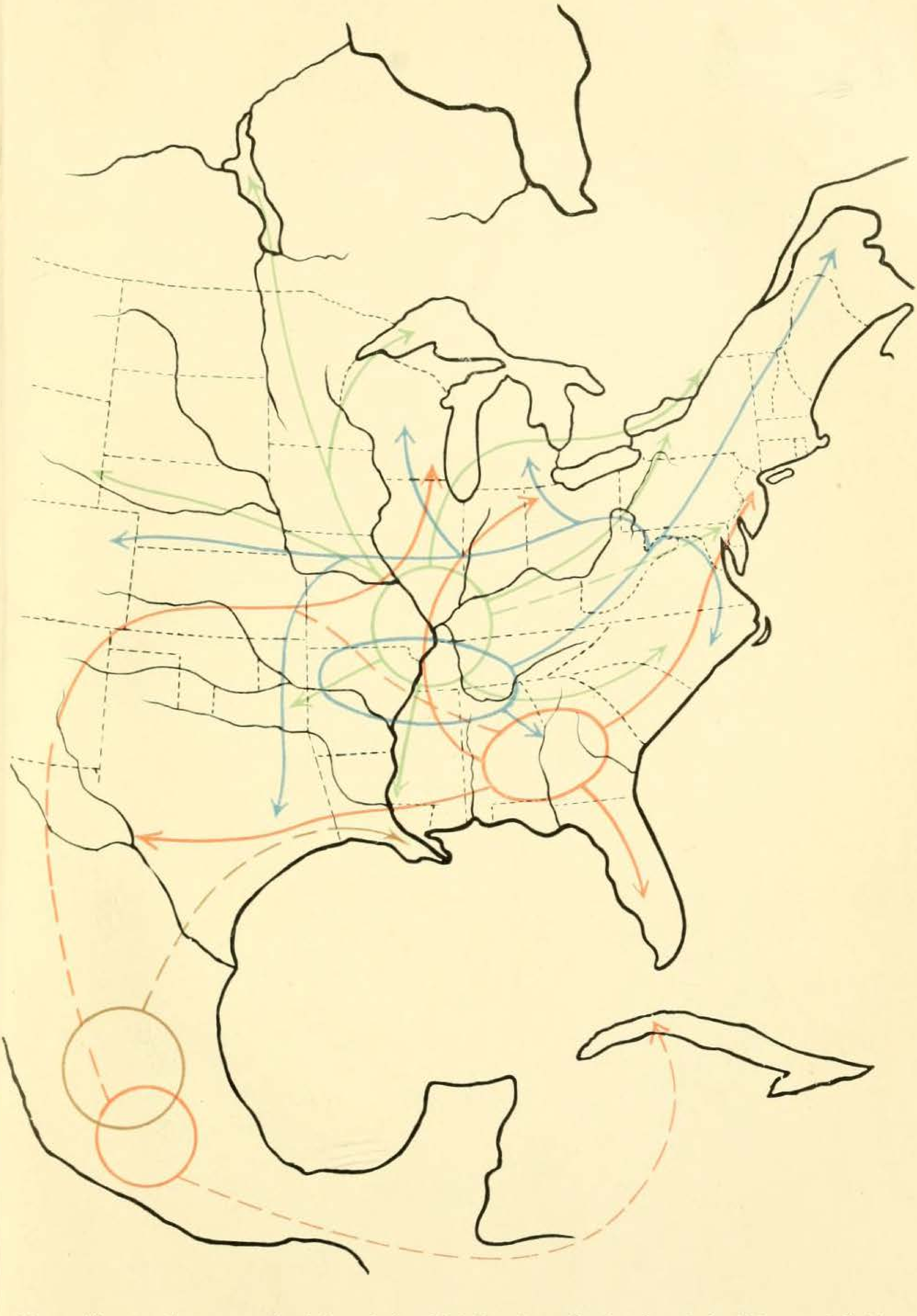
CARNEGIE MUSEUM,
PITTSBURGH, April 7, 1905.

EXPLANATION OF PLATE VIII. III

The plate is introduced to illustrate the *centers of origin*, and the *chief directions of migration* of the different subdivisions of the genus *Cambarus*. Circles or ellipses indicate centers of origin, the lines radiating from these, and ending in an arrow-point, indicate the migration. The different colors mark the different subgenera: *Red, Cambarus; brown, Cambarellus; green, Faxonius; blue, Bartonius.*

It will be remarked that two centers are given for the subgenus *Cambarus*: the one in Mexico marks that of the more primitive forms, the other in Alabama and Georgia, that of the more highly advanced forms (*blandingi-section*). This latter one, as well as the subgenera *Faxonius* and *Bartonius*, took their origin probably from a primitive stock of the subgenus *Cambarus*, immigrated into the southern United States along the broken red line running from Kansas to Alabama.

For further particulars see text, pp. 103, 106, 113, 121, and 124 ff.



Map to illustrate the centers of origin and the chief directions of migration of the different subdivisions of the genus Cambarus.