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PRELIMINARY SURVEY OF THE

AMPHIBIANS

OF THE RIUKIU ISLANDS

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INTRODUCTION

The purpose of this paper is to present a preliminary analysis of the amphibian fauna of the Riukiu Islands, both as to its nature and its origins. The Riukiu Archipelago, lying between Japan proper and Formosa, forms one of the great series of island arcs that fringe the eastern border of the Asiatic continent. Their animal life is especially notable for its considerable differentiation of species that are found nowhere else. This fauna affords a unique opportunity to examine the phenomena of the origin of species in a linear chain of islands of moderate age.

Unfortunately, information concerning the Riukius is either scattered in travelers' accounts or written in Japanese. In the latter case it is almost inaccessible; in the former, it is difficult to locate and assemble. Therefore, in certain instances I have included non-zoological data in greater detail than would be required by the scope of this paper, with the hope that they will facilitate future faunal studies. One case in point is the meteorological data; another is the geologic history.

I wish to acknowledge my indebtedness to the authorities of the California Academy of Sciences and the United States National Museum for the loan of material, and to the authorities of Chicago Natural History Museum for the use of collections and laboratory space. I wish to thank Messrs. David Zaid and Charles A. Wonderley of Philadelphia, Robert Burton of Evanston, Illinois, and James A. Slater of the University of Illinois for specimens collected by them and now in Chicago Natural History Museum. I am also indebted to Mr. D. Dwight Davis and Dr. Rainer Zangerl of Chicago Natural History Museum and Mr. Ernest N. Poll of the University of Chicago for assistance with photographs and to Mrs. Peggy Brown, formerly of Chicago Natural History Museum, for the drawings contained herein. To Messrs. Karl P. Schmidt and Clifford H. Pope of Chicago Natural History Museum, and to my wife, Mary Lee Inger, I wish to extend my gratitude for much helpful advice and criticism.

The Riukiu Islands, situated south of Japan, have been the subject of many investigations in fields ranging from ethnology to

herpetology. The spelling of the name of the archipelago in the papers that have been written about it has been as variable as the points of view of the men who have written them. Most of the early workers referred to the islands as Loo Choo, Liu Chiu, and Liu Kiu. More recently, and especially by the Japanese, they have been known as Ryu Kyu or Riu Kiu, written together more recently as Ryukyu or Riukiu. I am using the last form because it is the one that seems to be most frequently used at the present time.

Herpetological exploration of the Riukius began with the expeditions of Commodore Perry and Captain Rogers to the north Pacific in the 1850's. The type specimens of several of the species reported on in this paper were collected by Rogers' expedition and were described by Hallowell (1860). Between 1860 and the recent war most of the collecting was done by biologists from Japan, which had had possession of the islands during the period. The notable exception was the large collection made for the California Academy of Sciences by Victor Kuhn in 1910. During World War II medical units of the United States Navy made an excellent collection. Smaller series were collected by individual members of the armed forces.

Stejneger's (1907) volume, *The Herpetology of Japan*, contained the first complete account of the herpetofauna of the Riukius. Subsequent to that, a good, though not comprehensive, survey was made by Van Denburgh (1912b). In 1931 both Okada and Tago published their monographs on the frogs and salamanders of the Japanese Empire. It is with these two orders of amphibians that this paper is concerned.

GEOGRAPHY OF THE ISLANDS

The Riukiu Islands extend in an arc convex southeastward from south of Kyushu to a point northeast of Formosa (see Map 1). The numerous islands and islets (about 95) which make up the chain have been divided into groups by Tokunaga (1901) and subsequent geographers. These groups, together with some of the principal islands[1] of each, are as follows, with the groups (after Hanzawa, 1935) in geographic order from north to south:

Tokara (Linshoten) group: Takara, Kotakara.

Oshima group: Amami, Kikaiga, Tokuno, Okierabu.

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[1] Properly the names of the islands bear the suffix *-shima* or *-jima*. For the sake of uniformity and simplicity these suffixes are not used in this report.
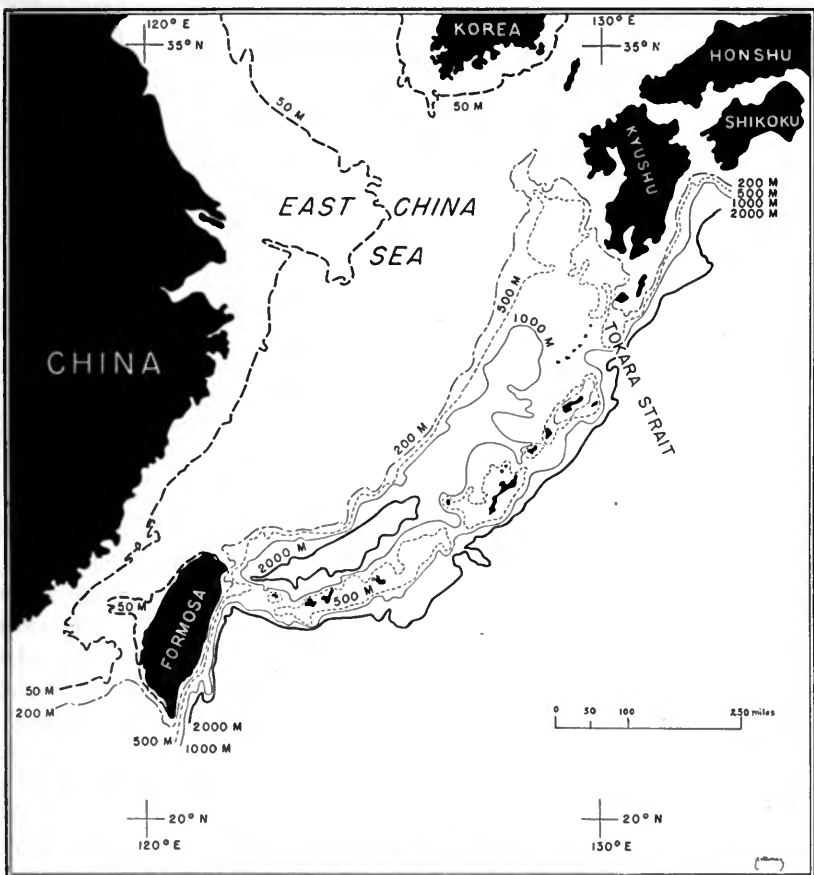
MAP 1. Bathymetric chart of northwest Pacific area.

Okinawa group: Okinawa, Ie, Iheya, Kume, Ke, Tokashiki.
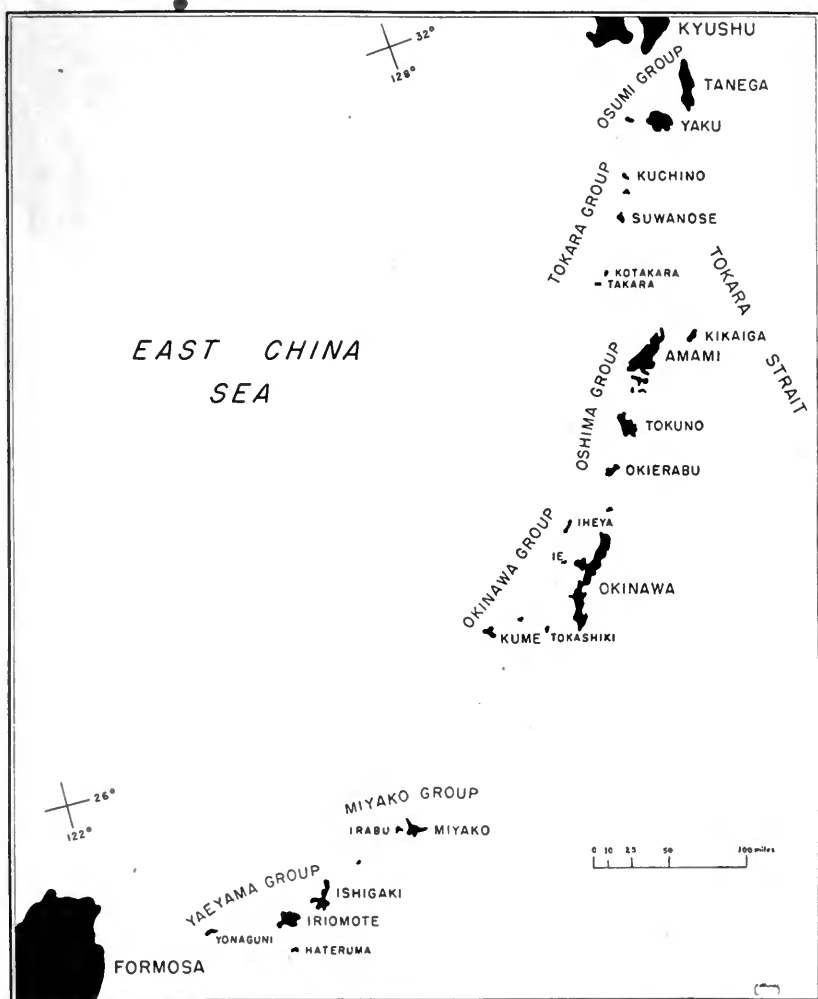
Miyako group: Miyako, Irabu.

Yaeyama group: Ishigaki, Iriomote, Hateruma, Yonaguni.

Map 2 shows these islands in greater detail. Hanzawa included still another group, the Osumi, lying just south of Kyushu. For reasons given below I do not consider that the islands of the Osumi group are part of the Riukius.
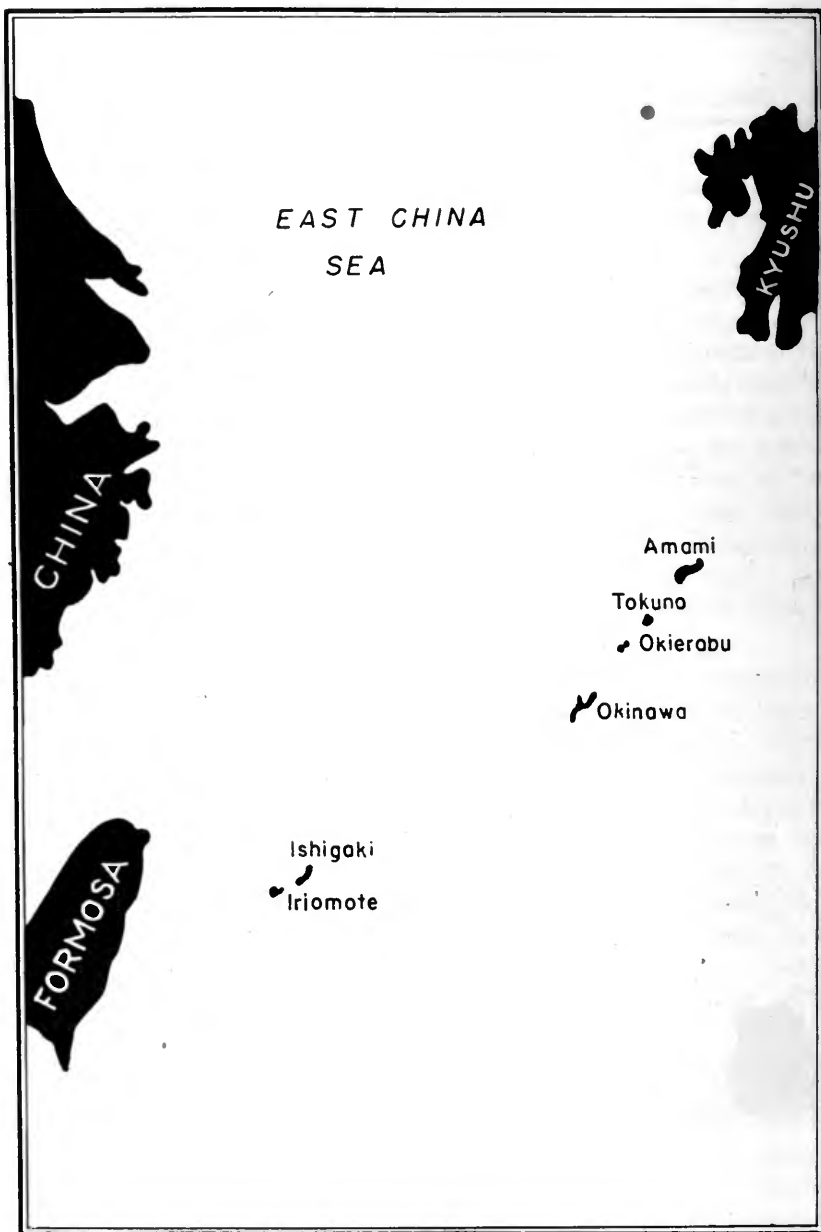
The topography and geology of the region has been worked out in some detail by Koto (1897) and Hanzawa. The account that follows is based largely upon these two authors, supplemented by the correlative work of Yabe and Aoki (1923). The islands may be divided into two curves. The inner or western curve, comprising the Tokara group, Kume, and several small islands lying to the northeast of Formosa, is of volcanic origin. These islands rise out of the trough at the eastern rim of the East China Sea. The outer curve includes all of the other islands. These are made up of Proterozoic, Paleozoic, and igneous rocks or Tertiary and younger rocks. In either case the islands of the outer curve are remnants of the Riukiu cordillera.

The different groups are separated from one another by sea basins from 400 to 2,000 meters in depth. The deepest of these, the Tokara Strait, lies between Amami and the Osumi group. The Osumi group is but 40 km. south of Kyushu and lies on the same submarine platform. The maximum depth of the channel between Kyushu and the Osumi group, 200 meters, is considerably less than the Tokara Strait. Thus, the Osumi group is more closely related to the Japanese Islands than to the Riukius on the basis of topography. This relationship is emphasized by the fauna, as will be shown later. The Okinawa group is separated from the Oshima group by a basin 800 meters deep, and from the Miyako by one slightly under 1,000 meters deep. The Miyako group is divided from the Yaeyama by a strait only 400 meters in depth. Formosa and the Yaeyama group are separated by a basin reaching 800 meters. The trough out of which the volcanic islands of the Tokara group rise is 800 meters deep and is directed north-northeast and south-southwest between the Tokaras and Amami. According to Koto, these straits, with the exception of the last, are developed across the strike of the Paleozoic rocks of the cordillera and are probably the result of faults.

The islands vary considerably in size, the largest, Okinawa, being 110 km. and 20 km. in its greatest dimensions. The maximum

KYUSHU

OSUMI GROUP

TANEGA

YAKU

TOKARA GROUP

KUCHINO

SUWANOSE

KOTAKARA
TAKARA

TOKARA STRAIT

OSHIMA GROUP

KIKAIGA
AMAMI

EAST CHINA
SEA

TOKUNO

OKIERABU

OKINAWA GROUP

IHEYA

IE

OKINAWA

KUME TOKASHIKI

26°
122°

MIYAKO GROUP

IRABU MIYAKO

0 10 25 50 100 miles

YAEYAMA GROUP

ISHIGAKI

IRIOMOTE

YONAGUNI HATERUMA

FORMOSA

32°
128°

MAP 2. Map showing islands of Riukiu Archipelago.

EAST CHINA
SEA

KYUSHU

CHINA

Amami

Tokuno

Okierabu

Okinawa

FORMOSA

Ishigaki

Iriomote

MAP 3. Probable land area of the Riukiu Islands at the climax of the land submergence between the Oligocene and the Pliocene. Present areas of China, Formosa, and Kyushu shown in black.

length and width of Amami are 57 km. and 30 km., of Miyako 25 km. and 15 km., of Ishigaki 35 km. and 20 km. The smallest islets are less than one square kilometer. In relief the islands also show much variation. Some, like Miyako, are relatively flat, with one or two low ridges. Iriomote consists of many flat-topped ridges. Ishigaki and Okinawa are mountainous in parts and relatively flat in others. The greatest elevation is 690 meters, on Amami.

GEOLOGIC HISTORY OF THE ISLANDS

The Riukiu cordillera arose in the late Permian or early Mesozoic Era. The history of the islands between the Permian and upper Eocene is uncertain. Nevertheless, it is probable that during that interval the cordillera was broken into a number of mountain masses by erosion and faulting. Subsequent to the Eocene there have been many fluctuations in sea level great enough to alter radically the area available for habitation by land animals. In the first of these fluctuations the islands were inundated from the upper Eocene through the lower Oligocene (Yabe and Aoki, 1923; Hanzawa, 1935). Only the Yaeyama group shows direct evidence of submergence at that time. The land rose during the middle and upper Oligocene.

Next began the most extensive submergence in the northwest Pacific since the end of the Paleozoic. Apparently only the highest points of Amami, Tokuno, Okierabu, Okinawa, Ishigaki, and Iriomote were above sea level. Toward the end of this stage, in the middle Pliocene, volcanic activity broke out. Hanzawa implied that the Tokara group owes its origin to this volcanism. At the height of the land emergence that followed, sea bottom that is now at a depth of 700 meters was raised above sea level (Yabe, 1929a, b). Thus during the late Pliocene the distance between the continent and the center of the Riukiu curve could not have exceeded seventy miles. This figure was determined by measuring the distance between the 500-meter submarine contours on Map 1. At this time the Riukius formed a more or less continuous peninsula projecting from the Formosa area.

Another period of inundation followed, during which only the tops of Takara, Kotakara, Amami, Tokuno, Okierabu, Okinawa, Iheya, Kume, Tokashiki, Ishigaki, and Iriomote remained above sea level. When the land arose in the earliest Pleistocene, Takara and Kotakara were united as a single island, as were all of the islands in each of the other groups. Hanzawa stated that the Oshima and Okinawa groups were connected, as were the Miyako and Yaeyama

groups. However, that would imply an emergence at least as great as that of the late Pliocene unless the channels separating the groups were not as deep then as now. Hanzawa also stated that in all probability the latest tectonic movements have given the channels their present depth.

The islands were once more inundated (early-middle Pleistocene) except for the tops of the islands listed in the preceding paragraph. In the following land emergence the larger islands were connected with their surrounding islets. Subsequent shifts in sea level have not exceeded 20 meters and have resulted in the present conformation of the islands.

In summary then, since the Eocene there have been three stages when the Riukius could have had direct land connections with Asia through Formosa: during the Oligocene, the late Pliocene, and the early Pleistocene. The entire Miyako group, Hateruma and Yonaguni in the Yaeyama group, Kume and most of the lesser islands in the Okinawa group, and Kikaiga in the Oshima group seem to have been most subject to inundation during the stages of land submergence. Maps 3 and 4 illustrate different stages in the geologic history of the Riukiu cordillera.

CLIMATE OF THE ISLANDS

From the standpoint of the physical requirements of life, the climate of the Riukiu Islands is almost ideal. The following tables are adapted from Simon (1914):

MONTHLY AVERAGE TEMPERATURES AT FOUR STATIONS

Average temperatures in degrees Fahrenheit
Maxima and minima in degrees Centigrade

	Kyushu	Amami	Okinawa	Formosa
January.........	44.6 (7 C)	58.8	61.7	62.1
February........	44.6	57.2 (14 C)	59.9 (15.5 C)	57.7 (14.3 C)
March..........	51.1	62.3	64.8	62.3
April..........	59.5	67.7	70.0	68.4
May............	65.3	71.8	74.3	74.3
June...........	71.1	76.6	78.4	78.3
July...........	78.1	81.0	82.0 (27.8 C)	81.5 (27.5 C)
August.........	79.5 (26.4 C)	81.0 (27.2 C)	81.9	81.1
September......	75.2	78.4	79.7	78.4
October........	66.2	72.9	75.0	73.4
November......	56.7	66.9	69.4	67.6
December.......	47.8	61.0	63.7	62.6
Number of years observed......	25	10	10	9
Positions of stations.........	31° 35′ N. 130° 33′ E.	28° 23′ N. 120° 30′ E.	26° 13′ N. 127° 41′ E.	25° 9′ N. 121° 45′ E.
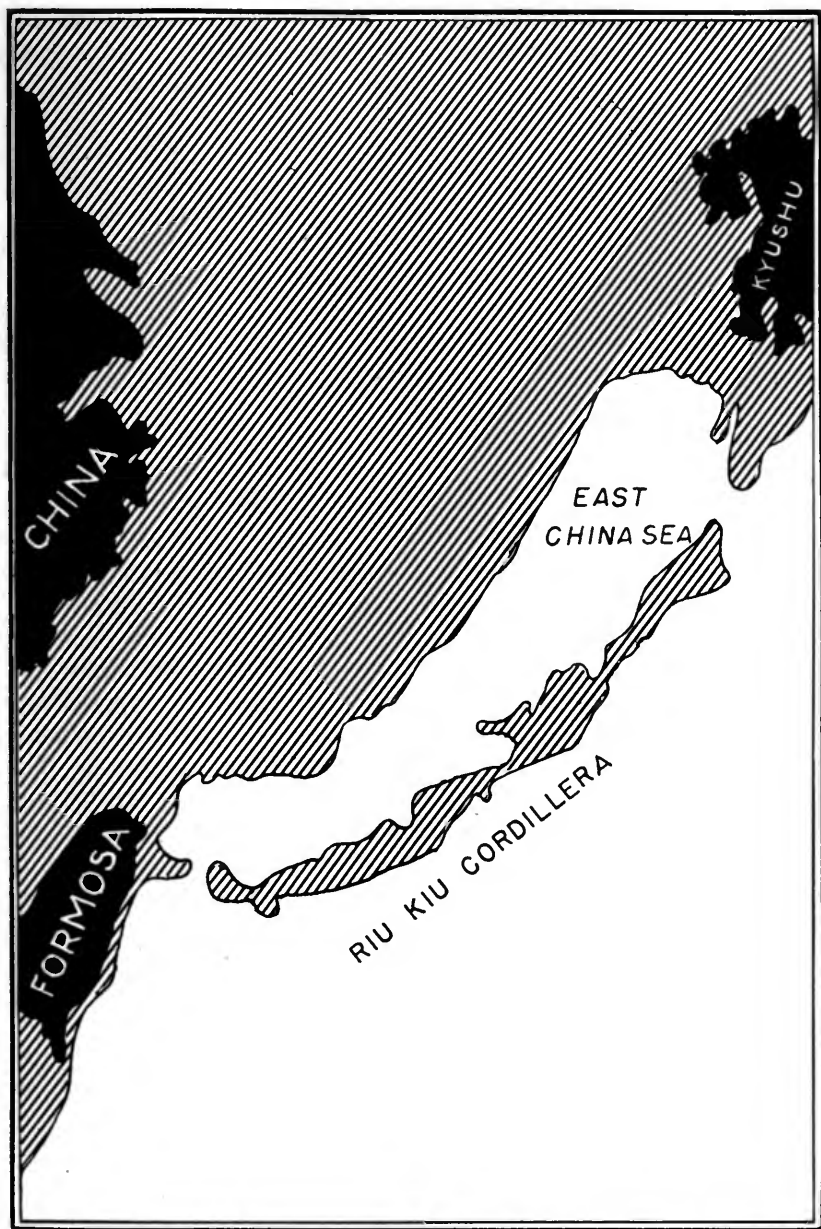
MAP 4. Probable maximum extension of land in late Pliocene. Present areas of China, Formosa, and Kyushu shown in black.

AVERAGE MONTHLY RAINFALL IN INCHES IN AMAMI AND OKINAWA

Positions of stations same as in table on page 304

	Amami	Okinawa
January	9.0	5.9
February	6.1	4.4
March	9.2	6.0
April	9.8	5.5
May	17.4	8.2
June	19.0	11.6
July	10.3	7.4
August	7.8	9.0
September	11.2	7.4
October	12.9	6.7
November	6.9	6.0
December	6.9	5.2
Total	126.5 (3213 mm.)	83.3 (2115 mm.)
Number of years observed	5	10

FLORA OF THE ISLANDS

Analyses of the flora of the Riukiu Islands have been made by Warburg (1890), Wilson (1920), and Masamune (1934, 1935). The best picture of the woody vegetation was given by Wilson: "In general the ligneous vegetation of the Liu Kiu Archipelago consists of a littoral fringe of plants wide-spread in warm temperate and sub-tropical regions. On the mountains are found a comparatively small number of Japanese and a considerable number of endemic species. Evergreen . . . is a marked feature of the vegetation. The presence of mangrove-like trees and the endemic *Cycas revoluta* and *Pinus luchuensis* are the three plants which give character to the vegetation." The pine, the commonest tree from sea level to mountain top, forms pure stands that usually have dense under-growths of evergreen shrubs, small palms, and the cycad. The palms accentuate the tropical relations of the flora. The coral fringes and sea cliffs frequently bear heavy growths of the cycad. Generally the mountains are wooded. The lower levels are under cultivation, principally with rice, sweet potatoes, and sugar cane. The extensive rice fields, of course, form a very important ecological niche for the amphibia.

Of the 351 species of woody plants found by Wilson in the Riukius, seventy-one are endemic. As might be expected, the flora of the Oshima group shows more affinities to the flora of Japan than does that of the southern islands. Interestingly enough, the Tokara Strait seems to have the same significance for the woody vegetation that it does for the fauna. As Wilson pointed out, most of the typical

ligneous plants of Japan reach their southern limit in the Osumi group lying on the north side of the strait.

FAUNAL ANALYSIS
Oriental Species

The amphibian fauna of the Riukius is made up primarily of two elements: endemic forms (derived presumably from Oriental species) and Oriental species that reach the islands without changes regarded as of specific grade. The following species are part of the general Oriental fauna: *Microhyla ornata, Rana limnocharis, Rhacophorus schlegelii, Rhacophorus eiffingeri, Rhacophorus japonicus.* *Microhyla ornata* is found in China, Formosa, and southeastern Asia, as well as the Riukius. *Rana limnocharis,* generally distributed in the East Indies, southeastern Asia, and China, is one of the few Oriental species reaching Japan. Outside of the Riukius *Rhacophorus japonicus* has been reported from Formosa only. Though *R. schlegelii* and *R. eiffingeri* either occur in Japan or are closely related to Japanese forms, the distribution of the genus is southern, being found in the East Indies, southeastern Asia, and Madagascar. *Rhacophorus* reaches its northern limit (approximately 40° N. Lat.) in Japan.

Endemic Species

Approximately one-half of the amphibian species of the Riukius are endemic. They are: Caudata: *Triturus ensicaudus, Tylototriton andersoni;* Salientia: *Hyla hallowelli, Rana holsti, R. subaspera, R. ishikawae, R. narina, R. namiyei, R. okinavana.* Of these, five show affinities to contemporary Oriental species. Only four other species of *Tylototriton* are known, and they are from isolated localities in southern and western China. *Hyla hallowelli* is similar to *chinensis* of Formosa (Van Denburgh, 1912b) and *Rana namiyei* to *kuhlii* of Formosa and southern China. Stejneger (1907) cites the relationships, which are open to question, of *R. narina* to *everetti* of the Philippines and of *R. okinavana* to *lateralis* of southeastern Asia. *Triturus ensicaudus* is closely related to *T. pyrrhogaster* of Japan. The genus is Holarctic in distribution. The remaining three species, *Rana subaspera, R. holsti,* and *R. ishikawae,* do not have clearly defined geographic relations.

The extent of endemism in the fauna of the islands is reflected in the inter-island differences of species endemic to the Riukiu chain, and even in the more widespread, relatively undifferentiated forms.

Illustrative of this is the local differentiation of *Rhacophorus schlegelii*. In this species the populations on the various groups of islands differ with respect to coloration, texture of skin, and body proportions. Also, within an island group there may be intra-specific differences such as exist between the Amami and Kikaiga populations of *Hyla hallowelli*. These variations are discussed in some detail under each species. However, it should be said that they may be qualitative, as in changes of color pattern in *Rhacophorus schlegelii*, or quantitative, as in the differences of body proportions in *Hyla hallowelli*. In *Rana limnocharis*, as in *Rhacophorus schlegelii*, there are inter-island differences in coloration and body proportions.

At this juncture it would be well to point out the suitability of the Riukius as a "natural laboratory." The one-dimensional range afforded by the elongate and narrow Riukiu chain has a decided effect on its populations. In this type of range, differentiation increases much more rapidly with increasing distance than in a two-dimensional range. The change in rate of differentiation is brought about by the reduction in the effective size of the population (Wright, 1940). The breaking up of the Riukiu cordillera would result in the introduction of discontinuities in any existing clines. Once the isolation produced by the division of the cordillera was established, local selection could act more effectively and would add to the increase in the rate of differentiation. Also, as the cordillera became divided into smaller units, the resulting fragmented populations would tend to show the Sewall Wright drift effect (Wright, 1940), with non-adaptive added to the increasing adaptive differentiation.

Although I am at present unable to demonstrate the adaptive nature of any inter-island variation that I have found, it is not unreasonable to expect that further intensive investigation will reveal inter-island adaptive differentiation. In *Rana holsti* and *R. subaspera* the metacarpal spine, which is of obvious value to the male during amplexus (see p. 328), presents a case in which differentiation has been adaptive. As an example of non-adaptive differentiation I offer the light mid-dorsal line found in *R. limnocharis* of Ishigaki but not in *limnocharis* of Okinawa. Investigation of the smaller islets that are not inhabited by man should reveal more examples of both the intensification of local selection and the increase of non-adaptive mutations due to the drift effect.

Palearctic Species

Bufo bufo gargarizans, with its distribution limited to Miyako, is the only strictly Palearctic form in the Riukius. The presence

of this toad on only one island and its similarity to *gargarizans* of China indicate that it may be a recent introduction. The fact that it is restricted to Miyako eliminates the possibility of its being the remnant of a form widely distributed in the archipelago at one time; for, as I have pointed out earlier, Miyako has been subject to complete inundation and has been, therefore, an unsatisfactory habitat over a long period of time.

In the Osumi group are found such Palearctic species as *Hyla arborea japonica, Rana japonica, R. nigromaculata, R. rugosa,* and *R. temporaria.* All of these frogs occur in Japan but none south of the Tokara Strait. None of the species found in the Riukius (as here restricted) has been recorded from the Osumi group, even though two are found in Japan. The split in the frog fauna at the Tokara Strait is parallel to the separation of Palearctic and Oriental mammalian faunas. This faunal division, known as Watase's Line (Okada, 1931), coincides with the geographic division mentioned previously. Apparently the channel between the Osumis and the Oshima group has proven a barrier to the southward migration of northern forms.

FAUNAL ORIGINS

The distribution of the non-endemic species and that of forms allied to the endemic ones indicate a southern origin for the amphibian fauna of the Riukius. As stated above, there were at least three periods of land emergence when the islands might have been connected with the continent. An examination of the bathymetric data of Map 1 indicates that less change in sea level would be required to link Formosa with the southern Riukius than would be needed to link the islands with Japan. Thus Formosa is a more probable "bridge" to the archipelago than is Japan.

An alternative mode of dispersal, by no means exclusive of the possibility of emigration by land from Formosa, is accidental transportation (waifing) on drifting masses of vegetation. If this method of dispersal is utilized at all by amphibians, it is of greatest importance where the water gap to be crossed is the least. On Map 4 is shown the probable maximum extension of land during the Pliocene. At this stage the easternmost points of the continent were not more than seventy miles from parts of the Riukius. Under this circumstance waifing from the continent becomes likely. It is apparent that waifing from Formosa, if there were no direct land connection, would also be facilitated at this time.

The importance of accidental transportation can be brought out by a comparison of the frog faunas of Japan and the Riukius. Such Oriental (and Riukiu) species as *Rana limnocharis* and *Rhacophorus schlegelii* are found in Japan. The bulk of the Japanese fauna, however, is composed of Palearctic forms, for example, *Rana nigromaculata*, *R. japonica*, *R. temporaria*, *Hyla arborea japonica*, and *Bufo bufo japonicus*. In the coastal provinces of China, *Rana nigromaculata* ranges as far south as Kwangtung, *R. japonica* as far as Fukien, and *Bufo bufo* as far as Kwangtung and even into Formosa. These ranges, which extend farther south than the Riukiu Archipelago, indicate that these species can tolerate the climatic conditions of the Riukius. *Rana limnocharis*, in China, is not found north of Shantung, approximately the latitude of southern Honshu. *Rhacophorus schlegelii* does not occur on the continent at all. The question arises as to the manner in which these last two species reached Japan. If they did not enter by way of Korea—and their present ranges place this avenue in doubt—perhaps they used a land bridge between the northern Riukius and the Osumi group; but this suggestion can be discarded at once because it assumes that the Palearctic species, which are not present in the archipelago, could not utilize the same land bridge to expand their ranges southward. The only explanation remaining is waifing: that *Rana limnocharis* and *Rhacophorus schlegelii* managed to reach Japan by accidental transportation on rafts of vegetation. Again, the Palearctic species of Japan must be considered. The waifing explanation still assumes some selective mechanism that the land bridge hypothesis could not supply. But in this case natural selective mechanisms exist, for the ocean currents, prevailing winds, and typhoon tracks along the coast of Asia are all directed northward. All three physical factors are obviously related to waifing and all are favorable to the idea presented above. Here, then, is a likely explanation for the significance of Watase's Line to the distribution of amphibians and mammals.

The direction of water and wind currents lends further support to the idea of a southern origin for the frog fauna of the Riukiu Islands. The presence of the salamander *Tylototriton* in the archipelago may also be the result of waifing from Formosa or southern China. The only form whose distribution seems to defy such an explanation is *Triturus ensicaudus*.

The differences in the distribution of the various forms is of significance to the study of the order in which they reached the archipelago. Generally, the endemic forms must be said to have entered

the islands earlier than those found also on the continent.   Forms found on the periphery of continents are frequently primitive.   The Riukius present an almost ideally peripheral area with respect to Asia.   Island forms are also released from selection pressures to which continental species are subject.   Given primitive forms and reduced selection pressure, it follows that the longer an island form is isolated the less able it is to expand its range in the face of immigrations of continental ones.   It is also true that the longer a species exists in an elongate and narrow range such as is provided by the Riukiu chain the more likely are discontinuities to develop in the distribution. In a chain of islands this will be a direct result of the fluctuations in sea level over a long period of time (see p. 303 ff.).   Therefore, from the preceding observations, an endemic form, found only on certain of the islands, probably has been in the archipelago longer than one found throughout the length of the chain and on the continent as well.

To utilize this idea, I have divided the frog fauna as follows:

Limited dispersal	Moderate dispersal	Wide dispersal
Hyla hallowelli	*Rhacophorus eiffingeri*	*Microhyla ornata*
Rana holsti	*Rhacophorus japonicus*	*Rana limnocharis*
Rana ishikawae	*Rhacophorus schlegelii*	
Rana narina		
Rana namiyei		
Rana okinavana		
Rana subaspera		

By limited dispersal is meant distribution limited to one or two island groups in the Riukiu chain.   By moderate dispersal is meant dispersal in more than two island groups, plus Formosa and/or Japan.   The final category, wide dispersal, indicates dispersal throughout the archipelago plus southeastern Asia.   If the hypothesis that restricted range is an indication of early entry is true, the "limited" species were in the early wave (or waves) of immigration, whereas the others entered later.   I am not prepared to distinguish between the last two groups of species.

It is possible to see the effect of fluctuations in sea level on the distribution.   *Rana okinavana*, for example, has been recorded from Ishigaki in the south and Okinawa in the north.   For this discussion I assume that the localities are correct and that exploration on Miyako will fail to reveal *okinavana* there.   The Miyako group (see Map 2) lies between Okinawa and Ishigaki, and geologic investigation of the Miyako group has shown that these islands are completely covered by early Pleistocene limestone formations.   The islands must have been entirely under water when those rocks were deposited,

and their populations of frogs would thus have been destroyed. If *okinavana* had a continuous distribution in the archipelago before the early Pleistocene, the subsequent changes in sea level would have interrupted that distribution by destroying at least the Miyako population. The distribution of *R. narina*, found in the Yaeyama and Okinawa groups, can be explained in the same fashion.

Hyla hallowelli presents a slightly different problem. This species occurs only on Amami and Kikaiga in the Oshima group. Its similarity to *H. chinensis* of Formosa seems to eliminate the possibility of a Japanese origin. One must assume either that the present population is the remnant of a species formerly widely distributed (in the Riukius) or that it originally entered the Oshima group as a waif from eastern Asia or Formosa and has never extended its range. Whichever of the above assumptions is true, the presence of *hallowelli* on Kikaiga cannot antedate the early Pleistocene because the entire island is covered with a Pleistocene limestone, indicating complete submergence. However, the date of entry into Amami cannot be so easily determined. Much depends on which of the assumptions is correct. It should be pointed out that the chances for waifing directly from the continent have been reduced since the Pliocene, when the water gap was narrowest.

The question of vagility cannot be ignored in these deductions. Waifing depends on the size of the animal and the size of the population from which it originates. Therefore, such forms as *Rana limnocharis*, *Microhyla ornata*, and *Rhacophorus japonicus* must possess a great deal of vagility as compared to the large *Rana namiyei*, which exists in relatively small numbers. It is probable that the presence of *Rana limnocharis* and *Rhacophorus japonicus* in so many islands is as much a result of waifing as of dispersal along land routes. Yet one is immediately struck by the contrast made by the relatively restricted ranges of *Rana okinavana* and *Hyla hallowelli*, which are of approximately the same size as *Rana limnocharis* and *Rhacophorus japonicus* respectively. Another factor in vagility is ecological opportunity. Obviously, to be strictly comparable, two species must be similar ecologically; for example, one should not be a tree frog and the other a grass frog. The pairs of species *limnocharis-okinavana* and *japonicus-hallowelli* satisfy this requirement. It might be argued that the differences in extent of range are due merely to differences in vagility and not related to length of occupancy in the islands. However, vagility is one of the attributes of biological "success." As I said before, the longer a

species remains in the islands the less successful it is likely to be. Therefore, if ecologically similar animals are compared, differences in vagility support the hypothesis that the "limited dispersal" species were the first to enter the islands.

The problem of the order of entry into the Riukius may be attacked from a slightly different angle. Let us suppose that Species A is found only on Amami and Okinawa, with no closely related form or forms either in other parts of the archipelago or on the continent. Species B is found throughout the islands and on the continent. Assuming that the emigrations of both are relatively limited by water, the last time the Amami and Okinawa populations of both A and B were able to interbreed freely (i.e. Amami A×Okinawa A; Amami B×Okinawa B) was at the time of the last connection of the two islands. Suppose that a comparison of the two populations of each species reveals that Species B shows more inter-island variation than A. We may then conclude that B has a more rapid rate of evolution than A. The fact that A has speciated (i.e. diverged farther from its continental allies) despite its slower rate of evolution, whereas B has not, indicates that A has been in the islands longer than B.

Again the question of vagility arises. Granting the relatively great vagility of small forms occurring in large numbers, once such a species has become established on any of the larger islands the effect of accidental introductions on the population is slight. It is inconceivable that the amount of waifing per year into any one of the larger islands should exceed one thousandth of one per cent of the population on that island in the case of a frog like *Rana limnocharis*. The number of individuals of *limnocharis* on the larger islands must be very large, judging by its abundance in other parts of its range. Consequently, the effect of the introduced individuals would be negligible. The fact that the effect is not enough to offset the divergence of two separate populations is apparent from the differences observed between the Ishigaki and Okinawa series of *limnocharis* that I have examined (see p. 336). In those species occurring in such small numbers that introductions would have a definite effect, the opportunities for waifing are reduced because of the small size of the population. Therefore, as concerns this second method of determining the order of entry of the fauna into the islands (i.e. using the criteria of speciation and inter-island variations), differential probabilities for chance introduction are not important.

I have used body proportions extensively as a means of determining inter-island distinctions within species. Primarily, three

ratios were used: body length/leg length; tibia length/leg length; and head width/body length. In addition, the body lengths were used directly for comparison. The body length dimension was measured from the tip of the snout to the posterior tip of the body. Leg length was determined by the distance from the vent to the tip of the longest toe. The width of the head was measured at the level of the tympanum. Tibia length is the length in the flesh. All measurements were made to the nearest half millimeter. Where the body lengths were used for comparison, they were converted to logarithms to the base 10, to bring their distribution closer to normality. Student's t test was applied in all cases to the differences between means. Because only preserved material was available, I have avoided color as a criterion of intraspecific variation. However, I have used the pattern of pigmentation, and, in one case, the intensity of pigmentation. The following common abbreviations have been applied to designate the collections of the various museums: C.A.S., California Academy of Sciences; C.N.H.M., Chicago Natural History Museum; U.S.N.M., United States National Museum.

CAUDATA

KEY TO RIUKIU SALAMANDERS

A series of conspicuous knob-like tubercles along each side.. *Tylototriton andersoni*
Sides without knob-like tubercles; venter light yellow with dark markings.
Triturus ensicaudus

Tylototriton andersoni Boulenger

Tylototriton andersoni Boulenger, Ann. Mag. Nat. Hist., (6), **10**, p. 304, 1892—type locality Okinawa; Fritze, Zool. Jahrb. Syst., **7**, p. 865, 1894; Boettger, Offenbach. Ver. Naturk., Ber. 33–36, p. 107, 1895; Barbour, Proc. New Eng. Zool. Club, **4**, p. 54, 1909; Wolterstorff, Blatt. Aquar. Terr. Stuttgart, **6**, p. 95, 1929; Tago, Imori to Sansyouo (Salamanders of Japan), p. 26, pl. i, 1931; Okada, Copeia, **1934**, p. 17, 1934.

Distribution.—This salamander has been recorded from Okinawa and Amami (Tago, 1931).

Specimens examined.—Okinawa, 41 (C.A.S.).

Diagnosis.—The series of conspicuous knob-like lateral glands characteristic of this genus serve to distinguish *andersoni* from the only other Riukiu salamander. The present species is uniformly dark brown with the exception of the lower margin of the tail and the under sides of the feet, which are pale orange or yellow.

Secondary sexual characters.—I have not observed any obvious morphological distinctions between the sexes. The lengths of both

body and tail are greater in the females, but these differences are apparent only in large series. Although the absolute lengths differ, the ratio of tail to body length does not. The data are presented in the following table.

COMPARISON OF MALE AND FEMALE *Tylototriton andersoni*

	Male	Female	Diff.	t	n	P
Log body length.	1.8450±0.0127	1.8976±0.0063	0.0526	4.200	38	0.001
Body length in mm..........	69.99	79.00				
Log tail length...	1.7988±0.0139	1.8375±0.0107	0.0387	2.113	35	0.05
Tail length in mm.	62.92	68.80				
Tail length/body length........	0.899 ±0.013	0.886 ±0.016	0.013	0.548	35	0.60

There are no other discernible sexual differentiations in body proportions.

Breeding habits.—There is no mention of the breeding habits of this form in the literature. The entire series I examined was collected between May 5 and May 11. Three females, the smallest of which had a body length of 83.8 mm., contained enlarged eggs. That such a small proportion of specimens contained eggs seems to indicate that the series was taken at the end of the breeding season, as is also likely in view of the late date.

Remarks.—In the series I have examined there is an interesting variability in the number and development of the toes. The majority of individuals have five well-developed toes, but there are many in which the fifth toe appears only as a small tubercle; in others there is no external sign of the fifth toe. Still another variation appears in six specimens with fused toes. X-ray analysis reveals that not only is the number of digits variable, but also that the number of tarsal bones is not constant. Considering the number of feet rather than individuals, seven are syndactylous, three have no fifth metatarsal or corresponding phalanges, twenty-five have a fifth metatarsal but no accompanying phalanges, and forty-five have a fifth metatarsal with one phalange. Nineteen of the feet show no external sign of the fifth toe. Thus, some of these apparently four-toed specimens have a fifth metatarsal that has no effect on the adjacent skin. Where syndactyly appears, the entire structure of the foot shows disorganization—the tarsals are reduced in number and/or the metatarsals are reduced.

Whether the population is in process of shifting from the five-toed to the four-toed condition or is in a state of equilibrium is un-

known at present. As the entire series was collected in 1910, it is possible that a new collection might provide the solution, even in the relatively short interval of thirty-five generations. Syndactyly may develop during regeneration of the limb. In one instance the leg bearing a syndactylous foot is abnormally short. Regardless of the circumstances surrounding syndactyly, whether it is associated with regeneration only or with embryogenesis, the condition must have a genetic basis. The occurrence of such an obviously detrimental character is typical of insular forms. The questions asked concerning the number of digits may be asked regarding syndactyly. In this case also, new collections may provide the answers.

Triturus ensicaudus Hallowell

> *Triton subcristatus* Hallowell, Proc. Acad. Nat. Sci. Phila., p. 494, 1860 (in part; not of Schlegel).
>
> *Triton ensicauda* Hallowell, Proc. Acad. Nat. Sci. Phila., p. 494, 1860—type locality Amami.
>
> *Molge pyrrhogaster ensicauda* Boulenger, Proc. Zool. Soc. Lond., p. 150, 1887; Boettger, Offenbach. Ver. Naturk., Ber. 33–36, p. 106, 1895.
>
> *Molge pyrrhogastra ensicaudus* Okada, Cat. Vert. Japan, p. 65, 1891; Fritze, Zool. Jahrb. Syst., 7, p. 865, 1894.
>
> *Molge pyrrhogastra ensicauda* Brown, Proc. Acad. Nat. Sci. Phila., p. 186, 1902.
>
> *Diemictylus ensicauda* Stejneger, Bull. U. S. Nat. Mus., 58, p. 21, figs. 9–15, 1907; Tago, Imori to Sansyouo (Salamanders of Japan), p. 39, pl. i, 1931.
>
> *Triturus ensicaudus* Okada, Copeia, 1934, p. 17, 1934; Gressitt, Proc. Biol. Soc. Wash., 51, p. 159, 1938.

Distribution.—This salamander occurs in the Oshima and Okinawa groups. It has been specifically recorded from Amami and Kakeroma in the Oshima group and from Okinawa; it is here recorded from Tokashiki in the Okinawa group. *T. ensicaudus* is found in rice fields, drainage ditches, and pools of standing water.

Specimens examined.—Okinawa, 153 (25 C.A.S.; 118 U.S.N.M.; 10 C.N.H.M.); Amami, 51 (C.A.S.); Tokashiki, 6 (C.N.H.M.).

Diagnosis.—The absence of large tubercles on the back and sides and the light coloring on the ventral surface immediately distinguish this species from *Tylototriton*. In many of the individuals of *ensicaudus* the sides bear light blotches or stripes.

Secondary sexual characters.—As in many other salamanders, the males may be distinguished from the females by the globular swelling of the cloaca. In females there is no enlargement at that region, the opening of the cloaca being at the free edge of a narrow dermal extension. The females are larger than the males in both body and

tail length. These differences are set forth in the following table, and a difference in the body proportions is also revealed in the table.

SEXUAL DIFFERENTIATION IN LENGTH IN *Triturus ensicaudus*

Amami	Male	Female	Diff.	t	n	P
Log body length.	1.7677±0.0050	1.7996±0.0052	0.0319	4.290	48	0.001
Body length in						
mm...........	58.56	63.04				
Log tail length...	1.7018±0.0070	1.8557±0.0080	0.1539	13.99	48	0.001
Tail length in mm.	50.32	71.73				
Okinawa						
Log body length.	1.7445±0.0027	1.7794±0.0039	0.0349	7.581	141	0.001
Body length in						
mm...........	55.52	60.16				
Log tail length..	1.6752±0.0037	1.8251±0.0052	0.1499	24.53	141	0.001
Tail length in mm.	47.33	66.85				

The tail in females is considerably greater than the body length, whereas in males the tail is less than the body length. Tago (1931) states that in males the tail is 1.5 times the length of the trunk and in females 1.3 times the trunk, with which my observations obviously do not agree. Based on a rough estimate from the table, the ratio of tail to body is 0.85 in males and 1.14 in females. Tago did not define his measurements beyond "trunk" and "tail." Nevertheless one obtains from his data the erroneous idea that the tail of the male is relatively longer than that of the female.

Breeding habits.—According to Tago, spawning takes place from March to June, with the peak period in April. The eggs are laid singly or in small groups and attached to submerged vegetation or rubbish.

Inter-island variation.—The ground color of the lateral and dorsal surfaces is dark brown or black. As stated in the diagnosis, frequently light markings of two types occur on these regions. The first type is a dorso-lateral line that may vary in length between the eye and the groin. The second type is a spotting most common between the dorso-lateral lines. The spotting, too, may vary from a few scattered spots to large confluent blotches occupying the entire mid-dorsal region. Some individuals display both types. A comparison of the Okinawa and Amami series indicates that the spotting is characteristic of the former and the dorso-lateral stripes characteristic of the latter. I have used a contingency table to test the significance of the observed differences between two series. For the spotting:

OBSERVED FREQUENCY

	Amami	Okinawa	Total
Spots present	1	75	76
Spots absent	50	74	124
Total	51	149	200

CALCULATED FREQUENCY

	Amami	Okinawa	Total
Spots present	19.38	56.62	76.00
Spots absent	31.62	92.38	124.00
Total	51.00	149.00	200.00

Chi-square computed from the above equals 37.74. With one degree of freedom, P is less than 0.001. Similarly, for the dorso-lateral lines:

OBSERVED FREQUENCY

	Amami	Okinawa	Total
Lines present	24	30	54
Lines absent	27	119	146
Total	51	149	200

CALCULATED FREQUENCY

	Amami	Okinawa	Total
Lines present	13.77	40.23	54.00
Lines absent	37.23	108.77	146.00
Total	51.00	149.00	200.00

Chi-square computed from these data is equal to 13.97. At this value, with one degree of freedom, P is less than 0.001. Consequently, the differences between the two series observed for both types of markings are statistically significant. The dark spots on the venter also show considerable variation; however, the nature of these spots is such as to make any comparison between the series extremely complex.

Differences between the two series are also found in the body proportions. Though in the table on page 317 the series appear to be different in length, the observed differences are not statistically significant. However, with regard to the two ratios shown in the following table, the series are significantly different. The head depth measurement was made immediately behind the orbit and varies somewhat with the size of the paratoid gland.

DIFFERENCES IN BODY PROPORTIONS OF TWO SERIES OF *Triturus ensicaudus*

	Amami	Okinawa	Diff.	t	n	P
Head width/body length	0.204±0.008	0.196±0.001	0.008	5.263	187	0.001
Head depth/body length	0.094±0.001	0.090±0.0004	0.004	5.000	187	0.001

The differences between the Amami and Okinawa populations are such as to warrant their nomenclatural distinction as subspecies.

Triturus ensicaudus ensicaudus Hallowell

Type from Amami.

Diagnosis.—As indicated in the foregoing, the typical form is usually uniformly dark on the dorsal surfaces with the exception of a dorso-lateral light line found in almost half of the individuals.

Triturus ensicaudus popei[1] subsp. nov.

Type from Kin, Okinawa. No. 45039 Chicago Natural History Museum. Adult female. Collected by Messrs. J. A. Slater and J. W. Faulk on October 3, 1945.

Diagnosis.—This form differs from the typical in that almost half of the individuals have light cream or yellow spots in the mid-dorsal region. In some specimens these spots occupy most of the dorsal surfaces.

Description of type.—Body moderately slender; fingers and toes touching when limbs adpressed; maximum width of head greater than width of body at shoulders; paratoid glands distinct, extending from upper posterior border of orbit to posterior of neck; nostrils small, situated at tip of snout; a median ridge from base of tail, bifurcating on occipital region but not reaching paratoids; tail long, compressed laterally; skin rugose except on anterior portion of head.

Ground color of dorsal surfaces very dark brown; scattered yellow blotches on mid-dorsal region from occiput to anterior two-thirds of tail; sides with irregular pale yellow green spots from orbit to post-femoral region; chin and throat yellow with six very small dark dots; rest of venter and under surfaces of limbs yellow with scattered dark spots of varying size; lower edge of tail yellow.

Measurements of type.—Snout to vent 57.5 mm., tail 53.0 mm., head width behind orbit 11.3 mm., head depth behind orbit 4.6 mm., snout to posterior of paratoids 15.5 mm.

[1] Named for Clifford H. Pope, Curator of Reptiles, Chicago Natural History Museum.

Paratypes.—C.N.H.M. 45037–38, 45040–46 (Kin, Okinawa); C.A.S. 22309–33 (Nago, Okinawa); U.S.N.M. 7451 (2), 36555, 122118–33, 123032–130 (Okinawa).

Provisionally, I am including in this subspecies the six specimens, C.N.H.M. 43696–701, from Tokashiki, in the Okinawa group. These differ from the others examined in having an extremely granular skin. An adequate series from Tokashiki might show this character to be typical of that population.

SALIENTIA

KEY TO RIUKIU FROGS

1. Epicoracoids overlapping at mid-line[1].................................. 2
   Epicoracoids not overlapping at mid-line............................. 3

2. Back warty; paratoid glands present..................*Bufo bufo gargarizans*
   Back smooth; no paratoids; green in life....................*Hyla hallowelli*

3. Center of back occupied by dark ⟨mark⟩ mark...............*Microhyla ornata*
   No such mark on back... 4

4. Large disks on digits... 11
   Tips of fingers and toes pointed or slightly swollen..................... 5

5. A "thumb" or "fifth digit" on hand................................. 6
   No "thumb"... 7

6. Large dorsal tubercles surmounted with small white granules; Oshima group.
   Rana subaspera
   No white granules on larger tubercles; Okinawa group...........*Rana holsti*

7. Front of lower jaw with two large projections................*Rana namiyei*
   Lower jaw without a pair of tooth-like processes:...................... 8

8. White or light line below eye parallel to mouth...................... 9
   No white line above mouth.. 10

9. Tympanum surrounded by bead-like white tubercles; usually three complete
   crossbars on tibia...*Rana narina*
   Tympanum not surrounded by tubercles; usually one complete crossbar on
   tibia..*Rana okinavana*

10. Large dorsal tubercles with radiating striations..............*Rana ishikawae*
    Dorsal tubercles without radiating striations...............*Rana limnocharis*

11. Dorsum with dark markings.. 12
    Dorsum uniform green (blue or gray when preserved)..*Rhacophorus schlegelii*

12. Leg short; tibio-tarsal articulation does not reach tip of snout when limb is
    carried forward....................................*Rhacophorus eiffingeri*
    Leg long; tibio-tarsal articulation reaches beyond tip of snout.
    Rhacophorus japonicus

[1] For identification of live material it is unnecessary to examine the epicoracoids if it is remembered that *Bufo b. gargarizans* has a dry warty skin and conspicuous paratoid glands, and that *Hyla hallowelli* is one of the two green species. The diagnoses will assist in distinguishing *hallowelli* from the other green frog, *Rhacophorus schlegelii*.

Bufo bufo gargarizans Cantor

Bufo gargarizans Cantor, Ann. Mag. Nat. Hist., (1), **9**, p. 483, 1842—type locality Chusan.

Bufo bufo japonicus Stejneger, Bull. U. S. Nat. Mus., **58**, p. 69, 1907.

Bufo bufo miyakonis Okada, Tailless Batr. Jap. Emp., p. 47, pl. iii, figs. 1–2, pl. xviii, fig. 3, pl. xxii, fig. 5, text figs. 19–20, 1931; Gressitt, Proc. Biol. Soc. Wash., **51**, p. 161, 1938.

Bufo bufo gargarizans Boring, Pek. Nat. Hist. Bull., **13**, pt. 2, p. 91, 1939.

Distribution.—The common large toad of central China is found only on Miyako in the Riukius. The presence of the toad on this particular island and the absence of the genus in the other islands indicate that this toad may have been introduced (see p. 309).

Taxonomic notes.—Okada (1931) described the Miyako population of this toad as a new subspecies, *B. b. miyakonis*. It is difficult to determine just how he differentiated it from *gargarizans*. He gave no diagnostic characters and his description of the type fits Chinese specimens of *gargarizans* perfectly. The obvious similarity to the latter plus the peculiar distribution seem to place Okada's name in the synonymy of *gargarizans*. No Miyako specimens have been available for examination, and this is obviously essential for decision regarding their relations to the mainland populations.

Breeding habits.—Okada reported seeing tadpoles with hind limbs in late March on Miyako. Probably breeding takes place in February or March.

Hyla hallowelli Van Denburgh

Hyla hallowelli Van Denburgh, Adv. Diag. Rept. Amph., p. 4, 1912—type locality Kikaiga; Van Denburgh, Proc. Calif. Acad. Sci., (4), **3**, p. 190, 1912; Okada, Tailless Batr. Jap. Emp., p. 67, pl. vi, fig. 1, pl. xxiii, fig. 5, text fig. 32, 1931.

Distribution.—This species is known with certainty only from Amami and Kikaiga. Okada (1926) reported it from Yoron; however, he later (1931) stated that it did not occur on any island of the Oshima group save Amami and Kikaiga.

Specimens examined.—Kikaiga, type locality, 24 (C.A.S.); Amami, 21 (C.A.S.).

Diagnosis.—The toe pads and green color (gray or slate blue in alcohol) distinguish *Hyla hallowelli* from all other Riukiu Salientia except immature individuals of *Rhacophorus schlegelii*. Both species are green in life, have digital pads, and approximately the same amount of webbing. There is a difference in the position of the

nostrils, however.   In *Hyla hallowelli* they are situated at the tip of the snout, whereas in *Rhacophorus schlegelii* they are set back about one-third the distance from the end of the snout to the eye. Furthermore, the snout of the present species is truncate.   Adults of *Hyla hallowelli* are small, averaging around 30.5 mm., which is only slightly larger than *Microhyla ornata* but much smaller than *Rhacophorus schlegelii* (see p. 343).

Secondary sexual characters.—The males have a median external vocal sac and a nuptial pad on the mesial surface of the first digit. As all of the males examined possess these structures, they are presumably mature.   The mean length will be given below.   Only one female, C.A.S. 23819, was in the series examined.   Consequently no comparison of the sexes was possible.   Suffice it to say that the female lay well within the ranges of size and body proportions of the males.

Breeding habits.—The specimens were collected between April 26 and May 1.   As only one female is included in the series of forty-five individuals, one might assume that the dates of collection fall just prior to the general emergence of that sex.   The female contained eggs that were ready to be shed.   The inference, then, is that breeding takes place from the end of April through the first part of May.

Inter-island variation.—The two groups of specimens display differences in coloration, size, and body proportions.   On the basis of these minor distinctions, this species is here broken into two subspecies.

Hyla hallowelli hallowelli Van Denburgh

Diagnosis.—In all of the specimens of the typical form examined, the dark dots on the posterior of the thigh are discrete.   The dorsal surface of the body is consistently light gray.

Hyla hallowelli schmidti[1] subsp. nov.

Type from Naze, Amami.   No. 23852 California Academy of Sciences.   Adult male.   Collected by Mr. Victor Kuhne, April 26 to May 1, 1910.

Diagnosis.—Most specimens of this form are darker than those of the typical subspecies.   In many individuals of *schmidti* the brown dots on the thigh unite to form reticulations.   The comparison

[1] The new form is named for Karl P. Schmidt, Chief Curator, Department of Zoology, Chicago Natural History Museum.

given in the following table demonstrates further differences between *schmidti* and *hallowelli*.

BODY PROPORTIONS OF TWO FORMS OF *Hyla hallowelli*

	hallowelli	schmidti	Diff.	t	n	P
Log body length.	1.4826±0.0034	1.5031±0.0041	0.0205	3.727	42	0.001
Body length in mm.	30.39	31.86				
Body length/leg length	0.611 ±0.004	0.619 ±0.003	0.008	1.638	43	0.12
Tibia/leg length.	0.313 ±0.002	0.301 ±0.002	0.012	5.591	42	0.001
Head width/body length	0.336 ±0.003	0.315 ±0.002	0.021	4.905	43	0.001

Only in the body length/leg length ratio is there no statistically significant difference.

Description of type.—Body moderately slender, tapering to inguinal region; head same width as anterior portion of trunk; snout blunt; nostrils at tip of snout; canthus rostralis distinct; lores deeply concave; interorbital distance greater than width of upper eyelid; diameter of orbit equal to its distance from snout tip; tympanum distinct, one-fourth diameter of orbit; legs long, heels overlapping, tibio-tarsal joint reaching between eye and nostril; disks of digits well developed, those of fingers larger; disk of third finger larger than tympanum; fingers one-fourth webbed; toes almost completely webbed.

Skin finely shagreened; venter coarsely granulated; color of dorsal surfaces dark slate; ventral surfaces except for chin immaculate deep cream, chin faintly mottled with brown; posterior aspect of thighs with brown dots, many of which fuse to form reticulations.

Measurements of type.—Snout to vent 30.5 mm., leg length 49.5 mm., tibia length 14.5 mm., head width 10 mm.

Affinities.—In the absence of large black spots on the thighs and the presence of the dorsal color on the digits, *hallowelli* resembles *H. arborea japonica.* As pointed out by Van Denburgh (1912b), the homogeneous dorsal coloration and the position of the vomerine teeth ally *hallowelli* to *H. chinensis.* *H. hallowelli* shows more similarity in size to *chinensis* than to *japonica.* Japanese specimens of *japonica* are frequently over 40 mm. in body length (Okada, 1931); of 35 male *chinensis* measured by Pope (1931), the largest was 32.5 mm.; the largest of the 45 individuals of *hallowelli* examined by me was 34 mm. When the general body form and the shape of the head are considered, the relationship of *hallowelli* to *chinensis* is obvious.

Microhyla ornata Dumeril and Bibron

> *Engystoma ornatum* Dumeril and Bibron, Erp. Gen., 8, p. 175, 1841—type locality Malabar coast.
> *Microhyla ornata* Boulenger, Cat. Batr. Sal. Brit. Mus., ed. 2, p. 165, 1882; Gressitt, Proc. Biol. Soc. Wash., **51**, p. 164, 1938.
> *Microhyla fissipes* Boulenger, Ann. Mag. Nat. Hist., (5), **13**, p. 397, 1884; Boulenger, Proc. Zool. Soc. Lond., p. 150, 1887; Okada, Cat. Vert. Jap., p. 66, 1891; Fritze, Zool. Jahrb. Syst., **7**, p. 865, 1894; Boettger, Offenbach. Ver. Naturk., Ber. 33–36, p. 106, 1895; Okada, Tailless Batr. Jap. Emp., p. 71, pl. vii, fig. 3, pl. xviii, fig. 7, pl. xxiii, fig. 6, text figs. 33–34.
> *Microhyla okinavensis* Stejneger, Proc. Biol. Soc. Wash., **14**, p. 189, 1901; Stejneger, Bull. U. S. Nat. Mus., **58**, p. 89, figs. 71–75, 1907; Barbour, Proc. New Eng. Zool. Club, **4**, p. 58, 1909; Parker, Ann. Mag. Nat. Hist., (10), **2**, p. 492, 1928; Parker, Mono. Microhylidae, p. 138, 1934.
> *Microhyla undulata* Brown, Proc. Acad. Nat. Sci. Phila., p. 186, 1902.

Distribution.—This species has been found in all groups of the Riukius south of the Tokara Strait with the exception of the Tokaras. In addition, its range includes southern China, Formosa, Hainan, and all of southeastern Asia.

Specimens examined.—Okinawa, 13 metamorphosed individuals, 9 larvae (C.N.H.M.); Ishigaki, 17 adults (U.S.N.M.).

Taxonomic notes.—Parker (1928, 1934) recognized *okinavensis* as the form generally distributed through the archipelago. His diagnostic characters were the lateral fringes and a trace of a dorsal cleft on the toes, though the appearance of the cleft was erratic. The first character does not serve to distinguish Riukiu specimens from *ornata* of the continent. I have observed lateral fringes on the toes of several specimens from Szechwan, China (C.N.H.M. 18875–6). Parker also indicated that the tibio-tarsal articulation reached slightly farther anterior in *okinavensis*. Though there was some difference in this point between the Riukiu and the Chinese specimens I have examined, the range of this character in each series overlaps that in the other to a large extent. The tadpoles from Okinawa are indistinguishable from some from Szechwan which Dr. C. C. Liu was kind enough to make available. It is possible that further investigation will reveal differences of a subspecific nature; however, at the present time there is no basis for maintaining *ornata* and *okinavensis* as distinct species.

Diagnosis.—This species is the smallest frog in the Riukius, adults rarely exceeding 31 mm. It can be distinguished from all other frogs in the islands by the brown mark on the back (see key, p. 320). This mark, extending from the tip of the snout to the in-

sertion of the legs, varies in form somewhat. *M. ornata* also differs from the rest of the frogs, with the exception of *Bufo b. gargarizans*, by the absence of teeth in the upper jaw. The smooth skin of *ornata* as well as the peculiar mark on the back separates it from the toad. In the field, *ornata* may be identified by the extremely long leaps it makes (approximately six feet).

Secondary sexual characters.—The males have a median internal subgular vocal sac, the openings of which lie in the anterior floor of the mouth. There are no nuptial pads. The gular region of the males is densely mottled with very dark brown or black. In the females this region is less densely mottled, with the same drab or light brown found on the dorsum.

The females are slightly larger than the males. In the Ishigaki series the three males average 25.33 mm., the fourteen females 28.32. The value of P for this difference is 0.005 ($t=3.458$), a significant figure even though very few males were used in the computations. The mean length of nine Okinawa males was 23.39 mm. Two mature females from Okinawa measured 22.0 and 22.5 mm. The smaller of these contained eggs. Okada (1931) reported that the male was larger than the female. Yet he presented data in which the males averaged 24.5 and the females 28.4 mm.

In the Okinawa series there appeared to be a difference between males and females with respect to the body length/leg length ratio. However, the same did not hold for the Ishigaki sample. The following is a comparison of the ratio in males and females of the two series:

	MALES		FEMALES				
	Mean	No.	Mean	No.	Diff.	t	P
Okinawa.........	•0.555±0.012	9	0.489±0.000	2	0.066	2.427	0.04
Ishigaki..........	0.583±0.011	3	0.589±0.005	14	0.066	0.583	0.56

Inasmuch as there were only two females from Okinawa and the value of the ratio for those was so much smaller than in the Ishigaki females, I believe that the difference observed in the former series is due to chance despite the apparent significance of P.

Breeding habits.—There has been no specific mention in the literature of the breeding season of the Riukiu population. The Okinawa tadpoles, some of which had hind-limb buds, were collected on May 5, giving an indication of the breeding period. Pope (1931) stated that *ornata* tadpoles in Fukien could be found in any small rain pool. Doubtless the Riukiu population breeds in similar

temporary water sites as well as in rice paddies. The larval period is very short, lasting approximately from 20 to 30 days (Pope, 1931).

Inter-island variation.—As indicated in the section dealing with sexual differences, the males of the Okinawa series are apparently smaller than those of the Ishigaki. *P* of the observed difference (1.94 mm.) is 0.03 ($t=2.808$, $n=10$). The Okinawa female (22 mm.), which contains eggs and is therefore adult, is smaller than the smallest Ishigaki female (25 mm.).

There are small but statistically significant differences in the body proportions of the two Riukiu series as follows:

	Okinawa	Ishigaki	Diff.	t	P (n=26)
Body length/leg length..	0.543±0.013	0.588±0.004	0.045	3.750	0.001
Tibia/leg length.........	0.302±0.003	0.288±0.002	0.014	4.117	0.001

In preparation of the above table, males and females were combined. Elimination of the two Okinawa females does not alter appreciably the value of *P*.

Rana holsti Boulenger

> *Rana holsti* Boulenger, Ann. Mag. Nat. Hist., (6), **10**, p. 302, 1892—type locality Okinawa; Fritze, Zool. Jahrb. Syst., **7**, p. 865, 1894; Stejneger, Bull. U. S. Nat. Mus., **58**, p. 105, fig. 84, 1907.
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> *Babina holsti* Van Denburgh, Adv. Diag. New Rept. Amph., p. 1, 1912; Van Denburgh, Proc. Calif. Acad. Sci., (4), **3**, p. 197, 1912; Okada, Tailless Batr. Jap. Emp., p. 173, pl. xiii, fig. 1, pl. xxi, figs. 2–3, pl. xxviii, fig. 1, text figs. 78–80, 1931.

Distribution.—This species is apparently restricted to the mountainous region of Okinawa.

Specimens examined.—Okinawa, 12 males (C.A.S.).

Taxonomic notes.—This species and the allied *R. subaspera* are remarkable in that the first metacarpal is elongated into a curved spine approximately 15 mm. long in mature individuals. The spine is encased in a fleshy sheath ventral and medial to the first finger. On the basis of this character, Van Denburgh (1912a) established the genus *Babina*. He believed the spine to be a defensive mechanism. Inasmuch as the structure is obviously a sexual character (Boulenger, 1918), and considering the diversity of sexual adaptations in the genus *Rana*, it is much more reasonable to assign these two species to *Rana*, which they resemble in all other respects.

Diagnosis.—The metacarpal spur or "fifth digit" serves to distinguish this frog from all others in the islands save *subaspera*. From

the latter it may be separated by the absence of large tubercles on the anterior portion of the back. There are numerous small white granules on the dorsum, but they are not concentrated on the large tubercles as in *subaspera*. The average body length of the series examined was 107.45 mm. (minimum 99.5, maximum 118.5). Judging by the presence of nuptial pads and vocal sacs, all were mature.

Secondary sexual characters.—The males have a median internal subgular vocal sac. Spiny nuptial asperities are present on the spur sheath and first finger of the males. Because of the great similarity between *holsti* and *subaspera*, it is a safe assumption that the sexual differences of the latter (see p. 328) apply also to *holsti*.

Inter-island variation.—The relationship of *holsti* and *subaspera* is sufficiently close to be discussed in this section. In addition to the distinctions already mentioned in the diagnoses there are other differences, not so obvious, between these species. The body proportions are compared in the following table. To eliminate any discrepancies of a sexual nature only the males are considered.

COMPARISON OF MALES OF *Rana holsti* AND *R. subaspera*

Mean	*holsti* n=12	*subaspera* n=15	Diff.	t	P
Log body length....	2.0312±0.0057	2.0663±0.0041	0.0351	5.089	0.001
Body length in mm..	107.46	116.50			
Body length/leg length..........	0.602 ±0.004	0.601 ±0.004	0.001	0.013	0.97
Tibia/leg length....	0.303 ±0.002	0.297 ±0.001	0.006	2.935	0.008
Head width/body length..........	0.397 ±0.003	0.408 ±0.003	0.011	2.697	0.012

Only the body length/leg length ratio fails to show a significant difference.

Okada (1931) indicated that the two species could be separated by a reduced web between the first and second fingers of *holsti;* I have found no web in the hand of either form.

Rana subaspera Barbour

Rana subaspera Barbour, Proc. Biol. Soc. Wash., **21**, p. 189, 1908—type locality Amami; Barbour, Proc. New Eng. Zool. Club, p. 58, 1909.

Babina subaspera Van Denburgh, Adv. Diag. New Rept. Amph., p. 1, 1912; Van Denburgh, Proc. Calif. Acad. Sci., (4), 3, p. 199, 1912; Okada, Tailless Batr. Jap. Emp., p. 171, pl. xiv, fig. 1, pl. xv, fig. 1, pl. xix, fig. 7, text figs. 76–77, 1931.

Distribution.—Barbour (1908) and Van Denburgh (1912b) recorded this species from Amami only. Okada (1926, 1931) added Tokuno to the known range.

Specimens examined.—Amami, 16 males, 5 females (C.A.S.).

Diagnosis.—This is the only frog in the Oshima group having a spur such as is found in *R. holsti*. *R. subaspera* is distinguished from *holsti* by clusters of white granules on the large tubercles of the back. The anterior portion of the back of the present species is warty.

Secondary sexual characters.—Adult males are readily identified by the light-colored spinules appearing on the dorsal surfaces of the fingers. These asperities are concentrated into nuptial pads on the spur sheath and first digit. Another diagnostic feature of the male is the granular nature of the venter; in the female this surface is smooth. In *holsti* the ventral granules of the male are restricted to the pectoral region. The males of the present species, like *holsti*, have median internal subgular vocal sacs.

Van Denburgh (1912b, 1920) maintained on the basis of the field notes of his collector that the spine had a defensive function: a specimen of *holsti* stabbed the thumb of the collector with the spurs; also several specimens of *R. namiyei* were badly slashed after being carried in a bag containing *holsti*. Boulenger (1918) explained the behavior of *holsti* by pointing out the well-known fact that male frogs will clasp other species and even inanimate objects during the breeding season. All of Van Denburgh's specimens of *holsti* were collected between May 5 and May 11, near if not within the breeding season.

Both Van Denburgh (1920) and Noble (1920) rejected the sexual interpretation because the spine appeared in both sexes. This is hardly a valid point. Both men and women have mammae; yet that does not alter the sexual nature of the glands.

In all of the adult males I have examined of both species (total 27), the sheath was punctured, whereas, in the five adult females of *subaspera*, there was no such perforation. The one available juvenile male of *subaspera* lacked the perforation also. These data indicate that the spine has a sexual function in males. Since the punctures vary in position and shape from male to male, and are not even constant from one hand to the other in a single individual, it is my opinion that the spine is forced through the sheath during amplexus. The extremely thick and tough skin protects the female from damage.

With the exception of the body length/leg length ratio, the body proportions show no sexual differentiation. A comparison of the sexes is given in the following table. The measurements of twenty

adults were used.   Maturity in the males was determined by the presence of nuptial pads and vocal sacs; maturity in the females was based on the presence of ovulated eggs.

SIZE AND BODY PROPORTIONS IN *Rana subaspera*

	Male	Female	Diff.	t	P (n=18)
Log body length....	2.0663±0.0041	2.0684±0.0067	0.0021	0.254	0.80
Body length in mm..	116.50	117.04			
Body length/leg length...........	0.601 ±0.004	0.636 ±0.008	0.035	3.944	0.001
Tibia/leg length....	0.297 ±0.001	0.299 ±0.003	0.002	0.960	0.35
Head width/body length...........	0.408 ±0.003	0.403 ±0.029	0.005	0.309	0.76
Tympanum/body length...........	0.0069±0.0002	0.0065±0.0002	0.0004	1.225	0.24

According to Okada the male has a blunter snout and a larger tympanum.   As for the first point, I found no such distinction, and the table shows that there was no difference observed in the tympana.

Breeding habits.—The specimens examined were collected between April 26 and May 1.   As all five females contained eggs ready to be shed, one concludes that breeding takes place during the last part of April and early May.

Rana namiyei Stejneger

Rana namiyei Stejneger, Proc. Biol. Soc. Wash., **14**, p. 190, 1901—type locality Okinawa; Stejneger, Bull. U. S. Nat. Mus., **58**, figs. 122–126, p. 136, 1907; Van Denburgh, Proc. Calif. Acad. Sci., (4), **3**, p. 194, 1912; Okada, Tailless Batr. Jap. Emp., pl. xii, fig. 1, pl. xxi, fig. 1, pl. xxvii, fig. 5, text figs. 69–71, p. 156, 1931.

Rana kuhlii Boulenger, Rec. Ind. Mus., **20**, p. 62, 1920.

Distribution.—Adults have been recorded from Okinawa only. This frog inhabits the pools and quiet water of the mountainous region.   In this respect it is similar.to *R. kuhlii* (Pope, 1931).   Okada reported seeing tadpoles of *namiyei* on Amami.

Specimens examined.—Okinawa, 7 males, 10 females (C.A.S.).

Taxonomic notes.—*Rana namiyei* has been considered a synonym of *kuhlii*.   The close relationship of the two forms is obvious.   The question of the validity of the former is dependent upon two factors, isolation and differentiation.   *R. namiyei* has not been found south of Okinawa.   The nearest population of *kuhlii* is on Formosa.   As exploration of the amphibian fauna of intervening Ishigaki has been extensive we can safely assume that the two are effectively isolated.

There has been some differentiation. Of ninety-nine individuals of *kuhlii* from Fukien, the largest measured by Pope (1931) was 67 mm. long. The largest of forty-three specimens examined by Boulenger (1920) was 87 mm. The latter's specimens came from various points in the range of *kuhlii*. In the Okinawa series the mean length of six mature males was 83.44 mm., with a maximum of 102.5. The mean length of eight females containing eggs was 75.10 mm., with a maximum of 88.5. Okada (1931) listed six males of which the mean length was 96.0 mm., with a maximum of 113. He also recorded a female that measured 102 mm. It is apparent that *namiyei* is larger than *kuhlii*. There are other minor differences. The band between the eyes is much wider in *namiyei*. As pointed out by Van Denburgh (1912b), in the present form the web and dermal margin of the fifth toe are more extensive. These differences, of course, reflect differences in the genetic make-up of the two forms.

Inasmuch as the two most important criteria of species are satisfied, namely, effective reproductive isolation (by virtue of the wide separation in distance and in geologic time) and genetic distinction, *namiyei* should be maintained as a distinct species.

Diagnosis.—*Rana namiyei* is distinguished from other frogs in the islands by the two projections in the anterior part of the lower jaw. These processes fit into depressions of the upper jaw. *R. limnocharis* is the only other frog with a similar structure; however, in *limnocharis* there is only a single median projection. The present species is one of the largest in the islands. Data on length are given elsewhere. The general aspect of the body is broad and flat.

Secondary sexual characters.—As stated above, the mean length of the mature males examined for this study was 83.44 mm., of the females 75.10 mm. The difference between these figures is not significant ($P=0.24$, $t=1.235$). Nevertheless, a large series probably would show a significant difference between the sexes. In *kuhlii* Pope has demonstrated the presence of such a difference, due primarily to the large size of the head in males. The same condition holds true in *namiyei*. The head width/body length ratio of males in the present series was 0.455, that of females 0.435. *P* of the difference was 0.05 ($t=2.125$). However, of more importance is the fact that in the males there was a correlation of $+0.79$ ($P=0.04$) of the head width ratio to the logarithm of body length. In the females the correlation had a value of $+0.02$ ($P=0.97$).

For the comparison of the lengths only sexually mature individuals were used. In the males, maturity was determined by the

presence of the secondary sex structures, paired internal subgular vocal sacs, and granular nuptial pads on the first digit. Maturity in the females was determined by the presence of ovulated eggs.

Breeding habits.—All of the specimens were collected in the period from May 5 to May 11. The imminence of breeding at the time of capture is indicated by the presence of ovulated eggs in all of the large females.

Rana narina Stejneger

> *Rana narina* Stejneger, Proc. Biol. Soc. Wash., **14**, p. 189, 1901—type locality Okinawa; Stejneger, Bull. U. S. Nat. Mus., **58**, p. 134, figs. 117–121, 1907; Okada, Tailless Batr. Jap. Emp., p. 153, pl. x, fig. 3, pl. xxvii, fig. 2, text fig. 68, 1931.
>
> *Buergeria ijimae* Stejneger, Proc. Biol. Soc. Wash., **14**, p. 190, 1901.
>
> *Rana ijimae* Stejneger, Bull. U. S. Nat. Mus., **58**, p. 121, figs. 99–103, 1907; Van Denburgh, Proc. Calif. Acad. Sci., (4), **3**, p. 193, 1912; Okada, Tailless Batr. Jap. Emp., p. 151, pl. xxvi, fig. 5, text fig. 67, 1931.

Distribution.—This species has been recorded from Okinawa, Amami, and Ishigaki. In addition, Okada has reported it from Formosa.

Specimens examined.—Ishigaki, 13 (C.A.S.).

Taxonomic notes.—The descriptions of *narina* and *ijimae* in Stejneger (1907) and Okada (1931) indicate that these are very similar. The position of the vomerine teeth, the characteristic tubercles surrounding the tympanum, the swollen tips of the digits, the blunt snout, and the general form and size agree in both. From Okada's figures of the skull and pectoral girdle, there is no basis for distinction. Furthermore, his colored plate of *narina* fits his description of *ijimae*. The only differences mentioned by Okada are the relatively narrower head and shorter limbs in *narina*. However, those cannot be differences of the species level. When one considers further that there is no way of knowing just how Okada distinguished between the two, the differences he mentioned can very well be interpreted as variations within a population.

Apparently Stejneger's designation of two specimens of this form as the types of two distinct species was the result of poor preservation. In his *Herpetology of Japan* are figured the hand and foot of the type of *narina*. The figures are obviously those of a dried specimen. When writing of *ijimae* in the same volume, Stejneger states that the type specimen was too soft to determine the nature of the dorso-lateral region. *R. ijimae* is here reduced to the synonymy of *narina*.

Diagnosis.—Characteristic of this species are the light line above the mouth and the white tubercles surrounding the tympanum. The tips of the digits are swollen but, as in *okinavana,* are not as large as the disks of *Hyla* or *Rhacophorus.* The snout is blunt. There are usually three complete crossbars on the tibia.

Secondary sex characters.—The average body length of eight apparently mature females was 86.2 mm. (minimum 78.5, maximum 99.0). Of the three males available, the largest was 67.0 mm. This specimen, C.A.S. 22827, was mature, having a well-developed nuptial pad and paired lateral internal vocal sacs. The other males, the smaller being 62.5 mm., lacked these structures and were presumably immature. The larger of two males measured by Okada (1931) was 79 mm. long. Although it seems probable that the females were larger than the males, the magnitude of the difference is impossible to determine with the few specimens at hand.

A comparison of the body proportions of the two sexes is given in the following table. Only in the head width/ body length ratio is there a significant difference.

COMPARISON OF MALE AND FEMALE *Rana narina*
(*3 males, 8 females*)

	Male (mean)	Female (mean)	Diff.	t	P (n=9)
Body length/leg length..	0.590±0.004	0.596±0.007	0.006	0.364	0.73
Tibia/leg length........	0.307±0.001	0.309±0.002	0.002	0.576	0.62
Head width/body length...............	0.328±0.004	0.350±0.004	0.022	3.089	0.014

Okada (1931) stated that the hind limb and tibia of the males were shorter than those of the females. Such differences should be reflected in the body length/leg length and tibia/leg length ratios. The table, though admittedly weak because of the few specimens involved, does not reveal either of these differences.

Breeding habits.—All of the specimens examined were collected between May 25 and June 2. As none of the females contained ovulated eggs, it is evident that the breeding season occurs earlier. There is nothing in the literature concerning breeding behavior.

Rana okinavana Boettger

Rana okinavana Boettger, Zool. Anz., **18**, p. 266, 1895—type locality Okinawa; Stejneger, Bull. U. S. Nat. Mus., **58**, p. 102, 1907; Van Denburgh, Proc. Calif. Acad. Sci., (4), **3**, p. 192, 1912.

Rana macropus Okada, Tailless Batr. Jap. Emp., p. 95, pl. x, fig. 5, pl. xviii, fig. 4, pl. xxiv, fig. 6, text figs. 42–43, 1931.

Distribution.—Only the type specimen has been recorded from Okinawa. It has also been reported from Ishigaki (Van Denburgh, 1912b) and Amami (Okada, 1931).

Specimens examined.—Ishigaki, 11 males, 12 females (C.A.S.).

Diagnosis.—The absence of tubercles from the area surrounding the tympanum and the single crossbar on the tibia distinguish this species from *R. narina*. *R. okinavana* is also considerably smaller than *narina*. The mean of the series examined was 39.7 mm., with a maximum of 43.0. Okada (1931) described a female that was 47 mm. long. The smallest *narina* I examined measured 62.5 mm. The white line above the lip and the swollen tips of the digits separate *okinavana* from other members of the genus (with the exception of *narina*). Though the tips of the digits are enlarged, they do not approach the size of the disks of *Rhacophorus* and *Hyla*. The skin of the back is smooth except near the vent.

Secondary sexual characters.—The sexes are indistinguishable by gross inspection. Examination of eleven males failed to reveal nuptial pads or vocal sacs. However, that may be due to immaturity.

Analysis of the body proportions indicates very little difference between the sexes. The following table summarizes the data on body length and proportions.

COMPARISON OF MALE AND FEMALE *Rana okinavana*
(*11 males, 12 females*)

	Male (mean)	Female (mean)	Diff.	t	P (n=21)
Log body length...	1.5934±0.0043	1.6025±0.0061	0.0091	1.206	0.25
Body length in mm.	39.21	40.04			
Body length/leg length..........	0.569 ±0.005	0.553 ±0.006	0.016	2.026	0.06
Tibia/leg length...	0.294 ±0.002	0.293 ±0.001	0.001	0.105	0.90
Head width/body length..........	0.355 ±0.006	0.346 ±0.003	0.009	1.467	0.16

The only distinction between the sexes in the series lies in the body length/ leg length ratio. Even that difference is just at the borderline of significance (*P*= 0.06).

Breeding habits.—Practically nothing is known about the breeding behavior of this frog. None of the females available to me contained eggs. As all were collected in the period May 25 to June 2, it is probable that the breeding season had already ended. That the larger females were mature was evident from the relatively large oviducts observed.

Rana ishikawae Stejneger

Buergeria ishikawae Stejneger, Proc. Biol. Soc. Wash., **14**, p. 190, 1901—type locality Okinawa.

Rana ishikawae Stejneger, Bull. U. S. Nat. Mus., **58**, p. 132, figs. 111–116, 1907; Okada, Tailless Batr. Jap. Emp., p. 166, pl. xi, fig. 1, pl. xxvii, fig. 1, text fig. 74, 1931.

The few specimens collected have come from the mountainous region of Okinawa. I have not seen any individuals of this species. According to Stejneger (1907) and Okada (1931) the large tubercles of the back have radiating striae which immediately set this frog apart from any other in the islands. The smaller tubercles lack these ridges. The ends of the fingers and toes are slightly expanded. This species approaches the size of *R. holsti*, one individual being recorded as 115 mm. long (Okada, 1931). There is no reference to secondary sexual characters or the breeding habits of *ishikawae*.

Rana limnocharis Wiegmann

Rana limnocharis Boie in Wiegmann, Nova Acta Acad. Leop. Carol., **17**, pt. 1, p. 255, 1835—type locality Java; Boulenger, Fauna Brit. India, Rept., p. 450, 1890; Fritze, Zool. Jahrb. Syst., **7**, p. 865, 1894; Boettger, Offenbach. Ver. Naturk., Ber. 33–36, p. 103, 1894; Stejneger, Journ. Sci. Coll. Tokyo, **12**, pt. 3, p. 217, 1898; Stejneger, Bull. U. S. Nat. Mus., **58**, p. 127, figs. 107–110, 1907; Okada, Tailless Batr. Jap. Emp., p. 138, pl. vii, fig. 1, pl. xix, fig. 5, pl. xxvi, fig. 4, text figs. 62–63, 1931; Gressitt, Proc. Biol. Soc. Wash., **51**, p. 162, 1938.

Rana gracilis Wiegmann, Nova Acta Acad. Leop. Carol., **17**, pt. 1, p. 257, 1835; Hallowell, Proc. Acad. Nat. Sci. Phila., p. 505, 1860; Gunther, Rept. Brit. India, p. 409, 1864; Martens, Preuss. Exped. Ost-Asien, Zool., **1**, p. 383, 1876; Boulenger, Cat. Batr. Sal. Brit. Mus., p. 28, 1882; Boulenger, Proc. Zool. Soc. Lond., p. 149, 1887; Boettger, Offenbach. Ver. Naturk., Ber. 24–25, p. 159, 1885; Okada, Cat. Vert. Jap., p. 67, 1891; Brown, Proc. Acad. Nat. Sci. Phila., p. 185, 1902.

Rana vittigera Gunther, Cat. Batr. Sal. Brit. Mus., p. 9, 1858; Martens, Preuss. Exped. Ost-Asien, Zool., **1**, p. 163, 1876.

Distribution.—This frog is found in Kyushu, Shikoku, southern Honshu, Korea, China, and other parts of southeastern Asia. In the Riukius it has been recorded from all groups except the Tokaras.

Specimens examined.—Riukiu Islands, 67 (Okinawa, 47, C.N. H.M.; Ishigaki, 20, U.S.N.M.); Formosa, 9 (C.N.H.M.); Indo-China, 29 (C.N.H.M.); Fukien, 12 (C.N.H.M.); Szechwan, 43 (C.N.H.M.).

Diagnosis.—The present species is one of the smaller representatives of the genus, the largest individual from Okinawa examined

being 49.0 mm., the largest from Ishigaki 53.5. The ground color may be gray or brown, with several short black bands crossing the center of the back. There are many scattered longitudinal ridges on the back, especially posteriorly. The characters in the key are sufficient to separate *limnocharis* from all other frogs in the islands, the only possible confusion being with *namiyei*. The latter has two large processes at the front of the lower jaw, whereas *limnocharis* has a single median enlarged projection.

Secondary sexual characters.—The males have a median external subgular vocal sac. Coincident with the development of this structure, the ventral fold anterior to the pectoral girdle is much more pronounced than in the females. The nuptial pad of the male is granular and located on the dorso-medial surface of the first digit. Another male characteristic is the presence of black on the throat, but the density of the pigment and its extent vary considerably. When the amount of pigment is greatest, it extends in an anteriorly directed arching band from the posterior corner of the mouth across the throat. The maximum width of the band is approximately 4.5 mm. The reductions in density and extent of pigment begin in the same area, the center of the throat, though not in all cases simultaneously. At the minimum the pigment is present in a short pale band along the posterior margin of the jaw.

The females are slightly larger than the males. The Okinawa series included fifteen mature males and fifteen mature females. The mean lengths of these were 35.56 and 39.07 mm. In the Ishigaki series the mean of the fourteen mature males was 48.68; of six females 51.16 mm. The probabilities that these sexual differences are due to chance are $P=0.03$ ($t=2.356$) and $P=0.05$ ($t=2.119$), respectively. The significance of these figures is emphasized by comparison with the samples from Indo-China and Szechwan. In the former the mean for the males is 36.44; for females, 44.41 mm. The value of P for this difference is 0.001 ($t=4.988$). In the latter sample the means are 37.64 and 41.02, P of the difference being equal to 0.02 ($t=2.482$). I have found no distinction between the sexes in body proportions.

Okada (1931) made several statements concerning sexual differences for which I find no support. He reported that the males were distinguished by the presence of "two distinct palmar tubercles on the inner lateral margin of the first finger." In my series the females are identical to the males in this respect. Okada also stated that in the males the tibio-tarsal articulations did not overlap when the

legs were folded at right angles to the body. In my series the articulations overlapped in almost one-half of the individuals of both sexes.

Breeding habits.—A detailed account of the breeding was given by Pope (1931) in his observations on Chinese amphibians. According to Pope, laying takes place in quiet water. Depending on temperature and availability of water, breeding may begin any time from March to July. Generally the season lasts but six weeks. Eight of eleven females collected on Okinawa between April 19 and April 25 contained eggs. Two of the Ishigaki females also contained eggs. These specimens were collected "April, 1899."

Inter-island variation.—Stejneger (1907) reported that individuals of *limnocharis* from Ishigaki were distinguished by a light mid-dorsal line. Nineteen of the twenty examined for this study displayed this character. The width of the stripe varied from 0.5 to 3.0 mm. None of the Okinawa frogs had so much as a trace of the line. There were also significant differences between the two samples in size and body proportions, as illustrated in the following table.

COMPARISON OF *Rana limnocharis* FROM OKINAWA AND ISHIGAKI

Mean	Sex	Okinawa	Ishigaki	Diff.	t	n	P
Log body length....	♂	1.5509±0.0087	1.6874±0.0064	0.1365	11.55	27	0.001
Body length in mm.	♂	35.56	48.68				
Log body length....	♀	1.5919±0.0133	1.7089±0.0034	0.1170	5.005	19	0.001
Body length in mm.	♀	39.07	51.56				
Body length/leg length..........		0.657 ±0.008	0.635 ±0.005	0.022	1.956	49	0.056
Tibia/leg length...		0.284 ±0.001	0.297 ±0.002	0.013	5.200	49	0.001
Head width/body length..........		0.335 ±0.003	0.331 ±0.002	0.004	1.023	49	0.32

Although the body length/leg length difference is on the border line of significance, only in the head width ratio is there clearly no distinction between the two groups.

When compared with specimens from the continent, the Ishigaki series is similar to the populations in Formosa, Fukien, and Indo-China. The resemblance lies in the frequency of the median line (present in seven of nine specimens from Formosa, five of twelve from Fukien, and twenty of twenty-nine from Indo-China), size, and proportions. Strangely enough, the Okinawa series shows remarkable similarity to the sample from Szechwan in these characters. Not one of forty-three individuals from this Chinese province has a median line. In other respects the various samples are all very much alike. It seems likely that there are at least two subspecies, one in western China and the other in southeastern Asia

including Formosa and, possibly, the southern Riukius. The relation of the Okinawa population to the rest of the species is not determinable at present, the final analysis requiring comparison with material from the Oshima group and Japan.

Rhacophorus schlegelii Gunther

Distribution.—This species is found in the southern half of Honshu, in Shikoku, Kyushu, all of the groups of the Riukius except the Tokaras, and in Formosa. It is the only frog known to have this range. All of the others that occur both in Japan and the Riukius are also found in China.

Specimens examined.—Total, 174: Japan, 8 (*schlegelii*); Amami, 14 (*amamiensis*); Okinawa, 47 (*viridis*); Ishigaki, 100 (*owstoni*); Formosa, 5 (*moltrechti*). Most of these were from the collections of the California Academy of Sciences; some specimens were from the United States National Museum.

Taxonomic notes.—The *schlegelii* group as here interpreted contains the following forms:

Form	Distribution
schlegelii schlegelii Gunther	Japan
schlegelii arborea Okada and Kawano	Japan
schlegelii amamiensis subsp. nov.	Oshima group
schlegelii viridis Hallowell	Okinawa group
schlegelii owstoni Stejneger	Yaeyama group
schlegelii moltrechti Boulenger	Formosa

These have been variously considered as species and as subspecies. Stejneger (1907), though recognizing the close relationship, believed they were separate species. Okada and Kawano (1924) considered *arborea* to be a subspecies of *schlegelii*. They also described another subspecies, *intermedia*, which is probably the intergrading population of *arborea* and *schlegelii* as it is intermediate between them in range and breeding habits. There are apparently no morphological differences among these three. Okada (1926, 1931) treated *viridis*, *owstoni*, and *moltrechti* as separate species. But his interpretation of the relationships of these forms was in error, for he reported both *viridis* and *owstoni* from Formosa and Okinawa. Van Denburgh (1912b) reduced the forms, with the exception of *moltrechti*, to the subspecies level.

Wolf (1936) added *moltrechti* and many currently recognized species to the list of subspecies of *schlegelii*. His forms can be divided into three geographically isolated groups: (1) an East Indies

unit consisting of *javanus, poecilonotus, acutirostris,* and *monticola;* (2) a Chinese unit of *davidi;* and (3) the present East China Sea group of *schlegelii, viridis, owstoni,* and *moltrechti.* From the ranges and the fact that the members of the first two divisions are spotted dorsally, one concludes that Wolf was dealing with three separate species complexes. It is apparent that his conception of a species differs from mine. I believe that these forms are related subspecies of the same species. The occurrence of *schlegelii* on every island group and the similarity between successive populations lead me to the conclusion that the populations have been separated for a relatively short period of time, probably not long enough to become reproductively isolated.

Diagnosis.—This is the only *Rhacophorus* with a uniformly green back. In preserved material the color may be blue or slate. Because of the disks of the digits, *schlegelii* will not be confused with any of the species of *Rana* or the only *Bufo* found in the islands. However, juvenile *schlegelii amamiensis* (the only form found in the range of *hallowelli*) are superficially very similar to *Hyla hallowelli.* Older specimens are larger than *hallowelli* (more than 40 mm. as compared to 35 or less) and have dark blotches on the sides and thighs. Juvenile *schlegelii* may be differentiated from the *Hyla* by the position of the nostrils (see p. 322).

Secondary sexual characters.—These are of the type so common among frogs. The males when mature have granular nuptial pads on the first two fingers and a median internal subgular vocal sac. The first metacarpal of the female, in contrast to the rounded one of the males, is blade-like. The relative breadth of the metacarpal increases considerably with age. In addition, the females are much larger than the males, as is shown in figure 55 and in the table on page 343. With regard to body proportions, there was no significant sexual differentiation.

Breeding habits.—Okada (1928, 1931) stated that breeding of the typical form occurs from mid-April to June. Among the specimens examined, all of which were collected between April 26 and June 2, only one female contained eggs. Apparently the active period of egg-laying had passed. Okada (1928) reported seeing on March 25 an egg mass at the edge of a rice paddy on Amami. As none of the five large females of *amamiensis,* collected from April 26 to May 1, contained mature ova, it is likely that, on Amami at least, the breeding season begins in March and ends in April. Presumably the more southerly forms breed slightly earlier.
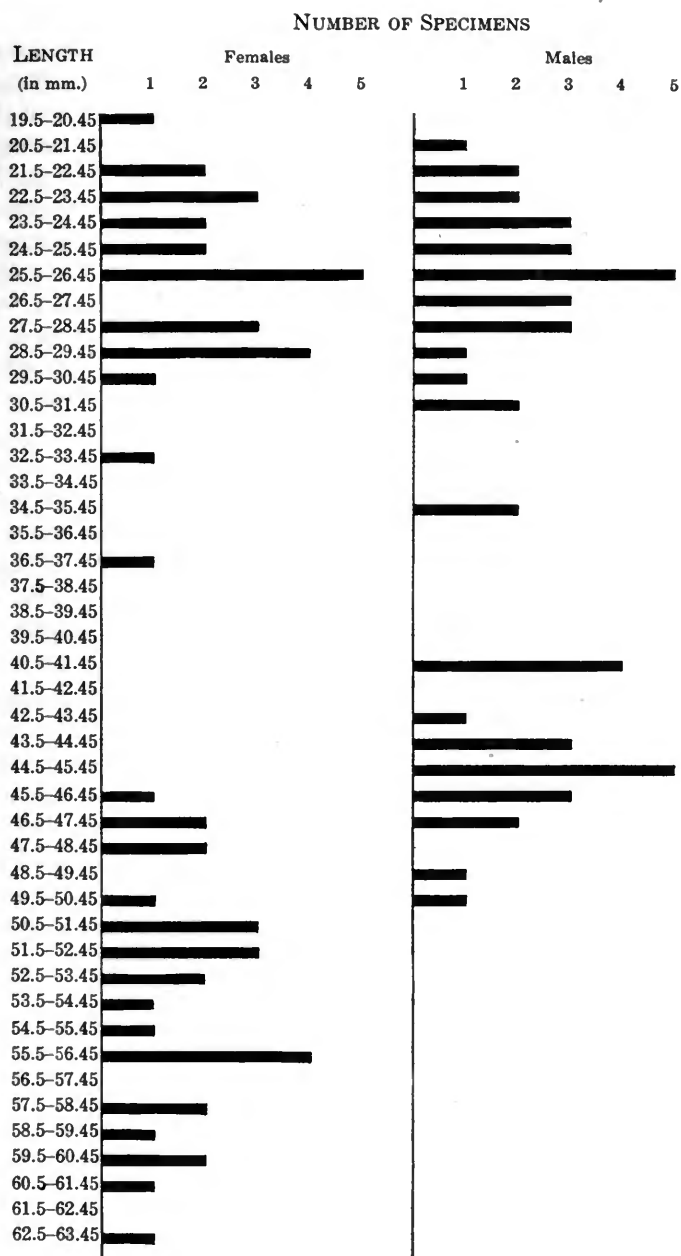
FIG. 55. Size frequency distribution of *Rhacophorus schlegelii owstoni*.

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The eggs of the typical subspecies are laid in a hole on the sloping banks of ponds and rice paddies (Ikeda, 1897; Okada, 1928). That the Riukiu forms have the same habit seems likely, in view of Okada's observation of the egg mass on Amami. On the basis of field observations Ikeda and Okada attributed the nest preparation to the female. The latter reported that prior to mating several males were frequently found in the same hole with a single female. During deposition both male and female beat up the gelatinous material covering the eggs into a white frothy mass. According to Ikeda the jelly becomes liquefied at about the time the eggs hatch. When the liquid reaches the proper consistency, it flows out of the opening through which the adults left the nest. The eggs will not develop in water.

Life cycle and growth.—Figure 55 is a graph of length frequencies of the Ishigaki (*owstoni*) series that was collected between May 25 and June 2. The frequencies are plotted at the center of one millimeter class intervals. There is a pronounced break in the distribution of both males and females. In the former the gap runs from 35.0 mm. (the actual measurement) to 41.0 mm.; in the females from 37.0 to 46.0 mm. This gap is probably the separation of two age groups which we shall temporarily call "younger" and "older."

In the Okinawa (*viridis*) series there were five individuals that were incompletely metamorphosed. The range of body length of these, which still retained the tail, was from 17.5 to 19.0 mm. The *viridis* series was collected from May 5 to May 11. As the distribution of the "younger" *owstoni* group falls immediately beyond the range of the tailed specimens, I conclude that the young of the two species were born at approximately the same time. The age assigned to the "younger" group depends on whether metamorphosis occurs shortly after birth or whether the tadpole stage lasts a full year. In the relatively cool climate of our Great Lakes region, *Hyla versicolor* metamorphoses when approximately 17 mm. long and within sixty-five days after hatching. It is difficult to believe that, in the much warmer climate (rarely below 50° F.) of the Riukius, it takes *R. schlegelii* a year to reach the same size. Consequently I assume that metamorphosis in *schlegelii* takes place about forty days after birth.

That assumption leads to the conclusion that the "younger" group consists of young of the year. In the table on page 341 it is shown that there is no significant difference between the sexes in this age group. However, the graph (fig. 55) shows a sexual differentiation in the "older" group, the significance of the difference

being shown in the table (bottom, p. 343). The explanation of the difference is that the growth rate of the females is greater than that of the males during the first year. Whether or not the females or both sexes grow appreciably after the second year cannot be determined from the data available; neither can the "older" group be broken into its component age groups.

In the Okinawa (*viridis*) series only ten specimens measured less than 40 mm. Of the ten, none was larger than 33.0 mm. Of those over 40 mm., the smallest male measured 40.5 and the smallest female 42.0 mm. None of the specimens from Amami (*amamiensis*) was under 42.0 mm. Thus we can split the entire series into two age groups in the vicinity of 40 mm.

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SUBSPECIES OF *Rhacophorus schlegelii*

Analysis of size of young of the year

</div>

Subspecies	Sex	Length in mm.	Mean	Diff.	t	n	P
owstoni	♂	26.70	1.4267±0.0100				
owstoni	♀	26.58	1.4246±0.0115	0.0021	0.001	51	0.99
viridis	♂	25.74	1.4107±0.0221				
viridis	♀	25.30	1.4031±0.0162	0.0076	0.021	8	0.97
owstoni	♂	26.70	1.4267±0.0100				
viridis	♂	25.74	1.4107±0.0221	0.0160	0.688	33	0.50
owstoni	♀	26.58	1.4246±0.0115				
viridis	♀	25.30	1.4031±0.0162	0.0215	0.623	26	0.54
owstoni	♂ ♀	26.61	1.4252±0.0075				
viridis	♂ ♀	25.64	1.4090±0.0154	0.0162	0.861	61	0.39

Inter-island variation.—Generally the differences between subspecies of *schlegelii* can be arranged in linear geographic series as suggested by Van Denburgh (1912b). This phenomenon is illustrated by the nature of the skin of the back. In a series ranging from north to south, the amount of granulation on the dorsum decreases until the skin is perfectly smooth in *owstoni* and *moltrechti*. Concurrently there is reduction in the amount of granulation of the throat and chin from *schlegelii*, which has a rough throat, to *owstoni*, which has a very smooth throat. The gular region of *moltrechti*, however, is slightly rugose.

Likewise, the dark markings change character. In the Japanese specimens they are in the form of fine reticulations; in *amamiensis* the markings become large, confluent blotches covering almost the entire posterior surface of the thigh; in *viridis* they are constricted into numerous discrete dots; in *owstoni* they are dots slightly reduced in number and with some tendency to unite; in *moltrechti* the markings are in the form of spots that are larger in size and fewer in number

than in *owstoni*. With the omission of *amamiensis*, these changes were pointed out by Van Denburgh (1912b). The gradation is illustrated in figure 56.
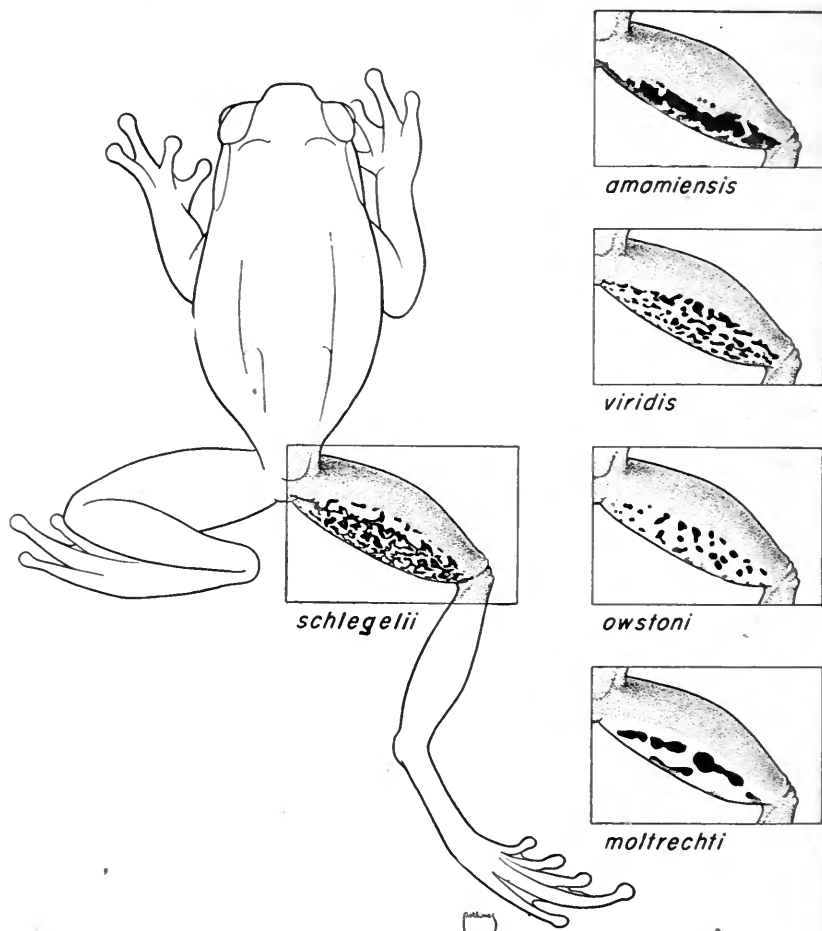
FIG. 56. Geographic variation in the color pattern in subspecies of *Rhacophorus schlegelii*. The subspecies are arranged in geographic order from north to south. The typical form is found in Japan, *amamiensis* in the Oshima group, *viridis* in the Okinawa group, *owstoni* in the Yaeyama group, and *moltrechti* in Formosa.

Further differences between these island populations are shown by the changes in body proportions. These ratios were not computed for *schlegelii* or *moltrechti* as too few specimens were available. Of the other forms only those individuals that were over 40.0 mm.

in length were used in the comparison below. It will be recalled that 40.0 mm. is approximately the lower limit of the individuals one or more years old.

SUBSPECIES OF *Rhacophorus schlegelii*

Comparison of body proportions

	No.	Body length / Leg length	Tibia / Leg length	Head width / Body length
amamiensis	14	0.666±0.008	0.296±0.001	0.348±0.003
Difference		0.001	0.006	0.003
t		0.175	2.940	0.672
Prob.		0.86	0.007	0.51
viridis	35	0.667±0.004	0.302±0.001	0.351±0.003
Difference		0.012	0.008	0.026
t		2.294	5.574	7.239
Prob.		0.03	0.001	0.001
owstoni	45	0.679±0.003	0.294±0.001	0.377±0.002

Only the means are cited. In all ratios used there is a significant difference between *viridis* and *owstoni*. However, *amamiensis* differs from *viridis* only in the tibia/leg length ratio. Undoubtedly the greater distinction between *viridis* and *owstoni* reflects a longer period of isolation, a conclusion supported by the geologic history of the islands.

SUBSPECIES OF *Rhacophorus schlegelii*

Analysis of size of specimens one or more years old

Subspecies	Sex	Length in mm.	Mean	Diff.	t	n	P
amamiensis	♂	46.03	1.6632±0.0084	0.0178	1.298	14	.0.22
viridis	♂	44.20	1.6454±0.0112				
owstoni	♂	45.07	1.6540±0.0055	0.0086	0.740	25	0.47
amamiensis	♀	70.70	1.8494±0.0115	0.0944	3.043	31	0.007
viridis	♀	56.87	1.7550±0.0128				
owstoni	♀	53.92	1.7318±0.0071	0.0232	1.563	53	0.13
amamiensis	♂	46.03	1.6632±0.0084	0.1862	13.181	12	0.001
amamiensis	♀	70.70	1.8494±0.0115				
viridis	♂	44.20	1.6454±0.0112	0.1096	4.144	33	0.001
viridis	♀	56.87	1.7550±0.0128				
owstoni	♂	45.07	1.6540±0.0055	0.0778	8.101	45	0.001
owstoni	♀	53.92	1.7318±0.0071				

The table indicates a statistically significant difference in size between females of *amamiensis* and *viridis*. There were only five specimens of the former available, all of which measured between 65 and 76 mm. Four females of *viridis* fell in the same range. Although there may very well be a size difference between these two subspecies I believe that it will not approach the magnitude shown in the table and that the difference shown is the result of the accidents of collecting.

Rhacophorus schlegelii amamiensis subsp. nov.

Polypedates schlegelii viridis Van Denburgh, Proc. Calif. Acad. Sci., (4), **3**, p. 202, 1912.

Rhacophorus viridis Okada, Ann. Zool. Jap., 11, p. 102, 1926; Okada, Tailless Batr. Jap. Emp., pl. xvi, fig. 3, pl. xxi, fig. 5, pl. xxix, fig. 1, text figs. 87–89, p. 188, 1931.

Type from Naze, Amami. No. 23823 California Academy of Sciences. Adult female. Collected April 26 to May 1, 1910, by Mr. Victor Kuhn.

Diagnosis.—This subspecies can be distinguished from the others by the large confluent dark blotches on the posterior aspect of the thighs and on the sides, as illustrated in figure 56. The dorsum and throat are granulated, more so than in *viridis* but less so than in the typical form. The gular region is faintly mottled with brown. Data on size and body proportions are given in the tables on page 343. This subspecies is known only from Amami.

Description of type.—Body tapering to inguinal region; head large, interorbital distance greater than width of upper eyelid; nostril one-third distance from tip of snout to orbit; canthus rostralis distinct, lores obliquely concave; skin of back and throat finely granulated; skin of venter more coarsely granulated; a dermal fold from posterior border of orbit over tympanum to insertion of arm; tympanum distinct, one-half diameter of orbit.

Fingers one-third webbed, first shorter than second; toes almost fully webbed; disks of digits well developed, those of fingers largest; heels touching.

Color of dorsal surfaces slate; throat faintly mottled with brown; venter and under surfaces of limbs immaculate cream; posterior aspect of thigh and lower portion of sides with confluent dark blotches.

Measurements of type.—Snout to vent 76.0 mm., leg length 109.5 mm., tibia length 32.5 mm., head width 26.5 mm., interorbital width 8.0 mm.

Paratypes.—C.A.S. 23824–6, 23830, 23839, 23842–43, 23848, 23856–58, 23860–61 (all from Naze, Amami).

Rhacophorus schlegelii viridis Hallowell

Polypedates viridis Hallowell, Proc. Acad. Nat. Sci. Phila., p. 55, 1860—type locality Okinawa; Stejneger, Bull. U. S. Nat. Mus., 58, p. 147, 1907.

Rhacophorus viridis Boulenger, Proc. Zool. Soc. Lond., p. 149, 1887; Fritze, Zool. Jahrb. Syst., 7, p. 865, 1894; Boettger, Offenbach. Ver. Naturk., Ber. 33–36, p. 106, 1895; Brown, Proc. Acad. Nat. Sci. Phila., p. 185,

1902; Okada, Ann. Zool. Jap., 11, no. 2, p. 102, 1926; Okada, Tailless Batr. Jap. Emp., pl. xvi, fig. 3, pl. xxi, fig. 5, pl. xxix, fig. 1, text figs. 87–89, p. 188, 1931.

Polypedates schlegelii viridis Van Denburgh, Proc. Calif. Acad. Sci., (4), 3, p. 202, 1912.

Rhacophorus schlegelii viridis Wolf, Bull. Raffles Mus., no. 12, p. 192, 1936.

Diagnosis.—The markings of the sides and legs distinguish *viridis* from the other subspecies (see fig. 56). The skin of the dorsal surface is smooth, with only the faintest indication of shagreening. There is no granulation of the throat. Occasionally the lower jaw has a few faint dark spots, but these never extend across the throat. Length and body proportions have already been discussed. The range of *viridis* as here understood is limited to Okinawa. There have been no specimens reported from the other islands of the Okinawa group.

Rhacophorus schlegelii owstoni Stejneger

Polypedates owstoni Stejneger, Bull. U. S. Nat. Mus., 58, p. 149, 1907—type locality Ishigaki; Gressitt, Proc. Biol. Soc. Wash., 51, p. 163, 1938.

Polypedates schlegelii owstoni Van Denburgh, Proc. Calif. Acad. Sci., (4), 3, p. 202, 1912.

Rhacophorus owstoni Okada, Tailless Batr. Jap. Emp., pl. xvi, fig. 1, pl. xxix, fig. 2, text fig. 91, p. 194.

Rhacophorus schlegelii owstoni Wolf, Bull. Raffles Mus., no. 12, p. 193, 1936.

Diagnosis.—The markings of the legs and sides are in the form of small dots differing from those of *viridis* in displaying a tendency to unite and in being fewer in number (see fig. 56). The lower jaw and throat are immaculate. There are no granulations of the dorsal surface and throat. *R. s. owstoni* has been reported from Miyako, Ishigaki, and Iriomote, all in the southern half of the Riukius.

Rhacophorus eiffingeri Boettger

Polypedates burgerii Hallowell, Proc. Acad. Nat. Sci. Phila., p. 501, 1860—not of Schlegel.

Rana eiffingeri Boettger, Zool. Anz., 18, p. 267, 1895—type locality Okinawa or Amami; Boettger, Offenbach. Ver. Naturk., Ber. 33–36, p. 104, 1895.

Polypedates eiffingeri Stejneger, Bull. U. S. Nat. Mus., 58, p. 153, fig. 147, 1907; Stejneger, Proc. U. S. Nat. Mus., 38, p. 97, 1910; Van Denburgh, Proc. Calif. Acad. Sci., (4), 3, p. 203, 1912; Okada, Tailless Batr. Jap. Emp., p. 210, 1931.

Rhacophorus eiffingeri Boulenger, Ann. Mag. Nat. Hist., (8), 4, p. 495, 1909.

Distribution.—This species has been recorded from Amami, Okinawa, Ishigaki, and Formosa.

Specimens examined.—Formosa, 9 (U.S.N.M.).

Diagnosis.—This species has the tips of the fingers and toes developed into the disks common to *Rhacophorus* and *Hyla*. The longitudinal dark lines on the back and the crossbars on the legs distinguish it from *Hyla hallowelli* and *Rhacophorus schlegelii*. The tibio-tarsal articulation of *R. eiffingeri* does not reach the snout as it does in *R. japonicus*.

Secondary sexual characters.—The nuptial pad of mature males is in the form of a large swelling on the medial surface of the first finger. The males also have a median internal subgular vocal sac with openings near the corner of the mouth. The largest male of the Formosa series measured 35.0 mm. The largest of three females containing eggs measured 41.0 mm.

Rhacophorus japonicus Hallowell

Ixalus japonicus Hallowell, Proc. Acad. Nat. Sci. Phila., p. 501, 1860—type locality Amami; Okada, Cat. Vert. Jap., p. 66, 1891; Fritze, Zool. Jahrb. Syst., **7**, p. 865, 1894.

Rana macropus Boulenger, Proc. Zool. Soc. Lond., p. 414, 1886; Boulenger, Ann. Mag. Nat. Hist., (6), **10**, p. 302, 1892; Fritze, Zool. Jahrb. Syst., **7**, p. 865, 1894; Boettger, Offenbach. Ver. Naturk., Ber. 33–36, p. 103, 1895.

Polypedates japonicus Stejneger, Bull. U. S. Nat. Mus., **58**, p. 155, figs. 148–153, 1907; Stejneger, Proc. U. S. Nat. Mus., **38**, p. 97, 1910; Van Denburgh, Proc. Calif. Acad. Sci., (4), **3**, p. 205, 1912; Okada, Tailless Batr. Jap. Emp., p. 207, pl. xvii, fig. 2, pl. xix, fig. 5, text fig. 97, 1931.

Distribution.—This tree frog is found in every group of the Riukius from the Tokara Strait southward. Van Denburgh and Okada have recorded it from Formosa.

Specimens examined.—Okinawa group, Tokashiki, 1 male, 1 female (C.N.H.M.).

Diagnosis.—The disks of the digits in combination with the dark ⟩⟨ shaped markings of the back distinguish this species from all other Riukiu frogs except *R. eiffingeri*. In *japonicus* the tibio-tarsal joint reaches beyond the tip of the snout, considerably farther than in *eiffingeri*.

Secondary sexual characters.—The male has a median internal subgular vocal sac and a granular nuptial pad on the first digit. According to Okada (1931) the female is larger than the male. The

mean of five males measured by him was 29.00 mm., that of sixteen females 31.07. The difference is not statistically significant, P being equal to 0.15 ($t=1.5$). Unfortunately not enough specimens were available to test the supposed sex dimorphism further. Okada also reported that in the male the head is as long as broad. Although he considered that condition diagnostic of males, he did not describe the condition in the female. In the literature there is no mention of the breeding behavior of this species.
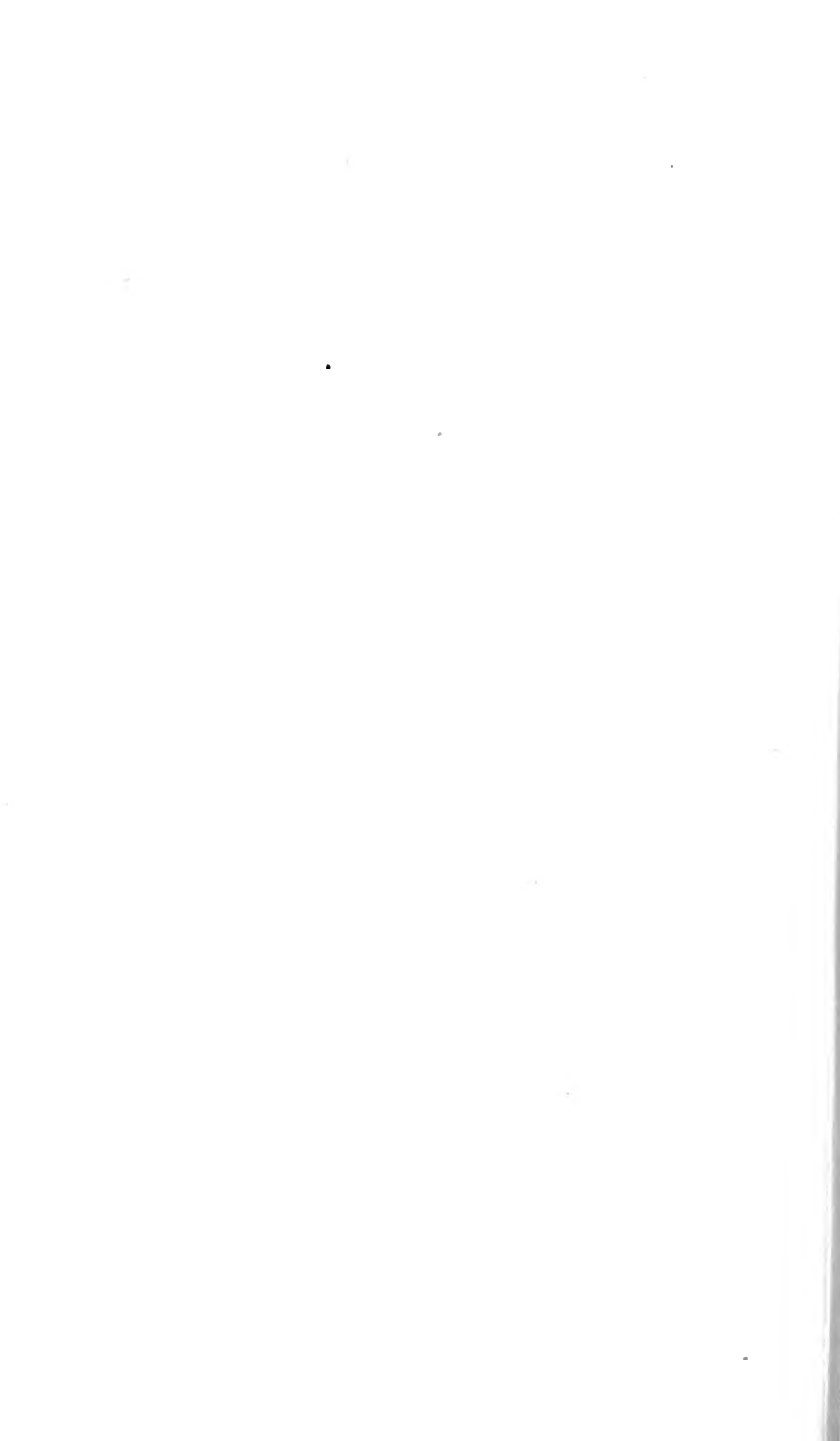
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