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On the History of the Distribution of the Genus Dendrocopos

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(with 29 text-figures and a Summary in Dutch).

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II SAMENVATTING.

Deze studie streeft er naar de geschiedenis van het geslacht *Dendrocopos* (Bonte Specht) te reconstrueren aan de hand van het morphologisch onderzoek en de kennis van het verspreidingsgebied van de soorten. Deze geschiedenis bezit niet alleen een faunistisch kenmerk, maar wijst bovendien op het dynamisch karakter van alle zoölogische systematische eenheden. Overgangen tussen meer of minder homogene populaties (Westeuropese *D. major* en *D. minor*), ondersoorten (*D. syriacus, D. leucopterus, D. atratus*), soorten (*D. nanus, D. maculatus*) en geslachten (*D. mahrattensis, X. albolarvatus*) worden met nadruk genoemd. Er wordt op gewezen, dat de hieruit voortvloeiende nomenclatorische moeilijkheden uitsluitend langs subjectieve weg zijn op te lossen.

De uitbreidings-historie laat zich in vele gevallen tot het begin van het pleistoceen vervolgen. Waar tertiaire gebeurtenissen het recente verspreidingsbeeld schijnen te hebben beïnvloed, laten deze invloeden zich slechts in algemeenheden vaststellen (*D. medius, D. stricklandi, D. kizuki*), of er worden parallelle verschijnselen genoemd uit het terrein van de plantengeographie of de geologie (*D. himalayensis, D. leucotos*). Met groter nauwkeurigheid zijn in bepaalde gevallen de invloeden van de verschillende pleistocene IJstijden op het recente verspreidingsbeeld herkenbaar (*D. major, D. leucotos*). Weliswaar blijft ook hier het hypothetisch karakter gehandhaafd, maar alle conclusies zijn — zo strikt mogelijk — uitsluitend op de verspreiding van de *Bonte Spechten* gebaseerd. Zij worden in het geval van *D. major* en *D. leucotos* getoetst aan soortgelijke conclusies, welke ontleend zijn aan de verspreiding van de Gaai (*Garrulus glandarius*) en verwanten.

In totaal worden 35 soorten (met vele ondersoorten) *Dendrocopos* en 1 soort (met 2 ondersoorten) *Xenopicus* erkend. Van alle soorten werden vertegenwoordigers persoonlijk onderzocht. De *Dendrocopos*-soorten worden zonder moeite verdeeld in 6 grote groepen, die de systematische waarde bezitten van *superspecies* of *subgenera*. Binnen elke groep is de historisch-geographische samenhang van de leden meer of minder duidelijk herkenbaar. Deze samenhang is niet ouder dan midden-tertiair. De morphologische samenhang tussen de groepen onderling is vrij groot. Hun geographische samenhang is niet direct herkenbaar. Wellicht is deze ouder dan midden-tertiair. De auteur heeft nadrukkelijk vermeden bespiegelingen te geven over een mogelijke samenhang van deze groepen. Evenwel lijkt het waarschijnlijk, dat hun geographische verbinding gezocht moet worden ergens in Z.O. Azië, van waaruit alle groepen (met uitzondering van de Noord- en Midden-Amerikaanse *D. villosus*-groep) zich over de continenten hebben verspreid. Wat de betekenis van dit Z.O. Aziatische ontstaanscentrum is, kan aan de hand van de Bonte Spechten alleen, moeilijk worden geschat. Tenminste ook voor de woud-vegetatie en voor de Gaaien, bezit Z.O. Azië het karakter van een ontstaans-centrum.

De auteur meent in de recente verspreiding aanwijzigingen te hebben gevonden van grote postglaciale en interglaciale verplaatsingen, waaraan een groot deel van de N. Aziatische en O. Europese populaties hebben deel genomen (*D. major, D. leucotos, D. minor*).

Discontinue verspreidingen worden beschreven van verschillende ondersoorten (*D. l. leucotos, D. m. minor*), welke zich postglaciaal vanuit O. Azië tot in Europa hebben uitgebreid. Door uitwendige invloeden hebben in dit geval de tussenliggende populaties (Siberië) kleine morphologische wijzigingen ondergaan. De auteur meent nieuwe argumenten te hebben gevonden dat veel recente ondersoorten door historische gebeurtenissen in hun verspreidingsgebied, hun morphologische kenmerken en ecologische eigenschappen hebben verkregen. Tevens hoopt hij te hebben duidelijk gemaakt, dat ook historische zoögeographie zich zeer nadrukkelijk met de ecologische verspreiding moet bezig houden.

III INTRODUCTION.

1. SCOPE.

The scope of this study is to determine whether historical influences upon distribution and taxonomy can be detected in the recent range of the genus *Dendrocopos* (Pied Woodpeckers). In order to reach this aim, cases of parallelism have been sought (1) in the distribution of a small number of other bird forms (especially *Garrulus glandarius*), (2) in the recent and former distribution of the arcto-tertiary forest vegetation, (3) in geologic (late tertiary and post-tertiary) occurrences. What has been reached is a reconstruction of the history of those populations of which the members are considered to be congeneric. The study is full of evidence that the historic successive cases of geographic isolation, and again conjunction of former geographically connected uniform populations have caused morphological, resp. ecological and physiological divergencies, which may be the base of — at all events — the superficial polymorphy of the recent bird forms. Various cases of the dynamic character of the species- and genus-concept have been mentioned in this work: the decisions whether certain forms have been ranked as a distinct *subspecies, species,* or even *genus,* are of a subjective value only. When this characteristic dynamic feature of the history of all organic life is called evolution, this study must be called an evolutionary one. Nevertheless, I have not been able to detect by this working method the pressure of that force that has ruled the system of organic life, of which the most characteristic feature is the adaptive cooperation of all its members, forming the only uniform natural entity that we know of: Nature. Still to the present author this study has had the charm of any historic study that counts with the existence of Him, who is the maker of every History.

2. CORRELATION WITH THE HISTORY OF FOREST VEGETATION.

The history of the genus *Dendrocopos* may be considered to be correlated with the history of the arcto-tertiary forest vegetation, since all members of the group are true tree-birds, occurring only very rarely on the ground; the few cases that *D. major* have been observed drinking, the birds were hanging clasped against the basic trunk of a tree that was standing in or nearby the water (Hagen, 1914). However, the author has more than once observed *D. major* on the ground, when bathing in a small pool. Apart from these normal occurrences *D. major* can be found on the ground in exceptional circumstances only: when migrating in very large numbers during years of autumnal invasions specimens from the N. European race *major* can be found in all localities, either suitable or not; in these periods they have been observed more frequently visiting the ground, but these are apparent exceptions: Pynnönen (1939: Finland) describes the following observations: „Auf ganz vegetationsfreien Dunenschären fand man sie Schwemmholz anhackend" (August 1909); 3 juvenile *major* „hüpfend im Heidekraut auf dem Boden". A few species only, mainly belonging to the "Ladder-backed" group have been observed on the ground more regularly. These species (*macei, atratus, analis*) are — at all events locally — known as ant-eaters. The most striking literature records known by the author of species of *Dendrocopos* being observed on the ground have been mentioned under the separate races.

The extremely multiformous arcto-tertiary forest vegetation, which at present is pushed back into a few widely separated ranges in Eurasia, and North and Central America had a continuous holarctic range in preglacial times, having been attacked by the mighty influences of the glacial periods. A tertiary uniform range is also supposed with reference to the distribution of *Garrulus glandarius* (Voous, 1945); besides, it may be the starting point of the theoretical considerations on the history of the distribution of *Dendrocopos*. Nevertheless, the present author may stress that he is doubtful whether he is correct or not. However, in spite of the fact that the configuration of the subspecific distribution of the preglacial bird fauna is the object of an up to now insoluble problem, "a uniform bird-population in the greater part of the palaearctic region — at all events geographically less varied than at present — proves to be no insufficient starting point in explaining the recent distribution of some landbirds by way of glacial isolation" (Voous, 1945, p. 22).

3. CENTER OF ORIGIN OF DENDROCOPOS.

Evidences of various kinds will be given in support of the assumption of an E. Asiatic origin of the genus. To these will be added here the fact that in S.E. Asia the greatest number of species of *Dendrocopos* are found: in Upper Burma, Manipur, Chin, and Cachin Hills 9 species occur: *catpharius, darjellensis, major, analis, atratus, macei, hyperythrus, canicapillus, mahrattensis*; in Yunnan 6: *catpharius, darjellensis, major, hyperythrus, canicapillus, obscurior*; in S. China 5: *catpharius, darjellensis, major, leucotos, canicapillus*; whereas in Peninsular India only 2 species occur: *nanus, mahrattensis*; in Europe 4: *major, medius, leucotos, minor*; in America, finally, maximum 4 species of *Dendrocopos* have been found side by side: *villosus, pubescens, scalaris, arizonae* (Arizona). It is possible that in this case also the amount of red on the head in the adult and juvenile birds can be used as an indicator of the center of dispersal of the genus: this is especially true with reference to the "Ladder-backed" group in which a total red upper head is only found in those species that inhabit S.E. Asia (*analis, atratus, macei, hyperythrus*), whereas other cases that a red crown occurs in adult birds (*major* group) apparently refers to historically old forms (*himalayensis, assimilis*), as also to the species *leucotos*, which is equally considered to be of a high age, since races are found as tertiary relicts in the Riu Kiu Islands, and in S. China. The red crown in the adults of both sexes, found in *medius*, must be considered to be obtained by mutation, which indicates that neither its origin, nor its taxonomic relation are known. Those species which in the adult stage have relatively less red on the head usually show a greater amount of red in the juvenile birds (*major*: juvenile with a red forehead and upper head!), but the juveniles of *leucotos, analis atratus* and *macei*, which in the adults have a total red crown, have less red than the adults! In the most recently separated species of the major group (*leucopterus*) no red is said to occur in the head of the juvenile female, which is the highest degree of development of this secundary sexual character in the juvenile female. It is very remarkable, however, that trustworthy experiments by Nowikow (1939) tend to show that sexual hormons do not influence the sexual dimorphism in either the juvenile or adult *D. major*! In conclusion the assumption, that a red crown in the adult male is an older character than a reduced amount of red on the head, seems to be a sound basis for theoretical considerations. It is clear that the center of distribution of a red crown is situated in S.E. Asia.

Although an E. Asiatic origin of *Dendrocopos* is apparent, and is also probable with reference to the genus *Picus* (Salomonsen, 1931), this cannot be a severe argument against the hypothesis of Mayr (1946) suggesting a probable "New World (but very early) origin for the family" (*Picidae*) (p. 15). Mayr (*in litt.*, 1946) is perfectly right in stating that "it is quite possible that the family as such could have originated in the Americas while there is, of course, no doubt that the genera *Dendrocopos* and *Picus* originated in the Old World".

4. INTERSPECIFIC COMPETITION.

Interspecific competition appears to be a factor of importance in the recent distribution of the species of *Dendrocopos*, since the manner of living in the different species of approximately the same size is almost the same, both regarding feeding habits and nesting methods. This is especially conspicuous in the distribution of *D. leucotos*, and *D. major* in E. Asia, both species inhabiting the same type of biotope: either light pine woods, or mixed vegetations (*Larix*, *Pinus*, *Betula*). According te Kozlova (1932) the range of *D. leucotos* in E. Asia consists of disconnected colonies only, whereas *D. major* has a general distribution. In the Upper Amur region *major* is a common bird in light pine wood vegetation, but here *leucotos* is rare. In the Lesser Khingan Mountains, however, *leucotos* is very abundant, whereas *major* is totally absent (Stegmann, 1930). A very fine review of the working division and the competition between the Woodpeckers inhabiting the Albanian forest region has been given by Ticehurst & Whistler (1932); especially in the paragraphs on *D. medius*, and *D. leucotos* the author has often referred to it. Interspecific competition has often been observed between the species *D. major*, and *D. medius* in Europe. Interspecific competition plays a role in the recent distribution of *D. assimilis*, and *D. mahrattensis* in N.W. India, and of *D. scalaris* in the S.W. United States; it probably has been of historic importance in the distribution of *D. analis* in Farther India and the Sunda Islands, and it has been thought to be one of the causes of the probable absence of *D. major* in S.E. Europe and of *D. medius* in S.W. Europe during the last glacial epoch. Interspecific competition has not permitted the penetration either of *D. canicapillus*, and *D. minor* into the Japanese Islands, which are inhabited by the much alike *D. kizuki*, the 3 mentioned species apparently only having been forced to live side by side in the Manchurian glacial forest refugium. Interspecific competition combined with a divergence in biotope has plaid a role in the distribution of *D. canicapillus*, and *D. moluccensis* in Malacca and the Sunda Islands. All cases of interspecific competition will be mentioned more in detail in the separate chapters.

5. RESULTS.

The method of reasoning followed in this paper is as strictly *induction* as has been possible to the author in this kind of zoogeographic research. The result is, however, that the author has totally *failed* with reference to the examination of various geographic and systematic problems. Perhaps the most severe one is the total neglecting of the relation of the genus *Picoides* to *Dendrocopos* but the lack of an examination of the great number of American species of *"Sapsuckers"*, which may be thought to have an historic relation with *Dendrocopos*, is equally of importance. The same may be said of the interrelationship of the Ethiopian Woodpeckers of close Dendrocopos-type, which have not been considered owing to lack of material.

Within the genus *Dendrocopos* several *groups* have been arranged, which have an historical zoogeographic value only. In systematics these may possess the subordinate value of either superspecies or subgenera. The working method followed in this paper does not permit to find any indication of the interrelationship of these groups, which, thus, remain independently of each other; in

the recent distribution of the many E. Asiatic forms no indication of this theoretically necessary connection could be found by the author.
Nevertheless, the author hopes, that in this paper at all events a few problems of glacial and postglacial zoogeography have been brought nearer to a solution.

6. NOMENCLATURE.

Relatively little attention has been drawn to nomenclature, since that was not the aim of the author. Therefore no complete synonymy of the species names has been given. In accordance with the fact, that the *generic* name *Dendrocopos* Koch (Baier. Zool. I p. 72, July 1816, type: *Picus major* L.) is not antedated by *Dendrocopus* Vieillot (Anal. Orn. p. 45, April 1816, type: *Picus certhia* Bodd., *Dendrocolaptidae*!) on account of a difference of one letter only (Intern. Rules Zool. Nomencl. Article 36) the generic name of the Pied Woodpeckers used here is *Dendrocopos* and not *Dryobates* Boie (Isis 1826, p. 977, type: *Picus pubescens* L.). The author is glad to be in agreement with Peters in the future VIth Vol. of his "Checklist" (*in litt.*, 1946), and with several other American ornithologists (*Delacour*, 1946, p. 2, footnote 1; Mayr; Van Rossem, *in litt.*, 1946).

7. MATERIAL.

The material upon which this paper is based comprises about 1250 specimens, belonging to the following museums, and private collections: Zoological Museum Amsterdam, Netherlands; Natural History Museum Basel, Switzerland; Royal Museum of Natural History, Brussels, Belgium; Zoological Museum Buitenzorg Java; Zoological Museum of the University of Copenhagen, Denmark; National Museum of Ireland, Dublin; State Museum of Natural History, Leiden, Netherlands; Transvaal Museum, Pretoria; „*Schweizerische Vogelwarte*", Sempach, Switzerland; Royal Museum of Natural History, Stockholm, Sweden; *Congo* Museum, Tervueren, Belgium; United States National Museum, Washington (exchange). — Coll. Van Dedem; coll. Harrison; coll. Van Havre; coll. Hens; coll. F. C. van Heurn; coll. Huber; coll. Ten Kate; coll. Van der Meer; coll. Meinertzhagen; coll. Neijssel; coll. Sillem-Van Marle (incl. *Netherland Karakorum* Expedition).

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Important note : *When reading the chapter on the history of a (super-) species, the corresponding systematic part should be consulted.*

IV KEY TO THE SPECIES OF DENDROCOPOS (INCL. XENOPICUS).

1. a Primaries with white spots .... (2)

   b Primaries black, partially white; not spotted (!) (fig. 18): *albolarvatus.*

2. a Median upper parts (interscapulary region, back, rump, upper tailcoverts, and central rectrices) uniform black or brown: .... *major* group (3)

   b Median upper parts not uniform, but wholly or partly barred or spotted with white; sometimes partly uniform white .... (13)

3. a Upper parts brown .... (12)

   b Upper parts black .... (4)

4. a Wing less than 112 mm; underparts heavily striped: .... *catpharius.*

   b Wing more than 112 mm; underparts either uniform or striped ...... (5)

5. a No opisthotical black band connecting the black malar stripe with the black of the hindneck .... (6)

   b Opisthotical black band present .... (9)

6. a Underparts either heavily longitudinally streaked, or with a distinct yellowish or orange tinge .... (7)

   b Underparts only slightly striped or uniform; no yellowish or orange tinge (apart from the lower tailcoverts and the crissum which may be red) ... (8)

7. a Black malar stripe distinct and fairly well developped; opisthotical region yellowish buff: .... *darjellensis.*

   b Black malar stripe obsolete or only indicated by black bases of the feathers of that region; opisthotical region white: .... *medius.*

8. a Wing less than 125 mm; crown in adult male red; lateral rectrices barred with black and white: .... *assimilis.*

   b Wing more than 125 mm; crown in adult male black, occiput red; lateral rectrices black, in some cases with a few small white spots only; ... *syriacus.*

9. a Scapulars black .... (10)

   b Scapulars white .... (11)

10. a Red on underparts confined to lower tailcoverts and crissum; adult male with the crown red: .... *himalayensis.*

    b Red on underparts extending in a median stripe up to the belly and lower breast; adult male with a red occiput only: .... *major cabanisi* and relative races.

11. a White spots on inner webs of primaries very large, more or less square, most of them reaching the shaft; outer webs of distal primaries make the impression to be white with small black spots (fig. 4): ...... *leucopterus.*

    b White spots on inner webs of primaries conspicuously smaller, rounded, only the basal ones sometimes reaching the shaft; outer webs of distal primaries make the impression to be black with white spots: ...... *major.*

12. a Malar stripe present: .... *arizonae.*

    b Malar stripe absent: .... *dorae.*

13. a Wing over 130 mm; in addition under tailcoverts and lower abdomen red or tinged with red: .... *leucotos.*

    b Wing under 130 mm; if above, no red on underside .... (14)

14. a Anterior part of upper head straw yellow: .... *mahrattensis.*

    b Anterior part of uper head not straw yellow .... (15)

15. a Crown grey or brown; if brown, wing less than 100 mm .... (16)

    b Crown white, red, or black; if brown, wing more than 100 mm ...... (25)

16. a Crown grey .... (17)

    b Crown brown .... (18)

17. a Crown bordered by a black line along the sides of the crown and the occiput: .... *canicapillus.*

b Crown bordered by a brown line along the sides of the crown and the occiput: .... *kizuki.*

18\. a Back and interscapulary region uniform brown: .... *obsoletus.*

b Back and interscapulary region slightly or conspicuously transversely barred or spotted with white .... (19)

19\. a Scapulars uniform brown, or with a few concealed white spots only; in addition a median dorsal stripe of white: .... *ramsayi.*

b Scapulars conspicuously transversely barred; upper back and interscapulary region equally transversely barred or spotted with white (in some cases slightly, but still present); no median dorsal stripe of white ... (20)

20\. a Upper back and mantle olive greenish with faint indications of light cross bars: .... *temmincki.*

b Upper parts either blackish or brownish, distinctly barred or spotted with white .... (21)

21\. a White stripe through eye not broken, running to the white patch on the sides of the neck .... (23)

b White stripe through eye interrupted posteriorly, forming a small white spot above and behind the eye, at all events not reaching the white patch on the sides of the neck .... (22)

22\. a Back, rump, and scapulars regularly transversely banded: .... *kizuki* (*partim*).

b Back, and scapulars irregularly and faintly cross barred; rump almost uniform white: .... *menagei.*

23\. a Throat or upper breast with dark rounded spots; lower underparts usually with sharply defined broad black longitudinal streaks: ... *maculatus.*

b Underparts with narrow dark shaft streaks, or even uniform white or brownish white .... (24)

24\. a Head dark brown with conspicuous blackish borders along sides of head and occiput; underparts longitudinally streaked: .... *moluccensis.*

b Head either dark brown, or much lighter brown, not or only very faintly bordered by a narrow dark line; underparts usually with very faint or without longitudinal streaks: .... *nanus.*

25\. a Crown white bordered with black (♀), or crown red with a white forehead and black occiput (♂) : .... *minor.*

b Crown not so coloured .... (26)

26\. a A median dorsal stripe of white, usually running up to the hind neck; a few slight indications of cross bars may be present .... (27)

b Back white, markedly transversely barred with black .... (28)

27\. a Exposed culmen less than 19 mm; lateral tailfeathers white, either distinctly barred with black, or with a few broken cross bars only: ... *pubescens.*

b Exposed culmen more than 19 mm; lateral tailfeathers uniform white or buffish, in some cases with a few irregularly shaped dark patches only: .... *villosus.*

28\. a Scapulars uniform sooty black: .... *stricklandi.*

b Scapulars distinctly transversely barred with black and white (fig. 20, 21): .... *Ladder-backed* group (29)

29\. a Forehead and fore crown brown, or umber brown: .... *brunnifrons.*

b Forehead and fore crown not so coloured .... (30)

30\. a Central rectrices barred with black and white .... (31)

b Central rectrices uniform black .... (33)

31\. a Under tailcoverts tinged with red: .... *analis.*

b Under tailcoverts without red .... (32)

32\. a Throat and upper breast white, longitudinally streaked with black; adult male with occiput red; adult female without red, and only a few whitish spots on the forehead .... *ligniarus*.

b Throat and upper breast fulvescent white, covered with rounded drop-like spots; adult male with two separate red patches on each side of the occiput; adult female with no red; the forehead profusely streaked with white shaft streaks: .... *mixtus*.

33. a Under tailcoverts with red .... (34)
b Under tailcoverts without red .... (36)

34. a Malar stripe well defined .... (35)
b Malar stripe obsolete or absent: .... *hyperythrus*.

35. a Upper breast very heavily and broadly streaked with black; chin whitish: .... *atratus*.
b Upper breast only faintly streaked with black, or streaks almost obsolete; chin fulvescent: .... *macei*.

36. a Dark eye-stripe well developped, broad, running to the sides of the neck .... (37)
b Dark eye-stripe narrow, forming a black spot behind the eye, of a few mm length only; sides of the head uniform white: .... *borealis*.

37. a Nasal tufts white, or whitish, conspicuously contrasting with the black of the forehead; forehead in adult male uniform black: .... *nuttallii*.
b Nasal tufts as well as a narrow frontal line brownish; forehead in adult male black, profusely spotted with white and red: .... *scalaris*.

V DENDROCOPOS MAJOR GROUP.

1. INTRODUCTION.

To this group those palaearctic and oriental species are referred which are characterized by the wholly black back, without any trace of black-and-white barring. The black areas include hindneck, interscapulary region, back, rump, upper tailcoverts, and central rectrices. No other species of *Dendrocopos* exist in which uniform black uppersides occur. In the majority of cases the scapulars and inner tertials are white, forming two conspicuous shoulder patches. There are several more characters which the members of this group have in common: medium to large size, absence of black eye stripe, red on under tailcoverts (slightly so in some races of *catpharius*!), and lower abdomen, dark cross bars on lateral rectrices.

This group encloses the following species: *catpharius, darjellensis, medius, himalayensis, syriacus, assimilis, major, leucopterus.*

Outside the palaearctic region members are found in China, E. Tibet, Burma, Indo China, Cashmere, and Afghanistan. The greater part of the area is inhabited by one form only. Three species are found side by side in S. W. China, E. Tibet, Burma (*darjellensis, catpharius, major*), two or three in the whole region inhabited simultaneously by *medius, syriacus,* and *major.*

This group may not be considered to be a superspecies, although all members are genetically closely related to each other. Nevertheless, it will be shown in the following paragraphs that clear evidence exists that all forms historically have originated from a common stock, of which the separate characters have been retained independently in the different species. The geographic origin of the group is thought to be situated in S. W. China, where a relative large number of presumed primitive characters have been retained in the three species that at the moment inhabit that country (*catpharius, darjellensis, major*).

In the following lines there will be many occasions to call attention for cases of parallelism in the distribution of *D. major* and *Garrulus glandarius*; of course there are many species of birds which have distributions that agree with the distribution of *D. major*; of these, however, *G. glandarius* is studied more or less thoroughly by the present author (1945).

The following either positive (a = primitive) or negative (b = newly acquired) characters are known to occur in the group.

1. a Adult male with whole crown red.
   b Adult male with a red hindneck only; in *darjellensis* including occiput.
2. a Absence of opisthotical black band.
   b Presence of opisthotical black band connecting the black breast band with the hindneck.
3. a Scapulars black.
   b. Scapulars white.
4. a Presence of a red breastband.
   b Absence of a red breastband.
5. a Undersurface striped; on the flanks ± cross barred.
   b Undersurface with no stripes or bars.
6. a Underparts with yellow lipochrome.
   b. Underparts without yellow lipochrome.

In the following list are mentioned the numbers of the primitive characters that occur in the different members of the group.

	adult	juvenile
catpharius	4.5	5.5
darjellensis	4	5
medius	4	4
himalayensis	2	3
major (*cabanisi* group)	2	3
assimilis	2	3
syriacus	1	4
major (*numidus* group)	1	2
major (*tscherskii* group)	1	2
major (*European* group)	0	1
leucopterus	0	0.5

It appears that in no form all primitive characters have been retained in one species (in the juvenile *catpharius* the yellow lipochrome on the underside appears to be faintly developped only), whereas in only two forms (*major, leucopterus*) newly acquired characters only are found. From this it may be concluded that at the moment only two primitive forms exist: *catpharius* and *darjellensis*, these inhabiting the S. Chinese and S. Tibetan regions from which it is thought that so much animal and plant life has originated. Nevertheless, among the remaining species primitive characters can be detected mostly in those forms that may be considered to be old members of the group, on account of their isolated or remote geographic areas only (e.g. *himalayensis, assimilis*). In conclusion the group appears to be composed of a number of genetic characters (at least 6 pairs) that can be found to occur in 118 of 120 theoretically known combinations (= 98.3%), only the combination in one species of the yellow lipochrome on the underparts (primitive) with a postauricular black band (newly acquired) being unknown. This may be an argument in favour of the theory that taxonomic characters are distributed among the different geographic members of the offspring of an historical primitive form, fully *independently* of each other. The distribution of the separate characters among different forms may have been facilitated by the fact that the group has been severely subject to the influences of the successive ice-ages, causing close contact between isolated and thus differently developped populations.

2. PRIMITIVE FORMS OF DENDROCOPOS MAJOR GROUP.

In the mountain regions of S. E. Asia two species occur that have been considered in the first paragraph on the *D. major* group to be primitive forms, both on account of their taxonomic characters, as on the geographic situation of their ranges: *catpharius* and *darjellensis*. In their adult plumages the following characters are found that in typical members of the *D. major* group occur in juvenile specimens only, or in the adults of isolated populations of relatively higher ages:

a. absence of opisthotical black band (as in *medius, assimilis, syriacus*).
b. black scapulars (as in *himalayensis*, and *major cabanisi* group).
c. presence of a red breast band (only in *catpharius*: as in *major numidus, syriacus juv.*, and ± *major cabanisi* group).
d. streaked undersurface (as in *medius*, ± *syriacus* (much stronger in juv.), and ± *major* juv.).

The present distribution of these species do not indicate the course of their history, although I think it quite clear that they have been derived from each other by geographic (incl. altitudinal) or ecological isolation. *Catpharius* is supposed to be the older form, since more primitive characters have been retained by it, and since it has a wider distribution, being rare or extremely rare in many regions (China). Besides, *catpharius* is the pigmy form of the group, which may indicate a state of degeneration.

In biogeographic theories S. E. China (Yunnan, Sechuan) including E. Tibet have become the most remarkable region of the world, since there is a gradual progress of evidence that most of the Eurasiatic animal- and plant-life has originated from these regions. A few arguments only will be given.

The present flora of the phytogeographic Sino-Himalayan region, including N. W. Yunnan, Sikang, W. Sechuan, E. Himalaya is characterized as compared with the whole Chinese region by the presence (a) of the largest number of species, (b) the highest degree of endemism, (c) the most varied vegetation, (d) the smallest phytogeographic influence from outside. It is supposed by Hui-Lin-Li (1944) that in this region "many of the plants of temporate E. Asia have originated, extending eastward to form important constituents in the other Chinese regions" (p. 257). Even the whole arcto-tertiary forest vegetation may have had here its distributional center; according to Diels (1908) Central China may be called "die Wiege vieler grosser und erfolgreicher Pflanzengattungen" (p. 125). In this region 447 species of *Rhododendron* occur, against 40 in Sikkim amd Bhutan, 6 in the central Himalayas, and 3 in Cashmere (cf. Meinertzhagen, 1928); in the same region 56 species of *Araliaceae* are found, of which 32%are endemic to China, whereas 10% are regionally endemic (Li, 1944). Finally, of the bird genus *Garrulax* 19 species occur in Yunnan, 15 in Nepal and Sikkim, 6 in the central Himalayas, and 4 in Cashmere (cf. Meinertzhagen, 1928). Hora (1938) assumes that S. China is also the centre of distribution of the fresh water fishes of the Oriental (incl. Himalayan) region: nor Peninsular India, nor the Himalayas, nor Malaya having peculiar forms without close relatives in that region. It must expressively be remarked that the present author does not know what is the exact meaning of what is known as a *"distributional center"* or a *"center of origin"*; nevertheless it cannot be denied that there is clear evidence that biogeographically the S. W. Chinese regions have had (or still have) all characteristics of a region where life-forms may have originated. At all events this theory furnish a useful working hypothesis both in phyto- and zoogeography.

In conclusion, it is suggested that the present areas of *catpharius* and *darjellensis* approximately indicate the centre of origin of all members of the *D. major*-group, whence they have spread approximately over the whole of Asia and Europe. *Catpharius* and *darjellensis* are thought to be the oldest members of the group, that have retained the greatest number of primitive characters. All members of the *D. major* group are directly generally related with these, both in time and in place.

D. catpharius catpharius looks like a minor edition of *D. darjellensis*; the remaining subspecies of *catpharius* differ more conspicuously from *darjellensis* as they have maintained an additional important primitive character in the complete development of a red breast band. The species occurs side by side in many regions and are confined to the forests of the high mountains, but *darjellensis* inclines to go generally higher than *catpharius*: For *catpharius* records are to be found in the literature ranging from 1200 to 2800 m, but it is usually found between 1200 and 2100 m (Stuart Baker, 1927); *darjellensis* has been observed between 1800 and 3900 m. In Bhutan Ludlow observed *catpharius* at 1800—1950 m, and *darjellensis* between 2300—3350 m (Ludlow & Kinnear, 1937); in Yunnan *catpharius* has been collected at 2100 m, whereas *darjellensis* has been obtained between 2400—2700 m (Rothschild, 1926).

Judging from the records in the literature *darjellensis* is an inhabitant of dense, and very dense mostly ever-green broad-leaved forest (cf. Stresemann & Heinrich, 1940), especially of Oak and *Rhododendron* (Stuart Baker, 1927; Stanford & Mayr, 1941), being only seldom found in coniferous forests, but occurring up to the highest mountain forests (cloudy forests in the Hsifan Mts.: Schäfer, 1938); in Bhutan, where it is said to be the most common Woodpecker it inhabits all kinds of forest (Ludlow & Kinnear, 1937). *Catpharius* also prefers dense broad-leaved forests of any kind (Stuart Baker, 1927), but it also particularly prefers Oak-woods (Stanford & Mayr, 1941). The habits of *darjellensis* appear to be quite similar to those of typical *D. major*, even its cry closely resembling that of the European *D. major* (Stresemann & Heinrich, 1940).

I **Dendrocopos catpharius** (Blyth 1843: Darjeeling).

Material examined: Darjeeling (3); Nepal (4). — (Amsterdam Mus.; Leiden Mus.; coll. Meinertzhagen).

Measurements:

Wing ♂ 99, 100, 103, 103; ♀ 103 mm.

Culmen ♂ 17.5, 18.5, 19, 19, 19.5; ♀ 17.5 mm.

Range: China, from Hupeh (Bangs & Peters, 1928), Kansu and Sechuan to E. Tibet (Ludlow & Kinnear, 1944), Bhutan (Ludlow & Kinnear, 1936) and Yunnan (Rothschild, 1926), through Upper Burma (Stanford & Mayr, 1941), Shan States, N. Siam (Deignan, 1945) to Tonkin (Delacour & Greenway, 1940); Naga Hills, Manipur, Khasia Hills; eastward to Sikkim and Nepal.

Subspecific characters: The races *pyrrhothorax*, *pernyi*, and *tenebrosus* differ mainly from *catpharius* in possessing a red to orange red gorget. No specimens could be examined; so it will be referred to the following described races only:

D.c. catpharius (Blyth 1843: Darjeeling).

D.c. pernyi (Verreaux 1867: Chingchuan, Sechuan) (cf. Bangs & Peters, 1928).

D.c. pyrrhothorax (Hume 1887: Aimole, E. Manipur).

D.c. tenebrosus (Rothschild 1926: Shweli-Salween Watershed, N.W. Yunnan), (cf. Stanford & Mayr, 1941).

D.c. innixus (Bangs & Peters 1928: Chang Yang Hsien Hupeh, China).

II **Dendrocopos darjellensis** (Blyth 1845: Darjeeling).

Material examined: Sikkim (3); Darjeeling (1); Nepal (5). — (Dublin Mus.; Leiden Mus; coll. Meinertzhagen).

Measurements:

Wing ♂ 127, 128, 130, 132, 134; ♀ 127, 130, 132, 133 mm.

Culmen ♂ 32.5, 34, 35, 35, 36.5; ♀ 30, 31, 33, 34 mm.

Range: W. Sechuan (Rensch, 1924; Hsifan Mts.: Schäfer, 1938), through Yunnan (Rothschild, 1926), Tonkin (Chapa: Delacour & Jabouille, 1940) and Upper Burma (Stanford & Ticehurst, 1939), Shan States and Assam, also Manipur, Cachin and Chin Hills (Mt. Victoria: Stresemann & Heinrich, 1940), to Bhutan (Ludlow & Kinnear, 1937), Sikkim (Meinertzhagen, 1927), Darjeeling, and Nepal.

Subspecific characters: A distinct W. Chinese race (*desmursi* Verreaux 1870: Chinese Tibet, Sechuan) is recognized on account of a shorter bill: culmen 26.5-28, against 33—35 mm (Rensch, 1924).

3. THE HISTORY OF THE DENDROCOPOS MAJOR GROUP IN ASIA

Dendrocopos major is considered here to be an autochthoneous element of the Asiatic fauna, having spread approximately from those regions that at this time are inhabited by *D. catpharius* and *D. darjellensis*, *viz.* S. W. China (E. Tibet), extreme E. Himalayas, Upper Burma, and Indo China. These being also the supposed centers of distribution of the other Eurasiatic species of the genus. Besides, these regions have been equally suggested by Hesse (1912) to be the distributional center of the Green Woodpeckers (*Picus canus-viridis*-group); it may also be correct for the genus *Garrulus*.

The following reflections are mainly based upon the recent distribution of different systematic units within the species *D. major*. No use could be made of the result of a revision of the E. Asiatic *D. major* by *Greenway*, which in August 1946 was in the press (Greenway, *in litt.* 1946).

The possession of black scapulars found in different E. Asiatic forms (*catpharius, darjellensis, himalayensis*, Chinese forms of *major*, formerly referred to the species "*cabanisi*") has led to detailed considerations given in the paragraph on *D. himalayensis*. Black scapulars are supposed to be a character of high age, as is that of a whole red crown in the male (*himalayensis*); these connected with the peculiar geologic history of the Cashmere region make it logical to suppose that *himalayensis* is a remnant of the preglacial Eurasiatic *major* populations to which also *medius* belongs (red crown!).

In the presence of a faintly developped red breast collar the Chinese forms possess an additional character, that can be considered to be antique, since the most splendidly developped red gorget is present in the *pyrrhothorax* group of *D. catpharius*, which is considered to be the most primitive form of the group; in the typical *catpharius* the red breast band is only faintly developped, the breast feathers having narrow red tips only. It is a noteworthy fact that in the races of *catpharius* the red gorget appears to be a real primitive character, since it is found in the adult of *tenebrosus* of N. Burma, whereas it is absent in the juvenile specimen of that race (among which is the type-specimen), thus, showing the reverse situation from that found in all taxonomically and historically derived forms of the *major* group, in which the red breastband may be present in juvenile specimens only (*syriacus*). By the presence of a faintly developped red breastband "*cabanisi*" is connected with the N. African race *numidus*, and with *D. syriacus*. The "*cabanisi*" group of *D. major* can be homologized with the *sinensis* group of *Garrulus glandarius*, both having the same type of Chinese distribution.

Apparently caused by interspecific competition with the many species of Woodpeckers present in the Himalayan forests, *D. major* has not been able to penetrate as far westward into the Himalayas as *Garrulus*, which extends its rangs as far westward as to the N.W. Himalayas and W. Tibet; nevertheless it is possible that the penetration of *D. m. stresemanni* in S. and S.W. direction is at present still going on.

No *major* forms exist that can be directly compared with the distinct Blackheaded Jays from Farther India and Burma. In Indo China, N. Siam, and Upper Burma only *D. catpharius* occurs, which may be historically too far remote from *major* to be compared with populations of a subspecific value only.

The Manchurian region, which is separated from the S. Chinese arcto-tertiary refugional region by a zone of löss, indicating a deforestated area at some time (Reinig, 1937), is inhabited by a race of *D. major* that is totally different from the S. Chinese ones: *tscherskii*. This form has white scapulars and shows very close resemblances with the Japanese forms, both with those inhabiting Hokkaido, and the Hondo group.

In the narrow forest zone in the coastal districts of N. China (Chih-li; Jehol) indications of what may be *intermediate* birds between *cabanisi* (black shoulders) and *tscherskii* (white shoulders) have been found, especially in the neighbourhood of Pekin (Kuroda, 1929; Meise, 1934). It does not appear to be settled whether these birds are odd transitional (hybrid) specimens, or whether they must be referred to intermediate populations to which the name *renschi* (Kuroda, 1929) must be applied. It is noteworthy that in the same region conspicuously polymorph hybrid populations of *Garrulus glandarius sinensis-bambergi* occur, which are known under the name *pekingensis* (Reichenow) (Voous, 1945).

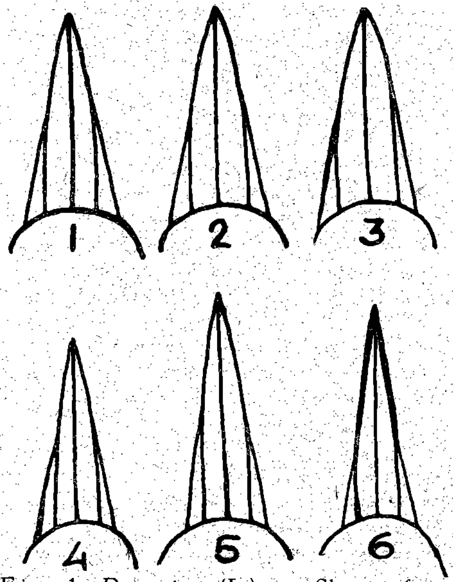

Fig. 1. *D. major* (L.) — Shape of upper mandible (natural size), showing the contrast between the Siberian (*major*) and the Manchurian-Japanese (*tscherskii, kamtschaticus, hondoensis*) types of bill: *major*: 1 ♂ Tatysh, Upper Yenissei; 2 ♀ Tunkun Mts.; 3 ♂ Amur region (January!). *tscherskii*: 4 ♀ Amur region (February!). *kamtschaticus*: 5 ♂ Kamchatka River. *hondoensis*: 6 ♀ Inab, Hondo, Japan.

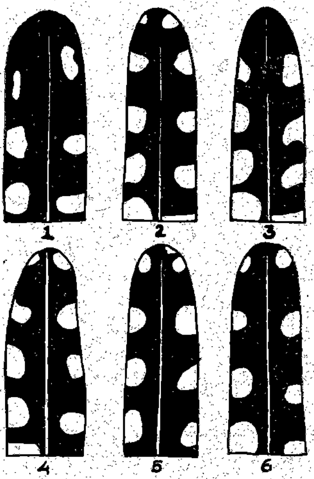

Fig. 2 *D. major* (L.) — Left inner tertials of adult specimens, showing the contrast in the amount of white spotting between the Siberian and the E. Asiatic races: *major*: 1 ♀ Tunkun Mts. *tscherskii*: 2 ♀ Amurregion. *kamtschaticus*: 3 ♂ Kamtschatka River. *hondoensis*: 4 ♀ Inab, Hondo, Japan. *cabanisi*: 5 ♂ Shanghai, China. *mandarinus*: 6 ♂ Foochow, China.

Contrasting with the E. Asiatic Jays conspicuous differences exist between the Manchurian and the Siberian races of *D. major*. The differences refer mainly to the shape of the bill and the pattern of the wing feathers (fig. 1, 2). Thus, it must be concluded, that during the last glacial period two separate N. Asiatic refugia have existed: one small and discontinuous in S. Siberia, and the Manchurian one. Reinig (1937) claims that no S. Siberian forest refugium should have maintained, apparently during none of the glacial periods, although he cannot deny the possible existence of small growths of *Larix sibirica-Picea* *schrenkiana*-vegetations, in which even *Surnia ulula, Picoides tridactylus, Turdus atrogularis, Prunella atrogularis,* and *Nucifraga caryocatactes* may have survived. Reinig is in contradiction with Stegmann (1932, *fide* Reinig, 1937) who has postulated a taiga refugium in S. Siberia during the last glacial epoch, in which a small number of only typical taiga birds should have survived (e.g. *Surnia*; *Cractes*; *Pinicola*; *Loxia*; *Bombycilla*; *Phylloscopus borealis*). Judging from its recent distribution *Garrulus glandarius* has been absent in these associations, whereas on the same grounds *D. major* must considered to have been a denizen of this last glacial taiga refugium. Thus, Reinig (1937) is not correct, when he catechorically states that E. Siberia and Manchuria ornithologically cannot be devided: the distinction between the Manchurian (*tscherskii*) and the Siberian ("*brevirostris*") Woodpecker being the result of the inhabiting of separate glacial refugia. In conclusion, during the last glacial epoch the Manchurian mixed-forest refugium has been inhabited by the *tscherskii*-type, whereas in the same period the "*brevirostris*"-type has survived in the S. Siberian taiga refugium.

Kamchatka is inhabited by a race (*kamtschaticus*), which greatly differs from the E. Siberian "*brevirostris*", showing resemblances with the Manchurian *tscherskii*. Its range seems to be connected with that of *tscherskii* by a narrow zone along the Sea of Okhotsk (Hartert, 1912), but in the mountains near Werkhojansk, and in the Yakuten Peninsula "*brevirostris*" is said to occur (Démentieff, 1934). It can be assumed that the Manchurian Woodpecker has been able to spread in northern direction along the coast, the extreme populations having become slightly distinguishable from the original ones. They can be separated as subspecies in nomenclature.

I regret not to have been able to examine material of *D. m. mongolus* (Lönnberg, 1909: Transbaicalia and Mongolia), which is said to have a long and slender bill, conspicuously different from „*brevirostris*", and agreeing with *tscherskii* and *japonicus*, but possessing less white on the wing quills than in these races (cf. Gyldenstolpe, 1927). I do not venture to make unfounded speculations on these highly interesting populations.

The races of *D. major* inhabiting Hokkaido and the S. Kurile Islands (*japonicus*) apparently have originated postglacially from the Manchurian region; those of Hondo and Tsushima (*hondoensis*) differ more conspicuously from the *tscherskii*-*japonicus* group and therefore I suppose them to be of an older age. Nevertheless, similar differences in relative geologic ages, as appear to exist between the Japanese Jays from Hokkaido (brown-headed: *bambergi*), and from Hondo and other southern islands (striped-headed: *japonicus*, a.o.) do not exist in the Japanese *D. major* populations. *Garrulus g. japonicus* and relatives belong to relict populations from which also the European and S. Caspian forms have originated, and which appear to have spread from the Manchurian area. No homologous antique forms, such as *Garrulus g. japonicus* and *Lalocitta lidthi* (Amami Oshima), are known from the Japanese *major* populations. They appear to me to have become exterminated by interspecific competition with *D. leucotos*, which also occurs in Japan, and which has left a relict form in Amami Oshima (N. Riu Kiu Islands).

Spreading from its Siberian glacial refugium "*brevirostris*" has penetrated into N. E. and W. Siberia, as far westward through Russia and Fennoscandinavia as to Norway and Poland, probably also invading into the coniferous zones of the Alps, where it seems to be gradually pushed back by the European populations. The extreme western populations (Sweden, Norway: *major sensu stricto*) only at the average appear to be slightly different from the Siberian ones ("*brevirostris*"), but separate specimens cannot be named without using the indications on the label; so the name *brevirostris* becomes a synonym of *major*. By far the greater part of Siberia has been populated by *D. major* postglacially! An additional *D. major* population has been isolated during the last glacial period in those regions in Central Asia, that have been situated south of the widely expanded inland sea, which was in contact at times both with the Arctic Ocean, and with the Sarmatic Sea, and which was partly formed by the waters of the yet immense large Siberian rivers, which, owing to the presence of a polar ice-cap could not flow into the Arctic Ocean. It appears, that this refugional range south of the recent zone of löss, can be indicated by the recent distribution of all *leucopterus*-like populations, which appear to have their geographic center in the Turkestan Mts., and in the northern slopes of the W. Kwen-Lun. Hence they have spread into Russian and Chinese Turkestan, and the Karakorum, wherever suitable localities are present. The *leucopterus* subgroup has the relative great amount of unpigmented areas on the wing feathers in common with the Manchurian populations, although in *leucopterus* this character has derived a much higher degree of development. It almost can be said to be a sorrowful accident that in several parts of its range *leucopterus* occurs side by side with a derivate of *"brevirostris"* (a.o. Naryn, Tian Shan; Boro-Khoro Mts.), thus, making it necessary for systematists to separate them as distinct species! The question will be fully discussed in the paragraph on *D. leucopterus*.

III **Dendrocopos himalayensis** (Jardine & Selby 1835: Mussuri).

Material examined: Simla (2); Ngari (4); N.W. Himalayas (2); Cashmere (7) "Himalayas" (3). — (Amsterdam Mus.; Brussels Mus.; Dublin Mus.; Leiden Mus.; coll. Meinertzhagen; coll. Sillem-Van Marle).

Measurements:
Simla, N.W. wing 125—135, average (6) 128.5 mm.
Cashmere: wing 128—133, average (6) 131.2 mm.

Range: N.W. Himalayas, including Garhwal, Simla States, and Kumaon, Cashmere, Gilgit, N. E. Afghanistan (Stuart Baker, 1927); it is also common in the Punjab, and in the Salt Range on the foothills of the Himalayas (Whistler, 1926, and 1930) and it is found in the Hindu Kush, and the Afghan Mts. west to about Safid Kuh (Hellmayr, 1929). It does not occur in Ladakh!

Subspecific examination: Little can be added to the distinction of the subspecies *himalayensis* and *albescens* (Stuart Baker 1926: Gond, Cashmere), nor to the ranges inhabited by these forms. Nevertheless, *himalayensis* does not appear in the first place to be distinguishable from *albescens* by the "more rufous or fulvous" underparts (Stuart Baker). In the material before me the underparts appear to be more greyish brown or even washed with greenish on the lower abdomen. *Albescens* has the underside dull greyish white, with a slight wash of yellowish green on the lower abdomen. No intermediate forms have been seen by me.

Young birds have a conspicuous rufous chin and breast. This juvenile character seems to be more prominent in *albescens* than in *himalayensis*, since a juvenile (autumn-) specimen of *himalayensis* from the Simla States is uniform dull brownnish grey on the underside. Flanks, thighs, and lower abdomen are faintly transversely banded and slightly streaked with black.

Biotope: The species appears to be confined to dense mountain forests, which may be either of coniferous or of deciduous trees; according to Stuart Baker (1934) it prefers mixed forests in which Oak prevails; Osmaston (1924) found it very common in Fir-forests. Nesting holes are found in *Quercus* (Stuart Baker), dead Firs (Osmaston), *Prunus padus* (Whistler, 1930). It is a bird of higher altitudes, being found mostly between 1400 and 3300 m. In most regions it appears to be common, or even abundant.

History: The species resembles to some extent the Chinese forms of *D. major* ("*cabanisi*" *s. l.*), from which it can be distinguished directly by the presence of a red cap in the male. As in these birds it possesses black scapulars, which is a character that also is found in the S. Chinese forms *catpharius* and *darjellensis*.

It is a known fact that the fauna of the Himalayas originates for its greater part from S. China; so the S. Chinese origin of *himalayensis* can easily be presumed. Not only in the relative high number of primitive characters *himalayensis* demonstrates its relative high age; its Cashmere range proves to be inhabited by a number of old palaearctic forms of birds and of mammals (cf. Meinertzhagen, 1928), that are absent in the other parts of the Himalayan chain: *Corvus corone* (black form), *Corvus monedula*, *Nucifraga*, *Garrulus lanceolatus*, *Sturnus vulgaris*, *Iynx*; — *Cervus cashmirianus*. In *Garrulus lanceolatus* a parallel case in the distribution of *Garrulus* and *Dendrocopos* can be detected. Both *lanceolatus* and *himalayensis* stand taxonomically somewhat apart. They are considered to be very old tertiary elements that have been separated in Cashmere from the main palaearctic range. This may have happened perhaps in middle tertiary times already, when a part of Ladakh north to the main Himalayan axis has been occupied by the waters of the retreating Middle Sea (*Tethys*) of which marine sediments have been left "in a long narrow tract in the Upper Indus valley from Rupshu to Kargil and Dras" (Wadia, 1939, p. 428), thus causing the isolation either as an island or as a peninsula of the recent Cashmere range, which, with a great deal of folding and fracturing, was busy rising out of the *Tethys*. This isolated range, which appears to have been surrounded by the sea to the south and to the north, could be reached both by northern palaearctic and eastern oriental forms; their isolation being the beginning of the history of the palaearctic *D. himalayensis*, *Garrulus lanceolatus*, etc., and from the oriental *D. brunnifrons*. It is a noteworthy fact that the recent ranges of *himalayensis* and *brunnifrons* do not cross the Indus valley into Ladakh, this having maintained for some reason or another its character as a boundary of the original insular or peninsular range.

The nearest living relative of *D. himalayensis* cannot be precisely defined; nevertheless, *himalayensis* most closely resembles the Chinese "*caranisi*" on the one hand (black scapulars, also present in *catpharius* and *darjellensis*), and both *medius* and *assimilis* on the other hand (total red cap). As all these forms are thought to be of a relative old age, *medius* probably being a remnant form even of the preglacial forms of the *major* group in Europe, the antiquity of *himalayensis* can be considered to be evident.

The nearest living relative of *Garrulus lanceolatus* appears to be *Lalocitta lidthi* of Amami Oshima, which is considered to be one of the tertiary relicts of the Riu Kiu Island-fauna, thus, furnishing an additional confirmation of the very high ages of both *G. lanceolatus* and *D. himalayensis*.

The nearest living relative of *D. brunnifrons* is thought to be found among the "*Ladder-backed*" forms of Farther India (*analis*, *atratus*, *macei*) and the North American pleistocene refugional areas (*borealis*, *nuttallii*, *scalaris*), from which it differs in the possession of only a yellow component in the lipochrome pigmentation of upper crown and forehead, so that a final evidence is given of the antiquity of at least this Cashmere element.

In pleistocene times relatives of all three forms coming through the Himalayan mountain forests have tried to penetrate once more into the Cashmere region. *D. m. stresemanni* ("*cabanisi*" group) has not been able to contact *himalayensis*, whereas the Brown-headed Chinese *Garrulus g. bispecularis* has penetrated along the whole mountain chain, thus, at the moment occuring in the same region as *G. lanceolatus*. It has to be remembered that the advancing Jay had only few specific competitors in the Himalayas, whereas the interspecific competition between the Woodpeckers appears to me to be a very severe one, thus explaining to some degree the marked difference in progress of the invasion of both Chinese forms of *Garrulus* and of *Dendrocopos*. Along the foot hills of the Himalayas the originally Burmese *D. macei* has reached the region of *brunnifrons*, although not extending its range into Cashmere.

Although terminal moraines, ice-transported blocks, smoothed and striated surfaces furnish sufficient geologic documents of the action of ice on land surfaces in the Himalayas during pleistocene times (Wadia, 1939), yet, the recent distribution of birds (and mammals) make us to conclude that the influence of the glacial periods in the Himalayas has not been so severe as to exclude the existance of all bird life in mountain forest zones. Trees may have survived in this region, since the N.W. Himalayas represent one of the disjunct areas of several arcto-tertiary broad-leaved trees (a.o. *Aesculus indicus* ! : Pax, 1928).

IV **Dendrocopos major (L) : Asiatic subspecies.**

Dendrocopos major major (Linnaeus 1758 : Sweden).

Synonym : Picus brevirostris Reichenbach 1854 : Irtysch, Siberia.
Material examined : Upper Jenissei River (4 : Abekans Mts., Owsjanka, Tatisch) ; Semipalatinsk (1) ; Altai (1) ; Tunkun Mts. (1) ; Amur region (1). — (Dublin Mus. ; coll. Hens ; coll. Sillem-Van Marle).
Measurements :
Wing ♂ ad. 139, 140, 143 ; ♀ ad. 142, 143, 143 mm.
Culmen ♂ ♀ 26.5—28.5 ; average (6) 27.4 mm.
Range : Siberian taiga up to the northern tree-line ; eastwards to the middle Amur River (Blagowechtchensk), the Greater Khingan Mts. and the Werkhojansk Mts. (Dementieff, 1934). Its occurrence in the Stanovoi Mts. is doubtful to the present author. The race is known as an occasional straggler in the area of *tscherskii* : Sakhalin (Hesse, 1915) ; Port Arthur, S. Manchuria ; Seoul, Corea (Kuroda & Mori, 1922) ; Buchedu and Kharbin, Manchuria (Meise, 1934).
Subspecific examination : The subspecific distinction of *brevirostris* was already doubted by Hartert (1904), although in his classic work he tries to give a sufficient diagnosis of the "race" (Hartert, 1912), mainly stating that the lower parts should be white without any trace of brown ; besides, the plumage should be softer and longer, and the red of the lower abdomen brighter than in typical *major*. These distinctions have been critizised by Gyldenstolpe (1926), Stegmann (1930 : hardly 50% distinguishable), and Kozlova (1932), but the race is maintained by Dementieff (1934) on account of the greater frequency of white underparts in Asiatic populations. No taxonomic differences between European *major* and the Siberian *brevirostris* could be detected by the present writer. White underparts occur both in Swedish and Siberian specimens, but the light creamy colour is subject to considerable fading. A freshly moulted adult specimen from the Abakans Mts. (August 21 ; coll. Sillem-Van Marle) has a distinct creamy brown underside, but an adult specimen from Tatisch (Oct. 14 ; coll. Sillem-Van Marle) is pure white. Shape of bill and measurements are exactly like those of the scandinavian ones (fig. 1, no. 1—3 ; fig. 12, no. 1,2) ; occasionally shorter bills and longer wings occur, but these can also be found in the European populations. Hesse (1913) mea-

sures 34 Altai specimens as follows: wing 135—150 mm; Dementieff (1934) finds in 61 Siberian specimens, wing 133—145.5 mm. From a nomenclatural point of view it is to be regretted that a name (*major*), which applies to the outermost populations (Sweden) of a widely spreaded race, which inhabits the whole Eurasiatic taiga, has priority over a name given to central populations. Swedish populations apparently have undergone slight influences of the penetration of the European *pinetorum* into S. Sweden. Nevertheless, no Siberian and N. European specimens can be distinguished as being *major* or *brevirostris*, without making use of the indications on the label. Thus, in this paper, *brevirostris* is treated as a synonym of *major*: nomenclatural type-locality: Sweden; historical-genetic type-locality: S. Siberia.

Biotope: Mainly the taiga („im ganzen ist er als Nadelwaldbewohner anzusehen", Johansen, *in litt.*, 1946), but in S. W. Siberia the species has been found breeding in scattered bushes in the steppes, apparently going as far south as trees occur; Sarudny (*fide* Grote, 1920) even mentions to have found in the Orenburg steppes a typical nesting hole "in der abschüssigen Wand eines Abzugkanals, der um eine vorjährige Heumiete gegraben war" (p. 60) and 5 newly fledged young feeding in the hay on grashoppers.

Dendrocopos major tianshanicus (Buturlin 1910: Kamenaia River, Dsharkent).

Dendrocopos major mongolus (Lönnberg 1909: Topka, Kentei Mts., N. Mongolia (Gyldenstolpe, 1927)).

From these races no material could be examined. They are said to have longer bills, in contrast to the heavy shape found in *major*. Nevertheless, their validity has been doubted by several authors, who have treated them as synonyms of "*brevirostris*":

as regards *tianshanicus*: Stegmann (1935).

as regards *mongolus*: Stegmann (1935); Kozlova (1932); Dementieff (1934).

The validity of *tianshanicus* has been defended by Dementieff (1934): the race is said to be confined to the central Tian Shan, where it is found in the coniferous mountain forests. The race may probably represent intermediate populations between *leucopterus* and *major*, as a conspicuous hybrid between these forms is described by Stegmann (1935) from Dshirgalan, Tian Shan.

The name *mongolus* has found practically no credit. Gyldenstolpe (1927) has once more propagated its validity, and it seems that he is right, for Lönnberg's sketches of the bills of Swedish *major*, and *mongolus* (1909, fig. 9, p. 25) represent totally different forms. Gyldenstolpe (1927) examined 6 specimens from N. Mongolia and S. Transbaicalia and found the white blotches on the secondaries as in *major*, and not as in *tscherskii*; the bill could not be distinguished from those of *tscherskii* and *japonicus*. *Mongolus* might perhaps consist of intermediate populations between *major* and *tscherskii*, the *tscherskii* influence dating back perhaps to the time that the northern boundaries of the Gobi were more abundantly covered with trees than at present.

Dendrocopos major tscherskii (Buturlin 1910: Khanka Lake, N. of Vladivostok).

Synonym: *Dryobates major seoulensis* Kuroda & Mori 1922: Seoul. C. Corea.

Material examined: 1: Amur Region (Dublin Mus.): ♀, wing 131; culmen 27 mm.

Range: Manchuria. Lower Ussuri River, and Corea; Sakhalin.

Subspecific characters: This race is conspicuously different from *major*. The secondaries and tertials have more and broader white blotches than in any other continental E. Asiatic race (fig. 2); the upper scapulars have broad black bases, a few of them also have narrow black edges; these are said to be often tinged with brown (Dèmentieff, 1934). The bill is slender and pointed, resembling the type of bill found in the Atlantic European populations. According to Meise (1934) the undersides of freshly moulted specimens are tinged with "blassbräunlich". Measurements are relatively small: wing of 15 Ussurian specimens 126—131.5 mm (Dèmentieff, 1934); wing of 7 Corean specimens 128.5—131 mm (Kuroda & Mori, 1922).

Dendrocopos major kamtschaticus (Dybowski 1883: Kamchatka).
Material examined: 1: Klutschewskoje on Kamchatka River (coll. Meinertzhagen): ♂, wing 137; culmen 33 mm.
Range: Kamchatka; according to Hartert (1912) also the coasts of the Sea of Okhotsk (Ajan) and according to Yamashina (1931) problaby also the N. Kurile Islands (Paramushiru).
Subspecific characters: The specimen examined can directly be distinguished from *major* by the slender pointed bill (fig. 1), and from *tscherskii* by the less amount of white on the secondaries (fig. 2) and tertials (although slightly more than in *major*) by the pure white underside, and reduced black bars on the lateral tailfeathers, and by the long bill. The race appears to be rare in collections; Dèmentieff (1934) saw among 625 Russian and Siberian specimens of *D. major* only 1 specimen from *kamtschaticus*. The race needs further investigation, especially its intergradation (if it exists) into the N.E. Siberian *major*.

Dendrocopos major japonicus (Seebohm 1883: Hakodate, Hokkaido, Japan).
Material examined: none.
Range: S. Kurile Islands (Uruppu, Kunashiri), Hokkaido Island, occasionally N. Hondo. The *Japanese Handlist* (Hachisuka, c.s., 1932) also mentions N. Corea, as does Yamashina (1932), but this may be a mistake. Corean specimens surely will have to be referred to the slightly different(!) race *tscherskii*.
Subspecific characters: The differences between *tscherskii* and *japonicus* appear to be very slight. No exactly labelled Japanese specimens originating from Hokkaido could be examined. Nevertheless, *japonicus* seems to differ from *tscherskii* by the more pronounced brownish tinge of the underside and the earcoverts, and by the average smaller size (cf. figs. 1, 2).

Dendrocopos major hondoensis Kuroda 1921: Shinano Prov., Central Hondo.
Material examined: Hondo (6): Tokyo, Yokohama, Inaba, Jao. — (Leiden Mus.; coll. Harrison; coll. Sillem-Van Marle).
Measurements:
Wing ♂ 128, 129; ♀ 128, 130, 133, 135 mm.
Culmen ♂ 28, 29.5; ♀ 25.5, 26, 27.5, 28 mm.
Range: Hondo; Tsushima. The *Japanese Handlist* (Hachisuka c.s., 1932) also mentions S. and C. Corea. If these records of the *Handlist* are trustworthy *tscherskii* would breed in Manchuria, *japonicus* in N. Corea, and *hondoensis* in C. and S. Corea! As the 3 mentioned races are only slightly different, these records apparently need further confirmation!
Subspecific characters (fig. 1, 2): *Hondoensis* seems to be slightly darker brown than *japonicus* on the under parts, earcoverts, and forehead. The specimens examined have broad black bases to the proximal scapulars, as in *tscherskii*; a

few possess apical white blotches to these. Besides, *hondoensis* appears to be slightly smaller at the average. Kuroda (1921) believes that 3 colour-phases can be distinguished among 39 Hondo specimens, which he could examine: pale underside (7); medium underside (14); dark underside (18): It is, however, most likely that these differences are nothing else than the result of the general process of fading of the brownish tinge on the underparts throughout the year, as has conspicuously been found in the series of Netherland, Belgium, and Danish populations. According to Kuroda (1921): wing of 45 ♂ ♀ from Hondo: 124—135.5 mm.

Dendrocopos major renschi (Kuroda 1929: Chihli N. China).
Material examined: none.
Although this race is apparently described on one ♀ with white scapulars (in the original description it is said that it is "similar to *seoulensis*" (= *tscherskii*) and "very distinct from *cabanisi*" (p. 61), nevertheless, this name applies to those populations in the coast regions of N. China (Chihli; Jehol), in which the characters of the *cabanisi* group and those of *tscherskii* intermingle. The scapulars in these intermediate populations, of which apparent stragglers occur as winter birds near Pekin, have been described to be irregularly barred with white and dark brown (Rensch, 1924; Kuroda, 1929), even the combination of wholly black scapulars (*cabanisi*) and a greater number of large white patches on the wing quills (*tscherskii*) have been found (Meise, 1934).

Chinese forms.
Dendrocopos major cabanisi (Malherbe 1854: China).
Dendrocopos major mandarinus (Malherbe 1856: Canton, Kwantung).
Dendrocopos major hainanus (Hartert & Hesse 1911: Cheteriang, Hainan).
Dendrocopos major stresemanni (Rensch 1923: Tsalila, Sechuan).
Dendrocopos major beicki (Stresemann 1927: Lau-hu-kou, Kansu).
Material examined:
Foochow: 3: wing ♂ 138, 133; ♀ 132 mm.
Shanghai: 1: wing ♀ 132 mm.
Tai-pai-shan, Tsinling Mts.: 4: wing ♂ 137, 139; ♀ 133, 139 mm.
Range: China, south of the region of *tscherskii* and south of the Gobi Desert, inhabiting also the Nan-Shan Mts, and the Richthofen Mts. (Stresemann & Meise, 1938); westwards as far as the forest vegetation penetrates into E. Tibet (Hsifan and Khams Mts.: characteristic of the altitudes between 1500—4000 m. especially in thick *Hippophaë salicifolia* thickets: Schäfer, 1938), also Yunnan (Lichiang Mts. 3300—3700 m: Rothschild, 1921), and Assam south of the Brahmapootra River, Manipur, Chin and Cachin Hills (2400—4000 m; Stuart Baker, 1934), Shan States (subspecies *cadwaladeri* Schauensee 1934: Keng Tung; synonym of *mandarinus*: Greenway, *in litt.*, 1946), and N. Indo China (Tonkin and N. Laos (Xieng Khouang: rather common): Delacour & Greenway, 1940); also Hainan, but apparently absent in Formosa.
Biotope: Apparently the same as *D. major* in Europe: both coniferous and deciduous forests are inhabited, but more frequently mixed forest types, gardens, and shadow-trees in cultivated areas are preferred; it appears to be common wherever there is sufficient timber of suitable size. In N. Burma it has been observed feeding on Insects in flowering *Rhododendron*; most specimens collected having the forehead heavily pollinated (Stanford & Mayr, 1941), but this may be an exceptional behaviour.
Subspecific examination (fig. 2): A systematic review cannot be attempted owing

to lack of material. I may refer to the revision undertaken by Greenway, which will be published in the mean time (Greenway, *in litt.*, 1946). The biogeographical value of the distribution of these black-shouldered populations, which were first considered to be subspecies of *D. major* by Rensch (1924), has already been discussed in a general chapter. The bill is always slender and pointed; the underparts are subject to a certain amount of variability (dark brownish buff to very light creamy white) caused both by regional differences and considerable fading during the year. Differences in the intensity of the red colour on the lower abdomen and under tailcoverts, as well as those concerning the development of the black barring on the lateral tail feathers are used in the subspecific discrimination of the populations.

V **Dendrocopos leucopterus** (Salvadori 1871: Yarkand).

Material examined: Transcaspia, on River Murkab (2: Imam Baba; Sary-Jasy); N. Afghanistan (2: Haibak); Tashkent, Ala Tau (2); Tarim Basin (8: Maralbashi, Akhdung, Abad, Pialma); N. Slopes of Kwen-Lun (3: Khotan; Sanju). — (Leiden Mus.; coll. Meinertzhagen; coll. Sillem-Van Marle (*Netherland Karakorum Expedition*)).
Measurements:
Tarim Basin; N. Kwen-Lun: wing ♂ 124—130, average (6) 127.2; ♀ 123—126, average (5) 124.8 mm. Culmen ♂ 29—32.5, average (5) 31.1; ♀ 27—29.5, average (5) 28.4 mm.

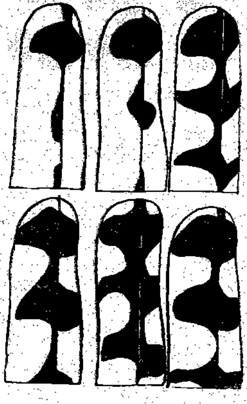

Fig. 3. *D. leucopterus* (Salvad.) — First (outermost) arm quill (secondary) to show gradual change of pattern correlated with geographic distribution. Upper row left to right: Sary Jasy on River Murkab (*albipennis*), Imam Baba on River Murkab (*albipennis*), Tashkent (*leptorynchus*). Lower row: Sanju, N. slopes of Kuen Lun (*leucopterus*), Abad, N. of Yarkand (*leucopterus*), Maralbashi on River Kashgar (*lencopterus*).

Tashkent: ♂ wing 125; Culmen 29.5 mm.
Afghanistan: wing ♂ 128; ♀ 127; Culmen ♂ 27.5 mm.
Transcaspia: wing ♂ 122; ♀ 123 mm; Culmen ♂ 29; ♀ 32.5 mm.
Range: Central Asia (Russian and Chinese Turkestan), from the Transcaspian region along the Middle Amu Darja and Lower Syr Darja (Sarudny, 1908), also along the rivers Murkab and Tedschen; Bukhara; through the N. Afghan Mountains (Meinertzhagen, 1938), N. Hindu Kush, Samarkand, Zarafschan, Ferghana along the Naryn Darja to the Alexander Mountains and Ala Tau, Semiretschensk, Dshungarian Ala Tau and Boro Khoro Mountains to Bogdo Ola (Ludlow & Kinnear, 1933); Tian Shan, Tarim Basin and N. Slopes of Kwen-Lun, eastward to Lob Nor.
Subspecific examination: Within this species there is a general inclination in the western birds to have more white in the wing quills (fig. 3), besides, these show slightly smaller measurements than the eastern ones. Based upon this consideration

it has become a tradition to recognize the following races: (Hartert, 1912; Hartert-Steinbacher, 1935):
albipennis (Buturlin 1908: Transcaspia)
leucopterus (Salvadori 1871: Yarkand)
leptorhynchus (Severtzov 1875: Tashkent).
Nevertheless, it is highly doubtful whether it is justified to distinguish separate races of which the geographically extreme birds only are clearly different from each other, whereas geographically intermediate birds can hardly be named subspecifically. Ludlow & Kinnear (1933) called attention for the fact that in the Bogdo Ola specimens occur which are intermedaite between *leptorhynchus* and *leucopterus*; besides, these authors think it doubtful whether these forms should be kept separate or subspecifically united. Finally, (Dementieff (1934), who could examine 36 specimens, has recognized only one form (subspecies of *D. major*). As I have seen 18 specimens only I do not like to decide whether subspecies should be recognized or not. I only refer to the sketch drawings of homologous feathers of various specimens, which should indicate that at all events a lighter western and a darker eastern form should be worth to be distinguished (fig. 3).

Fig. 4. *D. leucopterus* (Salvad.) — Fourth (externally) primary of *D. leucopterus* and *D. major* to show differences in pattern. From left to right: *D. leucopterus*: Sanju, N. slopes of Kuen Lun; *D. m. major*: Altai; *D. m. tscherskii*: Amur region.

Specific characters; *History*: Little has to be added to the history of this form in Central Asia during the pleistocene (See: *"History of D. major group in Asia*). Judging from its recent distribution and its taxonomic differences it is thought to have become separated from *major* apparently in relatively recent time (fourth glacial). The extreme reduction of melanine on the wing quills (fig. 4) has no parallel case in the genus, although juvenile birds of all races of *D. major* have much more white on the quils than in the adults. Adult *leucopterus*, however, have no white tips to the wing feathers, which is a conspicuous feature in juvenile *major*. In respect to the apparent total reduction of lipochrome in the juvenile ♀ (Hartert, 1912; Dementieff, 1934) in contrast to the total red crown found in the juvenile of either sex in all other forms of the *D. major* group, *leucopterus* proves to be the most differentiated form of this group. It also shows the highest degree of development in possessing a uniform unstriped undersurface in the juvenile bird (!), and in missing in adult and juvenile specimens any melanine pigmentation on the underside, which is pure white. Additional specific characters are formed by the great extension of the fiercely red coloration of the underside, reaching up to the breast, and by the long very slender and thinly pointed bill. Nevertheless, taxonomic characters would not be sufficient to warrant specific distinction. In fact, *leucopterus* is nothing but a race of *major*, which, owing to the simultaneous occurrence of *leucopterus* and *major* in several localities (Dshungarian Ala Tau; Boro Khoro Mts., west to the W. borders of Issyk Kul, Central and

E. Tian Shan; Stegmann, 1935) must be treated *in nomenclature* as a separate species. At all events in the Tian Shan *leucopterus* appears to inhabit exclusively broad-leaved trees, especially poplars which grow on the bottom lands along the streams, whereas *major* inhabits the coniferous forests (*Picea*) in the mountains, thus, preventing these species from meeting frequently. As ecological differences apparently have allowed these species to penetrate into each others regions, it can only be decided arbitrarily whether these forms should be kept conspecific or not (cf. *D. syriacus*; *D. atratus*!).
In the zones of contact between *major* and *leucopterus* transitional races have been described of both forms: *D. m. tianshanicus* (Buturlin 1910: Kamenaia River, Dsharkent), and *D. l. korejevi* (Sarudny 1923: Boro Khoro; Ala Tau). These making the statements of Stegmann (1935), that the species would not be able to interbreed frequently, somewhat doubtful. An intermediate hybrid, originating from Dshirgalan, Tian Shan, has been described by Stegmann (1935). I have been able to examine a ♀ from Tashkent (Mamkenna, 21.XII.1908, coll. Sillem-Van Marle), which neither is a pure *leucopterus*, nor a pure *major*: (1) bill short (25 mm) as in *major*, and, though relatively broad, pointed and thin as in *leucopterus* (fig. 5); (2) forehead brown as often found in *major*, but absent in *leucopterus*; (3) underside tinged with light creamy brown, directly distinguishable from the pure white underside of *leucopterus*; (4) abdomen and under tailcoverts much duller rosy red than in *leucopterus*; I found this colour once in a juvenile ♂ from Semipalatinsk (Sept. 5); (5) the red colour not so profusely developped as in the other *leucopterus* specimens, but still extending up to the lower breast; (6) wing pattern mostly resembling that of the darker specimens of *leucopterus*; (7) wing length as in *leucopterus* (125 mm). It is possible that this specimen represents a *hybrid* between *major* and *leucopterus*, although the influence of the penetration of *major* as far west as Tashkent is hardly to be expected.

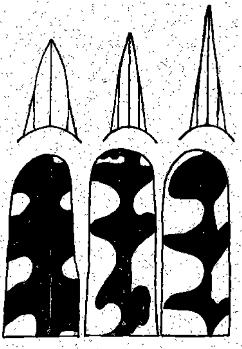

Fig. 5. *D. leucopterus* (Salvad.) — From left to rigth: bill and first outermost arm quill (secondary) of: *D. m. major*: Abakans Mts., Upper Yenissei River; hybrid *major* × *leucopterus*: Tashkent; *D. l. leucopterus*: Tashkent.

Russian ornithologists incline to treat *leucopterus* as a subspecies of *major* (Dementieff, 1934; Stegmann, 1935; Kozlova, *in litt.* 1946), but it seems that at the moment the available evidence, referated above, is in support of the specific distinction of *leucopterus*. Future observations, however, will have to decide, whether this proceeding has been right or not.
Biotope: As dense forests of whatever kind are absent in the greater part of its range (except in the mountain slopes in the north) the species has been found in sparsely wooded regions, generally occurring wherever broad-leaved trees are present. It usually has been found in cultivated areas, in gardens, and orchards near villages and in light *Populus* and *Salix* growths in river valleys.

In the Tarim Basin it is very common near the houses, even feeding upon the thatched roofs (Sillem, 1935), and in the S. parts it is described to be abundant in the oases vegetations of cornfields, cottonwoods, poplars, willows, apricots, peaches, vines, and melons (Ludlow & Kinnear, 1933). Equally in N. Afghanistan the species has been found by Meinertzhagen (1938) in oases amidst swampy grassland plains, being "abundant in the mulberry and plum orchards and gardens in the middle of May" (p. 698). In Transcaspia it appears to inhabit the light forests along the streams, but according to Sarudny (1908) it also occurs in Saxaul bush (*Haloxylon Ammodendron*).

4. THE HISTORY OF THE DENDROCOPOS MAJOR GROUP IN EUROPE.

The history of the *D. major* group in Europe (fig. 6) begins with the first penetration of *D. major*-like Woodpeckers from E. Asia into Europe. At all events in late tertiary times the species inhabited the whole of Europe and the regions surrounding the Mediterranean, as far as the habitat permitted its presence. The discovery of fossil bones furnish sufficient evidence of the preglacial occurrence of the *D. major* group in Europe: Upper Pliocene skeleton remains found in Hungary (Püspökfürdö) have been determined by Capek to belong to both *D. medius* and *major* (1917, *fide* Lambrecht, 1933). In post-tertiary times, however, the supposed continuous area has been disturbed at least four times by the climatic changes, known as glacial epochs. It is supposed that during the maximum glacial conditions the greater part of Europe was not covered with forests or park-like vegetations, thus, causing the *Dendrocopos* populations to retreat to the southern parts of the continent, including the mediterranean and the mesopotamian regions. The ranges of these retreating populations became separated from the main area of the species, thus causing morphological, and in course of time even physiological differences between the separated populations, induced by the unknown factors of geographic and genetic isolation. After each glacial period the tree-vegetation recovered the area lost by the extension of the land-ice, the *Dendrocopos* populations following simultaneously. It appeared, however, that the European range could be occupied either by trees and by Woodpeckers coming from *southern* or *eastern* direction. Thus, in each interglacial period a simultaneous re-occupation of the original area by southern refugional populations took place, together with a fresh invasion of new Asiatic elements. These populations may have been either physiologically indifferent from each other or not; at all events, the European range became fully recovered, the different invasion-elements extending not farther than after having established a distributional equilibrium on the respective boundaries. In general these boundaries may have been the same that existed in post- and interglacial periods between the original arcto-tertiary floral elements and the geologic younger taiga association, which invaded from the east. Thus, at the end of the first interglacial period races of *D. major* could be recognized originating already from a first and a second Asiatic penetration. The second glacial epoch caused the retreat of both these elements in southern direction, but it must be assumed that the area of the oldest populations retained their southern or distal situation with regard to the newly arrived ones. During each following interglacial period a new Asiatic penetration took place, occupying E. and N.E. Europe. Thus, at the end of the last (fourth) glacial period, in recent postglacial times, the number of invading Asiatic forms have become not less than five, the older elements having become pushed back to the very limits of the range of the eastern and western mediterranean refugional regions, forming the end of the long pathway of the series of E. Asiatic invasions. It will be shown that all 5 elements are thought by the present author to be traceable back to the present *Dendrocopos* fauna of Europe: four in the eastern and western part of the mediterranean refugium, in addition to one case of recent penetration into N. and N.E. Europe. Pleistocene records of *D. medius* and *D. major* in Europe are known through the finding of fossil bones in Hungary (38 specimens), Bohemia, Germany, Switzerland (?), Monaco, and Great Britain (Lambrecht, 1933). Even in Ireland, where in recent times no members of the genus *Dendrocopos* have bred, 2 femora have been found in pleistocene cave deposits in the S. W. part of the island (Clare Co); these remains were found in relation with bones of *Turdus ericetorum, T. musicus, T. merula, Erithacus rubecula, Sturnus vulgaris,* besides, with those of Irish Elk, Red Deer, Brown Bear, Arctic Lemming, as also with remains of human manufacture (Newton, 1906). It thus appears, that in some interglacial period *Dendrocopos* populations have been able to penetrate even into the extreme western part of Europe, having become exterminated there with the advancement of the polar climate in the following glacial time.

Postglacial.

The most recent Asiatic penetration is shown in the distribution of the race *major*. It is a noteworthy fact that between the races *major* and *brevirostris* no taxonomic differences can be found, their separation being mainly the result of tradition. *Major* appears to be more or less a typical bird of the taiga, having penetrated into E. Europe after the last glacial period. It has extended its range much farther westward than e.g. *Garrulus glandarius brandti,* which coming from the same direction has not reached Sweden and Norway, whereas in E. Poland, Finland, and in the greater part of European Russia hybrid populations between *brandti* and the European *glandarius* occur (cf. Voous, 1945). It is suggested that both *D. m. major* and *G. g. brandti* have spread postglacially into Europe from their last glacial Asiatic refugium, extending their ranges simultaneously with the extension of the taiga into N. Siberia. Contrary to former records N. Siberia appears to have been covered largely with polar as well as with mountain glaciers, at least during the last glacial periods (Obrutchev, *fide* Reinig, 1937). According to Reinig (1937 and 1938) most taiga birds, among which *Cractes infaustus,* and *Dryocopus martius* have survived in the Manchurian refugium only (*contra* *Stegmann*!), but, as principal differences appear to exist between Manchurian and Siberian *D. major* it may have been possible that in the case of *D. major* some smaller populations have maintained themselves in small isolated forests of *Larix sibirica* and *Picea Schrenkiana* in those southern parts of Siberia that have not been covered by land-ice nor by inland-sea. For the history of this Woodpecker in Europe this question is of minor importance, since it is undoubtfully that *major* is a recent Asiatic invader into Europe (cf. distribution of *D. leucotos*!).

As is the case in many taiga birds *major* also has been able to penetrate into the Central-European coniferous mountain forests, which bear some resemblances with the northern taiga. Thus, in the alpine regions, populations of *D. major* can be detected which are practically identical with the northern ones („*alpestris*"). The same type of distribution is found in *D. leucotos, Picoides tridactylus,* and *Dryocopus martius*. It remains an unsettled question, whether these alpine populations have been directly derived from the last postglacial invasion, or are the remnants of populations that have lived in alpine coniferous forests in the last interglacial period. The last glacial refugium of the alpine coniferous forests are clearly indicated by the recent distribution of *Abies alba,* combined with the result of pollen-analysis. This refuge has been situated S. E. of the Alps in the N. Balcans, from where *Abies* has spread postglacially in N. and N.W. direction, its area covering now, with a great deal of discontinuity, the greater part of the Alps, the Black Forest, and the Carpathian Mts., and being of minor importance, yet isolated regions in other Central-European middle mountains (cf. Bertsch, 1935). According to Reinig (1938) the alpine *Dryocopus martius* populations originate from the Manchurian refugium, from where the species has spread not before postglacial times. It is thought to be most likely that "*alpestris*" forms the S.W. outposts of the post glacial invasion of *major*. "*Alpestris*" seems to be only scarcely found in a pure state; in many regions it seems to be subject to elimination by the lowland form *pinetorum*, these going upwards even to the summits of the mountains in Germany and Bohemia. Two *pinetorum*-like specimens examined, originating from W. Austria (near Salzburg; coll. Hens) may be interpreted to represent an example of such recent penetration of *pinetorum* into the region of „*alpestris*". *Intermediate* populations between the eastward and northward invading *pinetorum*, and the westward invading *major* have been produced in those regions where they met with each other: Poland and extreme E. Germany, Denmark Bornholm Island: these populations having become a severe obstacle in subspecific nomenclature.

It is suggested that the recent postglacial distribution of *D. major* demonstrates those same events that happened during each interglacial period, when freshly arrived Asiatic populations covered a great deal of the coniferous forests in E. and N.E. Europe, causing the existence of at least two groups of geographic races of the species in Europe. Together with the already existing populations the newly arrived invader was deemed to retreat to the South at the advancement of the following glacial period.

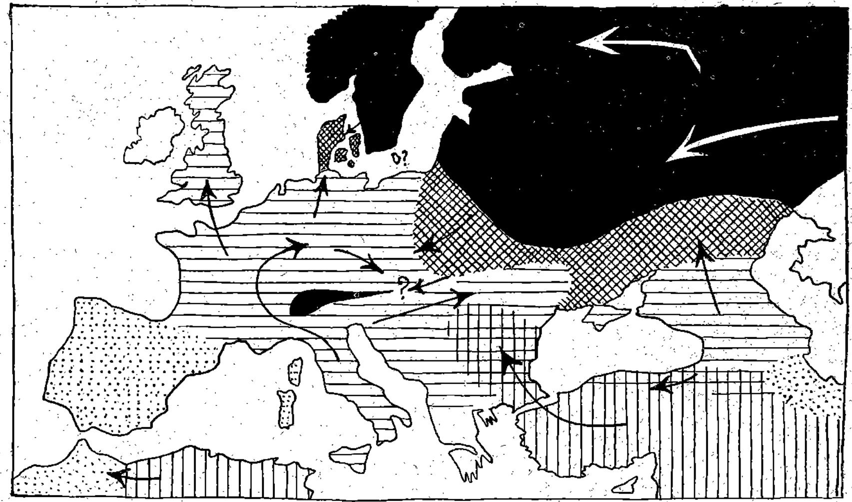

Fig. 6. *D. major* (L.) — Hypothetical postglacial dispersal of populations in Europe (indicated by the arrows): ■ new Asiatic invaders (*major*). ▤ 4th glacial generation. ░ 3rd glacial generation. ▥ 2nd glacial generation. ▦ intermediate populations.

Fourth Glacial (Würm).

Those populations that during the Riss-Würm interglacial period have become adapted to deciduous or mixed forests or park-like landscapes have been isolated in an *eastern* and a *western* European (*mediterranean*) refugium (cf. Salomonsen, 1931), which apparently during the last glacial period have been connected with each other, being situated south of the Alps, and north of the ranges of previous Asiatic invaders. The refugional areas may thought to have been situated in the Italian peninsula, in the southern part of France; doubtfully also in the N.W. part of the Balcans. During the Würm glacial period the greater part of the Balcans seems to have been devoid of *D. major*, its specific competitors *D. leucotos* and *D. medius* having here their most important refugional area.

The French, Italian, and Balcan races are considered to be the direct offspring of the populations out of these refugium, their close similarity in the general coloration (creamy underside), and the shape of the bill (slender) being considered to be the strongest argument in support of this hypothesis. French specimens on the one hand and Rumenian specimens on the other hand can hardly be distinguished from Italian ones, the differences between the French and the Rumenian populations being somewhat greater. Of the British Isles only England and Wales, and recently Scotland have been reached. In Ireland no species of *Dendrocopos* occurs as a breeding bird. The race *pinetorum* has originated from the French populations, and appears to have become subspecifically distinct not earlier than in postglacial times. From Germany it has spread into Denmark; slight influences of *pinetorum* — both in shape of bill, and colour of the underparts — may even be found in the S. Swedish *major*-populations. Which of the two generations, *major* or *pinetorum*, has been able to take possession of Bornholm Island in the S. Baltic Sea, appears to be not definitely established, since Schiöler (1922) refers them to *major* and Löppenthin (1946) to *pinetorum*. Shortly after the closing of my examinations I had the opportunity through the kindness of Mr. B. Löppenthin to examine 4 breeding birds from Bornholm Island. These proved to be intermediate between *major* (relative large measurements: wing 135, 138, 141, 141 mm) and *pinetorum* (rather slender and sharply pointed bill). Indeed, they would be worth to be named separately by those authors that like it to give distinct subspecific names to all intermediate populations. I agree with Löppenthin that the specimens before me can best be referred to *pinetorum*, rather than to *major*. Whether the Bornholm populations originate from the north (*major*) or from the south west (*pinetorum*) or from both directions, I should not like to decide. In the absence of typical *pinetorum* in eastern Central Europe one case more is contributed to the examples of the phenomenon that the E. European mountain masses form a barrier for postglacial floral and faunal occupation of Central Europe coming from the Balcans.

The same genetic relation that has been considered above to exist between the Italian, W. European, and German populations of *D. major may* exist in those populations of *Garrulus glandarius* inhabiting the same regions. The resemblance between *D. major italiae* and the French form *arduennus* stressed above, is also found in the Italian *G. glandarius albipectus* and the French Jays, which Kleiner (1935—38) has referred to one race (*albipectus*). Especially in Belgium and in the Netherlands the intermingling of the characters of the races *G.g. albipectus, rufitergum*, and *glandarius* represents a curious parallelism of the fact that the Belgian and Netherland Woodpeckers can hardly be named subspecifically owing to the intermingling of the characters of the races *D. m. arduennus* (*sive italiae*), *anglicus*, and *pinetorum*. In spite of my former doubts (Voous,

1944) I therefore sympathize with Verheyen (1941) who has identified Belgian populations of *G. glandarius* with *albipectus*, although personal examination has shown that Belgian Jays more closely resemble *rufitergum* (Voous, in press). Therefore, my former supposition that the Netherland populations of the Jay may represent the transition of three recognizable races (*albipectus*, *rufitergum*, *glandarius*) may be correct (1944, p. 47). Neither the Belgian nor the Netherland breeding birds of *Garrulus* and *D. major* can receive suitable names in modern trinominal nomenclature.

In conclusion the following historical and geographic parallelisms can be made:

D. m. italiae — *G. g. albipectus*
D. m. arduennus —
D. m. anglicus — *G. g. rufitergum*
D. m. pinetorum — *G. g. glandarius*
D. m. major — *G. g. brandti*

Northern- and Trans-caucasian populations (*tenuirostris*) probably also belong to the fourth glacial generation, although they may have survived here in small numbers only. They have been widely isolated from other forest areas by the mountain glaciers to the south and the extensive, yet, löss-covered areas of S. Russia to the north. Also in Crimea the species is called a pleistocene relict (Pusanov, 1933), since it is a breeding bird in the mountain forests only; the latter having been subject to considerable chopping during centuries of human cultivation. The Crimean forest fauna is a continuation of the Caucasian one, its insular separation dating back not further than to pleistocene times (cf. Pusanov, 1933).

In relation to the presence of small refugia in the Balcan Peninsula and on the N. side of the Caucasus, it becomes clear that *European Russia* has been populated by three different groups of glacially separated populations: from the East (Asia: *major*); from the South (Caucasus and Crimea: *tenuirostris*); from the Southwest (Balcans: *candidus*). It therefore is clear that the subspecific status of the recent populations in S. and C. Russia is rather complicated, all transitional forms between true *major*, *tenuirostris*, and *candidus* having been found; even Dementieff (1934) with his immense Russian material has failed to obtain clear results. Thus, the race *rossicus* (neighbourhood of Saratoff) may be interpreted to be somewhat intermediate between *major* and *tenuirostris*, although the original diagnosis clearly applies to *major* (Domaniewski, 1925); *artobolevskii* (Charlemagne 1934: Ukraine; winter birds!) may refer to intermediate birds between *major* and *candidus*. Going from N. to S. all shapes of bill can be found in Russia, beginning with the most heavily blunted shaped one of *major*, to the *pinetorum*-like bill of *tenuirostris*, and to the much more slender and pointed bill of *candidus*. *Candidus* appears to be the breeding bird in the Ukraine; in N., W. and N. Central Russia *major* is found; all other Russian populations being intermediate ones which therefore remain unnamed in modern nomenclature.

Caucasian and Crimean Black-capped Jays, like *D. m. tenuirostris*, have equally spread postglacially in N. direction into the present region of „*severtzovi*": Crimean-like Jays (*iphigenia*) have been recorded from Dnjepropatrovsk (Jekaterinoslav), thus clearly demonstrating the penetration of this race into S. Russia (Barabasch, 1933).

The sporadically distributed Asia Minor race *paphlagoniae* may probably be interpreted as an outpost of the *tenuirostris* populations into the region of *syriacus*, its range apparently being widely separated from the Balcan populations.

Third Glacial (Riss).

The third glacial epoch has caused the isolation of the European Woodpecker populations in an E. and a W. mediterranean refugium of which the remnants are to be found in those populations that are characterized by a very dark brown underside and a relatively smaller amount of white on the wing- and tail-feathers. They are found in remote areas, having been pushed back by successive new invaders: in the W. mediterranean areas: Corsica, Sardinia, Iberian Peninsula, Morocco, and Canarian Islands; in the E. mediterranean areas: extreme E. Caucasus, Lenkoran, and S. Caspian Mountains.

The Canarian Islands, which are of a volcanic origin (Miocene), situated on the continental shelf, and separated from the mainland not before holocene times, are inhabited by populations that are only scarcely distinguishable from the Sardinian ones. The red breast band is missing, indicating that no influence of *numidus* has reached them. They are separated from the original members of the same generation (Sardinia, Corsica) by the N. African and S. Spanish races, which possess a variably developped red breast band. Thus, the red breast band proves to be not an original character of the 3rd glacial generation, but to be the result of intermingling with *numidus*.

The historically caused taxonomic differences that exist between the Italian and the French *D. major* on the one hand and the Iberian form on the other hand can also be detected between the W. European (*albipectus*) and the Iberian (*fasciatus*) Jays, although the differences between the two races of Jay are by far not so conspicuous as in *Dendrocopos*. Nevertheless, *D. m. hispanus* is historically equivalent with *G. g. fasciatus*.

The resemblance of *D. m. poelzami* (E. Caucasus to S. Caspian Mts.) with the S. W. European races furnishes an additional case of parallelism in the distribution of *D. major* and *Garrulus glandarius*: *poelzami* may be compared with *G. g. hyrcanus*, the latter conspicuously resembling the western *glandarius* (cf. Voous, 1945).

In the zones of contact between the ranges of *poelzami* and *tenuirostris* in the S. E. Caucacus (Kura Valley, Gouv. Elisabethpol) specimens have been collected ("*kurae*"), which Laubmann (1915; somewhat confused description!) has referred to intermediate *populations* between the two mentioned races, but which by Dementieff (1934) are considered to be intermediate *specimens* only. At all events, hybrid forms of *Dendrocopos* between two races of successive geological ages occur in approximately the same area, in which hybrid Black-capped (*krynickii)* and Striped-headed (*hycanus*) Jays have been found: "*caspius*" (Lenkoran).

Second Glacial (Mindel).

The second glacial period has left the remnants of its mediterranean refugional populations even farther distally away from the entrance of the original Asiatic invaders into Europe. They are characterized by the presence of a red breast band either in all plumages, or in the juvenile stage only, and by the light creamy or almost white coloured undersides which distinguish this geologic generation directly from the succeeding (brown) populations. They inhabit Tunesia and Algeria (*numidus*) on the one hand, and Asia Minor, Syria and the S.E. Balcans (*syriacus*) on the other hand. *Syriacus* has preserved a more or less distinct barring or striping on the flanks and thighs, either in the juvenile stage or in the adult plumage. The most remote offspring of this generation is found in *assimilis*, still inhabiting the S.E. Persian refugium only. *Assimilis* is a minor edition of *syriacus*, but it has an either newly developped, or originally maintained red crown in the adult male.

In Morocco *numidus* has come into contact with representatives of the formation of the yet more or less stabilizised race *mauritanus* with a varying degree of development of the red gorget and a general colour of the under surface intermediate between the creamy colour of *numidus* and the coffee brown of *hispanus*. Pure *numidus* occurs as far W. as extreme E. Morocco (Merada Mts.: coll. Meinertzhagen); *mauritanus* inhabits coastal lowlands of Morocco. The dark brown colour of the underside in S. W. European populations is maintained in the Hispanian (*hispanus*) and the Atlas (*lynesi*) races, but the influence of the penetration of the *numidus*-element is observable in the fact that all degrees of development of the red breast band in these races can be found, varying between being totally absent, and being fairly well represented. In *hispanus* a wholly developped red gorget occasionally occurs, but only in S. populations. Relicts of *numidus* characters which may be called "atavisms" are found throughout the whole European range: red tips to a greater or smaller amount of breast feathers occur more frequently than is usually thought (personally found in Dutch and Danish specimens: cf. also Stresemann, 1920).

Contacts between races of different geologic generations can also be found in the range of *syriacus*. In certain parts of Asia Minor, Caucasus, and the S. Caspian Mts. *syriacus* lives side by side with other forms of *D. major*. This is also the case in S.E. Europe where in historical times it is extending its range very rapidly, apparently without, or only exceedingly rarely, producing, hybrids. It therefore appears justified to call *syriacus* a separate species in nomenclature, although — as *numidus* — it seems to be an equivalent historical race of *major*; only on distributional grounds *numidus* still will be treated here as a subspecies of *major*. *Syriacus* differs from *major* in missing the continuous black band surrounding the earcoverts, which in *numidus*, however, is completed. Details are given under *D. syriacus*.

For the sake of uniformity with *syriacus* the form *assimilis* will also be treated as a separate species.

Different E. Asiatic forms of the *D. major* group have retained peculiar characters, which are also to be found in the *numidus-syriacus* group: traces of red to the tips of the breast feathers, forming a more or less conspicuous faint red breast band, occur in the Chinese races of *D. major* (*cabanisi* a.o.). Fully developped red gorgets form the splendid characters of some races of *D. catpharius*; in this species and in *D. darjellensis* the opisthotical black band is absent, as is the case in *syriacus* and *assimilis*.

The recent distribution of the 2nd glacial generation of *D. major* agrees with that of the mediterranean Blackcapped group of *Garrulus glandarius* (N. Africa, Syria, Asia Minor, Caucasus, Crimea; cf. Voous, 1945). Thus, both groups may be of the same age and may belong to the same faunistic generation. Different cases of parallelism can be remarked. The N. African Jays have also produced a hybrid or intermediate zone in N. Morocco; the Asia Minor forms have penetrated into the region of Constantinople, producing there a hybrid population, as also one in the plains of Lenkoran. So the Jays prove to be unchanged either physiologically and ecologically, whereas *syriacus* has been differentiated from *major* perhaps ecologically only. Black-capped relatives of the mediterranean *G. glandarius* occur in Farther India and Burma, but comparable forms of the *D. major-group* cannot be detected (unless *D. catpharius* and *D. darjellensis* should be considered to represent these).

The occurrence in the Caucasus and in Crimea of Blackcapped Jays only, contrary to the occurrence in these regions of Woodpeckers belonging to an older geologic generation (*tenuirostris*) can be explained by the presumption that during the fourth glacial period Black-capped Jays remained undisturbed in the small Transcaucasian and Crimean refugia from invaders of the third interglacial period (*glandarius*-type). Thus, the Black-capped Jays prove to have spread wider than *D. syriacus*, which is of the same age.

Picus vaillantii (Malherbe) of N. Africa probably belongs to the same geologic generation as *D. m. numidus* and the Black-capped N. African Jays. *Vaillantii* is taxonomically closer to *Picus canus* than to *P. viridis*, to which its range borders (grey sides of head; black moustachial streak in both sexes). The systematic position of *P. canus* may be compared with that of *D. m. major* and its Asiatic races. Even in detail the distribution of *P. canus* in Europe is very like that of *D. l. leucotos*: both species showing the same type of postglacial extension into W. Europe (*canus* has been recorded even as far west as to the Vosges Mts., E. France).

First Glacial (Günz).

In *D. medius* the first glacial epoch has left the eldest European remnant of the offspring of the *major* group. Its preglacial occurrence in Europe has been proved by the presence of fossil bones, which are said to be of *upper pliocene* age (Hungary, Püspökfürdö: Capek, *fide* Lambrecht, 1933). As it is stated that from the same period remains of *D. major* are known, the separation between *major* and *medius* should go back to a tertiary date already, although it can hardly be assumed that in tertiary times the same differences between the two species *major* and *medius* would have existed as to-day. The specific distinction is still more pronounced in *medius*, than in *D. syriacus*. *Medius* is taxonomically higher differentiated, and ecologically differently adapted than either *major* and *syriacus*, but it appears to have developped a high degree of interspecific competition. Probably together with *D. leucotos* it has caused the practical absence of an additional form of *D. major* in the Balcan refugium during the last glacial period. *D. medius* has also retained the original character of heavily striped underparts, and a great amount of yellow and red on the abdomen and lower breast, which characters are also — but still more pronounced — found in the Chinese *D. cafpharius* and *D. darjellensis*. The red crown in *medius* is also a primitive peculiarity, but its presence in the female also, appears to be newly acquired, since it is unique in the whole genus: in the female of *all* other forms of *Dendrocopos* no red on the head is present.

It thus appears that all European forms of *Dendrocopos* with a wholly black median upperside (neck, interscapulary region, back, rump, upper tailcoverts, middle tail feathers) and with a white scapular patch, have been united within one genetic group, of which all members are of an Asiatic origin.

Summary (fig. 6):

I. First Glacial: *D. medius.*

II. Second Glacial: *numidus, D. syriacus, D. assimilis.*
Intermediate population: *mauritanus.*

III. Third Glacial: *harterti, parroti, canariensis, thanneri, hispanus, lynesi, poelzami.*
Intermediate birds: *kurae.*

IV. Fourth Glacial: *italiae, arduennus, anglicus, pinetorum, candidus, tenuirostris, paphlagoniae.*
Intermediate populations: *artobolevskii,* (*rossicus*).
Postglacial: *major* (incl. "*alpestris*").

Nomenclatural System of Verheyen (1941).
This may be the place to compare the nomenclatural propositions of Verheyen (1941) with the above results. Verheyen tries to express in nomenclature the genetic heterogenity of those taxonomically distinct bird populations that are generally called subspecies. Every ornithologist will agree with Verheyen that both phaenotypic and genotypic characters are used as subspecific distinctions, these causing the existence of unequivalent subspecific application. But I disagree with him to call every extremely geographically situated race a "geographic race" indicating that the racial characters are *either genotypically* or *phaenotypically* established, in contrast to the intermediate geographic populations which should be *always phaenotypically* determined ("geographic population"). Based upon the gradual taxonomic changes in the recent N. Asiatic and European populations of *D. major* and *G. glandarius* the following subdivisions are proposed by Verheyen:
Dendrocopos major (p. 10—11) :
brevirostris : geographic race.
italiae < *brevirostris*, that is : *major* : geographic population.
italiae > *brevirostris*, that is : *pinetorum* : geographic population.
italiae : geographic race.
hispanus : geographic race.
hispanus < *brevirostris*, that is : *anglicus* : geographic population.
Garrulus glandarius (p. 15—16) :
glandarius : geographic race.
glandarius > *hibernicus*, that is : *albipectus* : geographic population.
glandarius < *hibernicus*, that is : *rufitergum* : geographic population.
hibernicus : geographic race.
The objections against the treatment of referring apparent equivalent races as e.g. *G. g. rufitergum* and *hibernicus* to different genetic units without having proved it, are at once apparent. W. Europe has been peopled postglacially from the S. mediterranean refugional regions. So the series (1) *albipectus, rufitergum, hibernicus*, and (2) *albipectus, glandarius* consist of fully equivalent races. Much more serious are the objections in the case of *D. major*. Here *brevirostris, italiae*, and *hispanus* only are considered to represent geographic races, whereas *major, pinetorum*, and *anglicus* would have the value of geographic populations, their characters being phaenotypically defined (*sic* !). *Anglicus* and *pinetorum*, which are considered by the present writer to represent the outermost populations of the spreading of *italiae*-like forms out of the mediterranean refugium into W. Europe, are treated by Verheyen as intermediate populations between *hispanus*, resp. *italiae* on the one hand, and *brevirostris* on the other hand. Next to the fact that *anglicus* and *pinetorum* are considered here to have the same historical origin, and thus cannot be genetically differently interpreted, yet, the consideration that *hispanus, italiae*, and *brevirostris* are thought to belong to invasionary elements of a subsequent age, makes it improbable to the present author to accept the more or less subjective treatment of Verheyen, in which no method is indicated to avoid comparing of inadequate races, as has been done in the case of *D. major* !
Equally in his supplementary work on the definition of the units in ornithological nomenclature Verheyen (1946) maintains the distinctions between subspecies, geographic race, and geographic population. However, I fail to see whether in any particular case the mentioned criteria suffice to determine whether a group of populations to which in recent nomenclature the third (subspecific) name refers, must be called by one of the three nomenclatural units proposed by Verheyen. Verheyen seems to be correct that the species is "une unité

dynamique, autonome et naturelle" (p. 4), but this verdict refers more to the characteristic feature of the "species" than that it is sufficient to be a definition!

VI **Dendrocopos medius** (Linnaeus 1758: Sweden).

Material examined: Sweden (6); Denmark (13: Zealand); Netherlands (2); Belgium (3); Germany (14); Switzerland (3); Hungary (3); Rumenia (6); S. Italy (1: Taranto); European Turkey (2); Asia Minor (5: Marash; Taurus; Aidin); Caucasus (3: Kuban). — (Amsterdam Mus.; Basel Mus.; Brussels Mus.; Copenhagen Mus.; Dublin Mus.; Leiden Mus.; coll. Huber; coll. Meinertzhagen; coll. Sillem-Van Marle).

Measurements:

Sweden	wing	♂ 126—128,	♀ 124—130;	culmen	♂ 24—26;	♀ 21—25 mm.
Denmark	,,	♂ 121—128,	♀ 123—127;		♂ 22—26;	♀ 22—25 mm.
Netherlands Belgium	,,	♂ 124—129,	♀ 125—127;		♂ 23—26;	♀ 23—26 mm.
Germany	,,	♂ 121—128,	♀ 122—126;		♂ 23—25;	♀ 22—24 mm.
Switzerland	,,	♂ 125—128,	♀ 123;		♂ 24;	♀ 23 mm.
Hungary	,,	♂ 123,	♀ 126;		♂ 23;	♀ 22 mm.
Rumenia	,,	♂ 122—128,	♀ 123;		♂ 23—26;	♀ 23—26 mm.
Italy	,,	♂ 126,			♂ 24 mm.	
Eur. Turkey	,,	♂ 127—128,			♂ 25—26 mm.	
Asia Minor	,,	♂ 122—123,			♂ 25—26 mm.	
Caucasus	,,	♂ 122,	♀ 121—123;		♂ 24;	♀ 22—23 mm.

Judging from these measurements it appears that the rule of Bergmann is neither confirmed nor contradicted, although populations live under quite different climatic conditions (e.g. S. Sweden; Asia Minor, and Mesopotamia). Nevertheless, the winglengths of specimens of Asia Minor seem to be a trifle shorter than those of European birds. Two ♂ ♂ from Marash, Taurus (coll. Meinertzhagen) measure 122 and 123 mm, whereas 3 unsexed specimens from Aidin (Leiden Mus.) have winglengths resp. 116, 117, 120 mm. Hartert (1912) already mentions the fact, that the Asia Minor subspecies *anatoliae* appears to have the wing 3—9 mm shorter than those of typical *medius*. Personal measurements of specimens from the European range of the species, combined with those of Parrot (1905) give the following result:

Wing: 34 ♂ ♂ 121—129, average 125.0 mm.
Wing: 31 ♀ ♀ 121—130, average 124.5 mm.

The constant measurements prove the species to be in a stable, not evolutionary state.

Range (fig. 7): The greater part of Europe, from S. Sweden (Skane and Blekinge; absent in Norway: Kolthoff & Jägerskiöld, 1898: Wollebaek, *in litt.*, 1946; also absent in Finland), Denmark, Germany, Netherlands, Belgium, France (apparently only irregularly in Normandy and Brittany; besides absent in the Central Massif and in the mediterranean plains: Mayaud c.s., 1936) south to the Pyrenees (the few Pyrenean records being not trustworthy: Mayaud, *in litt.*, 1946); Central Europe, and Italy, where it is rare in Sicily (breeding?) and totally lacking in Sardinia and Corsica (Arrigoni, 1904); Balcan Peninsula; Rumenia, Poland, W. Russia, breeding at all events eastwards as far as Woronesh (regularly breeding: Ognew & Worobjev, 1923; although "rather seldom east of the river Oskold": Gladkov, *in litt.*, 1946), Tula and Kaluga (Johansen, in litt., 1946), in the latter district recorded in winter only (Gladkov, *in litt.*, 1946), Smolensk (breeding) and Pskov (breeding: Grote, 1926), but absent in the vicinity of Leningrad (Kozlova, *in litt.*, 1946), and very rare or lacking (Tischler, 1941)

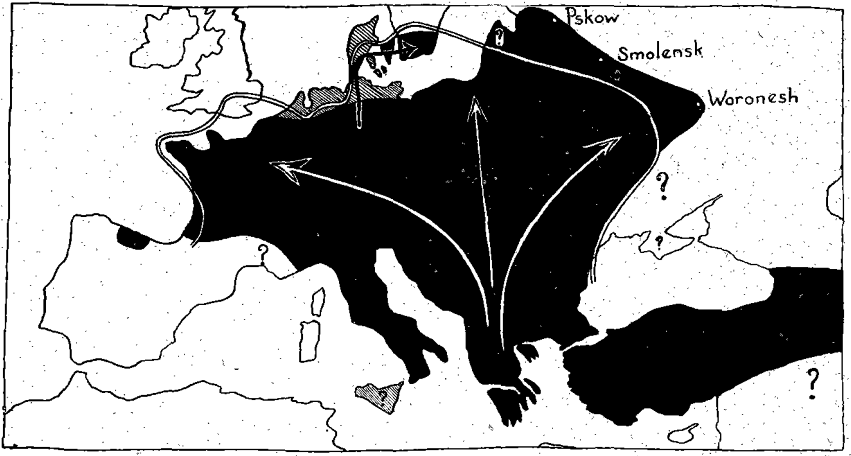

Fig. 7. *D. medius* (L.) — Distribution in Europe; the arrows showing its postglacial dispersal. In the Northsea countries (striated area) its occurrence as a regular breeding bird is uncertain. The northern limit of the range corresponds with that of *Carpinus betulus*, as shown by the white line (Bertsch, 1935, fig. 46).

in the Baltic States, the exact eastern limits in N.W. Russia being unknown; Asia Minor, Caucasus (plentiful in the region of Sochi and Gelendkik, in the basin of the Kuban: Gladkov, *in litt.*, 1946), irregularly breeding in Crimea (Pusanov, 1933); Mesopotamia, S. Caspian Mts., and S. W. Iran (Zagross Mts.); an isolated population inhabits the Cantabrian Mts. near Santander and Nordleon in N.W. Spain (Witherby, 1921 and 1922).

Subspecific examination: Concerning the extension and the intensity of the yellowish colour on the underside of the body, it appears that Balcan and Italian birds are generally more richly coloured than most of the central and Northern European specimens examined, but equally intensively yellow coloured adult specimens have been seen from the Ardennes (Belgium: Leiden Mus.) and from Hungary (coll. Sillem-Van Marle). Young specimens incline to have more yellow on the underside than the adult ones. So I am in agreement with many recent authors that the subspecies *sordidior* (Parrot 1905: Greece) is but poorly characterized so that it seems desirable to omit the name. Nevertheless, it must not be forgotten, that rich yellow coloured specimens are not quite so numerous in northern than in southern populations: all 13 Danish specimens examined have conspicuous grey undersides with only faint tinges of yellow. Connected with the yellow coloration, the intensity of the red coloration on the abdomen and the under tailcoverts, as well as the striations on the flanks and breast sides increase from North to South, apparently reaching the optimum in the Caucasus. Caucasus specimens (Ashej River, Kuban) have a light orange yellow heavily striped underside and a carmine red abdomen and under tailcoverts. These must be separated as *caucasicus* (Bianchi 1904: N. Caucasus). Specimens from Asia Minor have equally orange yellow undersides and are most heavily striped. The rosy red colour of the abdomen and under tailcoverts of the European birds (even present in 2 specimens from Constantinople) is substituted in the Asiatic birds by a more clear red colour. Apart from the different colour on the outermost tailfeathers, the Asia Minor subspecies *anatoliae* (Hartert 1912: Xanthus) must be recognized already on this point only. Birds of southern populations seem to have white throats, not tinged with grey as in central and northern European specimens; this character, however, is not sufficiently pronounced to be used in subspecific discrimination. The colour pattern on the lateral tailfeathers (fig. 8) proves to be very variable. The variability does not only concern specimens of one sex and one country, but in one German ♀ (Eythra, Leipzig: Brussels Mus.) even the right and left outermost tailfeathers are distinctly assymetrically marked with black and white.

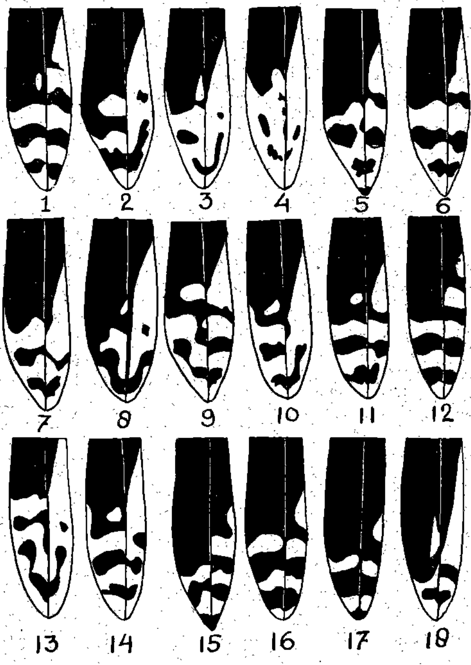

Fig. 8. *D. medius* (L.) — Lateral tailfeathers of adult specimens. The individual variability is too high for using the pattern as racial characters. 1 ♀ Sweden. 2 ♀ Sweden. 3 ♀ Denmark (Zealand: darkest type). 4 ♂ Denmark (Zealand: lightest type). 5 ♀ Netherlands (Heino, Overijsel). 6 ♀ Belgium (Fouron-le-Comte, Liege). 7 ♀ Germany (Leipzig). 8 ♂ Switzerland (Basel). 9 ♀ Switzerland (Basel). 10 ♀ Hungary (Halogy, prov. of Vas). 11 ♂ Rumenia (Cernica). 12 ♀ Italy (Tarento). 13 ♂ EuropeanTurkey (Constantinople). 14 ♂ Idem. 15 ♂ Asia Minor (Aidin). 16 ♂ Asia Minor (Cilicia). 17 ♂ Idem. 18 ♂ Caucasus (Kuban).

Only in the Asia Minor specimens the predominancy of black on the outermost tailfeathers is as sufficiently pronounced, that it can be used as a suitable racial character. It is probable that this is also the case in the subspecies *sanctijohannis* (Blanford 1873: Schiras) from the Zagross Mountains region (not examined). In the other cases the pattern of the lateral tailfeathers has no subspecific value. An additional slightly distinguishable race, described from Santander, N.W. Spain (*lilianae* Witherby 1921) seems worth to be recognized (not examined): wing measurements as in all other populations (4 ♂, 4 ♀: 124—129 mm); bill perhaps longer.

Biotope and history: D. medius has a typical European (i.e. mediterranean) distribution, which means that the species directly originates from the mediterranean, without having had — at least during the last glacial epoch — a central or east Asiatic refuge. From the fact that the species apparently is absent in the Sierra Nevada, the Atlas regions, and in the *Quercus*-forests of Algeria and Tunesia, one may conclude that it inhabited only the eastern mediterranean, including the S. Caucasian forest refugium during the last glacial epoch. Oakforests in the S. Pelopponesus (Niethammer, 1943) and in S. E. Iran (Paludan, 1938) are a favourite haunt of this Woodpecker. Thus, the needed biotope is present in the western mediterranean also, its absence being the result of historical circumstances.

D. medius seems to be a bird which is connected with the original deciduous mixed European forest. Apart from its missing in the western mediterranean region, its range shows many similarities with those of several European broad-leaved trees, which extend not farther east than to central Russia or to the Ural Mountains (e.g. *Tilia, Fagus, Quercus sessiliflora*). The western and northern limits of the range of *medius* especially correspond with those of *Carpinus betulus* (fig. 7) and *Fraxinus excelsior*; thus, these trees showing the same postglacial history as the Woodpecker; *Carpinus betulus* is also absent in the Iberian Peninsula and in N. Africa. Originating from the Balcan forests both *medius* and *Carpinus* have spread postglacially over the greater part of Europe, but at the moment *medius* appears to be a rare and scarce breeding bird, which is very locally distributed and which is even missing in many regions within the limits of its range.

D. medius is common only in very few localities, notably so in the mixed forest of Mamuras, north of Durazzo, Albania, which possesses all characteristics of the more or less swampy European virgin forest with many dead trees and rotten stumps, consisting mainly of Turkish Oaks, Poplars, Alders, Ashes, and Hornbeams. Here *medius* is the most common Woodpecker, obviously surpassing all other species that also inhabit this forest (*minor, leucotos, major*; *Picus viridis, P. canus*: Ticehurst & Whistler, 1932). In this region the species is living without disturbance perhaps at least since the last glacial epoch. In the E. European original mixed forest of Prypec and Rokitno on the former Polish-Russian boundaries *medius* has a second region where it is abundant ("überaus häufig"; Grafsmann, 1918). The kind of these forests is the same as those from Albania: marshy virgin forest with many dead trees and decayed wood, broadleaved trees predominating (Birch, Alder, Poplar, Willow, Hazel, Hornbeam, Beach, Oak, Lime, Ashe), whereas only few Pines occur (Zedlitz, 1920).

The invasion in northern direction ultimately has reached Denmark, where in recent times it apparently only breeds in the Island of Zealand (north of Copenhagen: Heilmann & Mannicke, 1939; Jespersen, 1946); from here it has spread to Sweden, where it inhabits the southern mixed Oak-forests. Here the species reaches its northern boundary. The most N.W. records are those from Borkum and Artland (Detmers, 1912), where it once has been observed as a straggler, apparently coming from over the Northsea. As a breeding bird *medius* just has reached the Netherlands and Belgium. In the Netherlands only 3 breeding cases in the 19th century are known; most observations refer to the E. and S. E. provinces and the regions along the great streams (cf. Eijkman, c.s., 1941). In Belgium it is supposed to have bred in the Ardennes and in the region of Liege: besides, several observations in all seasons and in all provinces are known (Verheyen, 1943). In France *medius* is a breeding bird, but it is rare in the extreme W. and N.; in the mediterranean plains and in the Pyrenees the species is absent, at all events as a breeding bird (Mayaud, c.s., 1936). In its absence in the British Isles and in Ireland the species once more demonstrates its postglacial S. E. origin, and the relative recent date of its immigration into W. Europe.

In its whole European range *medius* can be found wherever a convenient biotope may be present, but owing to the diminution of the original European mixed forests the species will be rare everywhere, or it will prove to be a common breeding bird in very restricted localities only: Oak-forests of the W. and S. Pelopponesus in Greece (Stresemann, 1920; Niethammer, 1943);

Dobrudsha (Stresemann, 1920); neighbourhood of Basel, Switzerland (Masarey, 1931; Sutter, *in litt.*, 1946); also Luzern in Switzerland (Haller, 1938); Oak-forests north of Copenhagen (Jespersen, *in litt.*, 1946); Tourraine (Mayaud, c.s., 1936) and Haute-Vienne (d'Abadie, 1922) in France. How much locally the species can be distributed, is demonstrated by the fact, that in Servia it is called "numerous" by Stresemann (1920), whereas Gengler (1920) called it "die für Serbien seltenste Form der Buntspechte" (p. 143).

In all regions *medius* conspicuously appears to love old Oak-forests, *Quercus-Carpinus*-forests, and all sorts of light mixed forest, being especially fond of forests on the bottomland of great rivers, in which Oak mostly predominates. For Europe I have collected the following records of the biotope:

Denmark (Zealand): Beech- and Oak-forests (Heilmann & Mannicke 1939).
Germany (Berlin): old Oak-forests (Heinroth, 1926).
(Lausitz, Saxonia): Oak-forests (Hantsch, 1903).
(Stuttgart): old decayed Oaks (Frieling, 1940).
Netherlands (Amerongen): once breeding in Beech (Snouckaert, 1908).
France (Loir- et Cher): once breeding in Poplar (Reboussin, 1929).
(Calvados): Oak-forest; probably breeding (Le Dart, 1930).
(Bretonne, Normandy): once breeding in Beech (Olivier, 1928).
Switzerland: Oak, "Auenwälder", mixed forests (Baumann, 1943).
Poland (South): Oak-forests (Stolz, 1917).
Italy: Oaks (Arrigoni, 1904).
Macedonia: Oaks (Stresemann, 1920).
Greece (S. Peleponnesus): Oaks; very seldom Pines (Niethammer, 1943).
Spain (Cantabria): Walnut-trees (Witherby, 1922).

Oak-forests are also preferred in Asia Minor (Kastamonu: Kummerlöwe & Niethammer, 1935), and especially so in the Zagross Mts. in W. Iran, where in the park-like vegetations *Quercus persicus* is a dominant tree, and where also *Pistacia, Acer, Platanus,* and *Ficus* regularly occur (Paludan, 1938). In these historically old Oak-forests the species has lived quite undisturbed, thus even outnumbering in many places *D. syriacus* (Witherby, 1903). Coniferous trees are avoided in most parts of its range; only in those places where the species is abundant its ecological valenz appears to be high enough to settle in coniferous trees (Asia Minor: Kastamonu: Kummerlöwe & Niethammer, 1935; Smyrna, on the mountain slopes: Lynes, 1912) in rare occasions even breeding holes, supposed to be of this species, have been observed in a Pine (Peleponnesus: Niethammer, 1943).

Compared with *D. major* the bill of *medius* is very much more pointed, besides, conspicuously weaker and smaller, making it easily to understand that wood-boring animals in more or less sound wood are not easily for him to obtain. It therefore is of importance that Ticehurst & Whistler (1932) have found that in the Albanian Mamuras mixed forest *D. medius* mostly is feeding by collecting tree-ants and beetles from the trunk of the trees, these being easily picked up with the pointed bill out of the crevices in the bark, leaving the wood-boring larvae especially to *D. leucotos* with its much stronger bill (fig. 9) (*major* is practically absent!). According to Madon (1930) stomachs of *D. medius* largely consisted of Ants and *Anthribus;* wood-boring insects being absent in all 9 stomachs examined. Meylan (1931) has found apparently in Swiss material that 17 stomachs of *medius* did not contain wood-boring insects (*Buprestidae and Cerambicidae)* (0%), whereas in *D. major* they were found in 19 of 61 stomachs (14.7%) and in *Dryocopos martius* even in 36 of

58 stomachs (69%). Finally, Zollinger (1933: Switzerland) mentions to have observed that *medius* often clings to the outermost small branches of the trees at the manner of Titmice, searching for Insects that can be picked up from the branches and the leaves; besides, the species could often been observed sitting cross-wise to the branches of the trees. In conclusion, the structural adaptation of *D. medius* to more or less soft or decayed wood for feeding and nesting habits is easily apparent. Probably in relation to the weakness of the bill drumming of this species in spring is less frequently heard and also seems to be less strongly performed (cf. Haller, 1938).

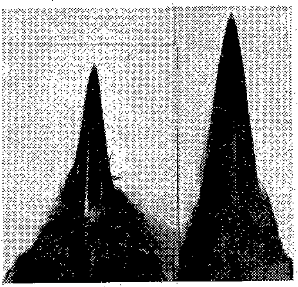

Fig. 9. *D. medius* (L.) — Bill from above of *D. medius* (left) and *D. leucotos* (right), both from the neighbourhood of Constantinople (coll. Meinertzhagen). Note the different shapes of bill, which correspond with different feeding habits.

History and systematics: *D. medius* belongs to the relative small group of species of Dendrocopos which have a black back and white shoulder patches, thus on the upperside more or less resembling *D. major*. In the heavily striped undersurface, the yellow tinge of the underparts, and the absence of a connecting black opisthotical band *medius* resembles to some extent *catpharius* and *darjellensis*, in which equally a number of primitive characters have been retained. The moustachial streak is poorly developped; this is rare in the genus, and does not represent a primitive character.

It now appears that all European species of *Dendrocopos* have come from S. E. Asia. In *D. major* this fact is quite easily recognizable in the map showing its

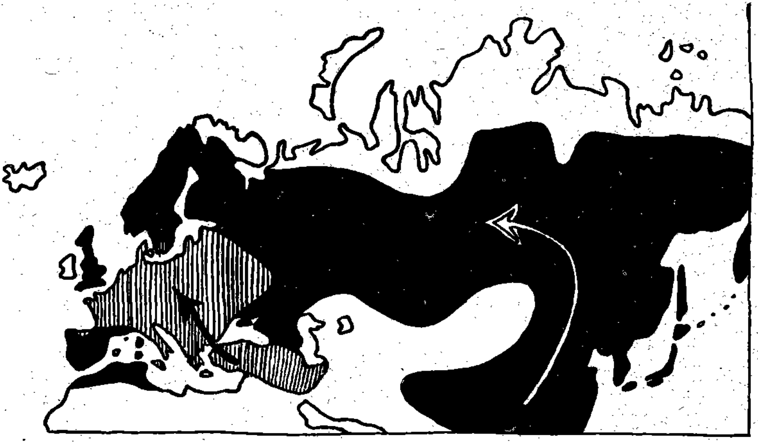

Fig. 10. *D. medius* (L.) — Schematical map showing the geographic relation between *D. medius* and *D. major* (incl. *syriacus*, *leucopterus*, and *himalayensis*). The white arrow indicates the pleistocene and postpleistocene dispersal of *major*; the black arrow indicates the postglacial dispersal of *medius*. ||||||||| range of *medius*. ■ and ||||||||| range of *major*. The situation in Central Asia is not correctly drawn.

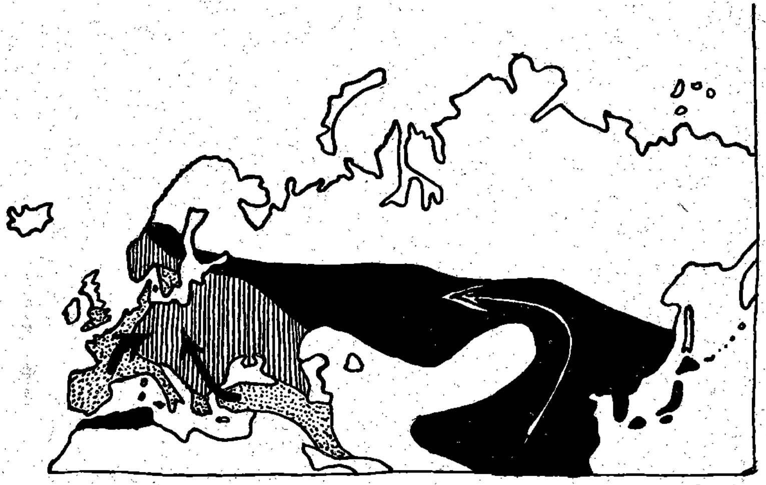

Fig. 11. Schematical map showing the geographic relation between *Picus viridis* L. and *P. canus* Gm. (after Salomonsen, 1931). The white arrow indicates the pleistocene and postpleistocene dispersal of *canus*; the black arrow indicates the postglacial dispersal of *viridis*. ░ exclusive range of *viridis*. ■ exclusive range of *canus*. ▥ regions where *viridis* and *canus* occur side by side. It is suggested in this paper that the N. African *P. vaillantii* (Malh.) is a race of *canus*, and not of *viridis*!

total distribution. It is suggested that during the first glacial period the species has left a relict population in some mediterranean refugium. Owing to probably unknown causes, and with the help of the results of isolation and of the still unknown phenomena, usually called mutations (red crown in the female!) this relict population not only has become changed, but also has retained a number of original characters (striped undersurface, inclining to cross bars on the flanks). After the postglacial re-invasion of *D. major* into Europe the population proved to be physiologically indifferent, this being the criterium for recognizing it as a distinct species. The geographic isolation of *medius* must be of a relatively old age, because of the rather strongly developped taxonomic differences that exist between *D. major* and *medius*, as well as because of the presence of a wholly red crown in both sexes, which in the *major* group is for the rest only to be found in the males of the very strongly isolated species *himalayensis* and *assimilis*.

It is a noteworthy fact that the combined distributions of *D. major* and *D. medius* on the one hand and *Picus canus* and *P. viridis* on the other hand show so many corresponding features that is is suggested that both *medius* and *viridis* have originated along a parallel way through isolation in a mediterranean glacial refugium (fig. 10, 11). Differences are conspicuous in the respective distributions of both groups, probably owing to the fact, that *medius* has split from *major* in a much earlier period than *viridis* from *canus*, the latter penetrating into Europe again in postglacial times, like the subspecies of *major* in the respective interglacial and postglacial periods. Apparently caused by interspecific competition with *major*, *D. medius* could occupy only one mediterranean refugium (eastern) during the last glacial time, whereas *P. viridis* has survived in an eastern and in a western one (Salomonsen, 1931).

(The supposed cross *major* x *medius*, shot by Madarász (1900) in Hungary proved to be a juvenile specimen of *D. leucotos* (Greschik, 1939)).

VII DENDROCOPOS MAJOR (L.): EUROPEAN SUBSPECIES (fig. 12).

Dendrocopos major major (Linnaeus 1758: Sweden).

Material examined: Lethonia (3); Sweden (15: Västerbotten, Dalarne, Upsala, Stockholm, Delsbö); Norway (1: Voss). — (Brussels Mus.; Dublin Mus.; Stockholm Mus.; coll. Hens; coll. Sillem-Van Marle).

Measurements:

Wing ♂ 138—149, average (12) 143.1; ♀ 140—147, average (9) 142.6 mm.

Culmen ♂ 27—29.5, average (10) 28.4; ♀ 25—28, average (8) 26.4 mm.

Range: Norway, Sweden, not Bornholm Island (Löppenthin, 1946, *contra* Schiöler, 1922), Finland, Baltic States, N. and Central Russia (taiga-zone), almost extending up to the arctic tree line. The range of this race in Asia is discussed in another place.

Subspecific characters: The race is characterized by the blunted form of the bill (fig. 12, no. 3—6), which is rather broad, both at the base and at the apex, the culminal ridge extending over a very great length along the sides of the bill. Slender bills, slightly approaching the Central European type, also occur, even in the N. part of Sweden (Stallfjäll, Västerbotten: 27.II. 1926: Stockholm Mus.), but the general type of bill is always more robust than in *pinetorum*. The under surface is usually very pale, and except in a very worn state, it always has a buff and creamy tinge, especially in freshly moulted plumage, when the general colour in some cases can be called dark creamy brown (♀, 10.X.1922, Upsala: Stockholm Mus.). The only one Norwegian specimen examined (♂, 25.XII.1930, Voss: coll. Sillem-Van Marle) has the underside rather dark earthy brown; by this character it could not be distinguished from Dutch specimens of the same season. The red colour on the under tailcoverts and lower abdomen is clearer than in Central European races, and tends to vermillion, rather than to bloodred. The large size of this race is in most cases directly apparent in the skin, as well as it appears to be in living specimens in the field.

It is probable that influences of the European *pinetorum* may be recognizable in the populations of S. Sweden, in those regions that has also been reached by *medius via* Denmark. This penetration may be responsible for the occurrence of *pinetorum*-like bills and brownish undersides in Swedish birds, although in Norwegia the influence of the Atlantic climate may also be of some importance. From this it is apparent that Fennoscandinavian populations do not represent the pure type of the postglacial Asiatic invaders (*major*). Nevertheless, *major*, although representing the W. outpost of a series of uniform populations and inhabiting an extensive Eurasiatic area, will prove to be the correct name in systematics for all Eurasiatic taiga Greater Pied Woodpeckers (*exc.* Manchuria, and Kamchatka) on account of priority over *Picus brevirostris* Reichenbach (1854).

D. m. rossicus (Domaniewski 1925: neighbourhood of Saratoff) is a synonym of *major* without question, being separated from *major* on account of the white and not brownish tinged forehead: a white forehead also occurs in some Swedish specimens.

Biotope; *Migrations*: In Europe *major* more or less appears to be a bird of the taiga, inhabiting forests of a mixed type, and only rarely nesting in pure coniferous forests. Pynnönen (1939), who noticed 40 finished nests of *major*, never found it in pure *Pinus* forests: 6 nests were found in mixed forests in which coniferous trees prevailed; 33 nests were situated in deciduous forests mixed with *Pinus* and *Picea*; 1 nest in pure deciduous forest. During the greater part of the year pine-cone seeds form the majority of its food, not only in this race, but also in other races of Central and W. Europe (*pinetorum*), even locally in England (Tracy, 1938)! Pynnönen (1939) has calculated the amount of calories which in the Finnish winter one specimen of *major* consumes *pro* day (± 100 cones). It is clear that failures of the pine-cone crop enforces the birds to look for other food, thus causing irregular migrations which apparently include whole populations. Consequently Pynnönen found that the number of nesting birds was very small after each combined pine -cone crop failure and migration: after the migration winter 1935-36 the normal number of Finnish breeding birds was re-established not earlier than in the spring of 1938! As odd specimens of northern stragglers are found in the invaded regions up to March or even April of the following year. one may conclude that the majority of the migrating birds does not return to their nesting grounds.

The occurrence of northern stragglers in areas inhabited by W. European races has furnished in some cases the occasion of examining the differences in weights and measurements of part of the skeleton, that exists between the heavier *major* and the smaller W. European birds:

Netherlands: Ten Kate (1930: *weights* of 3 indigenous adult birds (Nov., Jan., March): 71, 74, 75 g.; 2 ad. ♀♀ (*major*) caught in the same winter (Dec.): 88, 89 g.

Germany: Stresemann (1931) gives the *weights* of 3 *major* specimens from Reipzig on Oder (Nov.): 87, 91, 96 g. Lindner (1930): 2 *major* specimens from Saxonia (Dec.): 83, 84 g.

Netherlands: coll. Ten Kate: the length of the *humerus* could be measured in 1 indigeneous specimen: 23.8 mm; 3 *major* specimens measure: 25.5, 25.4, 26.3 mm. The length of the *crista* sterni in 3 indigenous specimens (coll. Hens; coll. Ten Kate): 28.7, 28.8, 30.7 mm; whereas 3 *major* specimens measure 31.3, 31.3, 32.6 mm.

The migrating flocks appear to be composed for the greater part of juvenile birds, they have been found at great distances, mainly in S. and S. W. direction of the breeding range. A short summary of personal examination of specimens and of literature references is given below.

Material examined:

Bornholm Island (coll. Löppenthin): 24.VII.1931; 16 and 19.X.1930; wing ♂ 139, 149, 142 mm.

Denmark: Zealand (*Copenhagen* Mus.): Oct., Nov., Jan. March; wing ♂ 139, 141, 143; ♀ 140, 144 mm.

Germany: Leipzig (Brussels Mus.): ♂ 28.XI.1920; wing 142 mm.

Netherlands: From 93 specimens, collected after 1890, 12% more or less certainly belong to *major*. In the series they are conspicuous by the white or creamy white undersurface when compared with indigenous specimens of the same date. The form of the bill will be either typical or somewhat slender, a phenomenon also found in Swedish birds. The race does not occur so frequently in the Netherlands as the number of specimens in collections would suggest, because the northern stragglers often occur in localities where breeding birds usually are absent, besides, making themselves conspicuous by their tameness, so that they are often collected in these countries as a curiosity. The form of the bill is indicated as "typical" (*t*; blunted and broad) or, as "slender" (*s*; i.e. more or less intermediate between the typical *major* and the *pinetorum* form) (u = underparts: br = brown; wh = white):

Leiden - Texel Island	28.X.1903	juv.,	wing 137,	bill (t),	u. light br.
Leiden - Texel Island	2.XI.1905	♀ ad.,	,, 139,	,, (t),	,, white
Leiden - Harderwijk	12.X.1909	♂ juv.,	,, 133,	,, (t),	,, white
Leiden - Workum	25.XI.1909	♂ ad.,	,, 148,	,, (s),	,, light br.

Hens - Linne	11.X.1910	juv,,	wing 138,	bill (s),	u dirty wh.
Leiden - Winterswijk	27.XII.1917	♀ ad.,	,, 143,	,, (t),	,, —
Ten Kate - Kampen[1]	6.XII.1929	♀ ad.,	,, 143,	,, (t),	,, white
Ten Kate - Kampen[1]	18.XII.1929	♀ ad.,	,, 142,	,, (s),	,, creamy
Rotterdam - Hendrik Ido Ambacht	28.XII.1929	♂ ad.,	,, 140[2],	,, (t),	,, white
Ten Kate - Kampen	16.XI.1932	♂ ad.,	,, 139,	,, (s),	,, light br.
Ten Kate - Soest	24.III.1944	♂ ad.,	,, 140,	,, (t),	,, dirty wh.

Belgium: From 64 specimens examined 10.9% surely belong to *major* (B = Brussels Mus.; H = coll. Van Havre).

B- Laeken (Brabant)	1900—1914	♀ ad.,	wing 142,	bill (s),	u white
B- Nivelles (Brabant)	28.IX.1930	♀ ad.,	,, 143,	,, (s),	,, dirty wh.
H- Kessel (Flanders)	14.II.1931	♀ ad.,	,, 139,	,, (t),	,, white
B- Namur (Namur)	12.X.1932	juv.,	,, 141,	,, (t),	,, white
B- Vedrin (Namur)	17.XI.1932	♀ ad.,	,, 137,5	,, (t),	,, white
B- Falaen (Namur)	21.II.1933	♂ ad.,	,, 146,	,, (s),	,, creamy
B- Brasschaet (Antwerp)	12.II.1934	♀ ad.,	,, 145,	,, (t),	,, creamy

Very instructive records of the irregularly occurring migrations are given by Drost & Schüz (1935), Thienemann (1910), Musílek & Cerny (1936). Migrations usually start in the middle of August, or even July, and will go on until the beginning of November. The number of migrating birds can be very large (on Sept. 9, 1935 not less than about 60 specimens occurred in Heligoland Island, whereas on Sept. 8 only ± 8 specimens had been observed: Drost & Schüz, 1935). S. W. directed migrations do not exclusively follow the continental boundaries, as stragglers have been collected in the Faroes (Salomonsen, 1942), the Shetlands (Brit. Birds 23, 1930, p. 229; Scott. Nat. 1929, p. 138), the Outer Hebrides (Witherby & Ticehurst, 1908), Scotland, and Ireland. In the latter locality it has been observed more than 40 times in Oct.-Febr. (Humphreys, 1937). In S. direction Bohemia and the Tatra Mts. have been reached (Mùsilek & Cerny, 1936: Wing of 44 migrationary specimens 136—146 mm, average 141.3 mm), as also perhaps Bulgaria (Rila Mts.: Boetticher, 1919). The type specimen of *Dryobates major bulgariensis* Gengler 1920: ♀, 26.I.1917. Nevscha, Bulgaria, may also be a northern straggler, as it is said that it possesses "einen viel kürzeren, breiteren Schnabel" (p. 139) than *pinetorum* (either Bulgarian and German specimens). Because of its brown underside and its wing length of 135 mm only (in spite of being "viel grösser und stärker"), the specimen may originate from the E. European transitional *pinetorum-major* zones.

Transitional Zones: I. *Bornholm Island.*

Material examined: 8 (coll. Löppenthin). Four specimens collected by Löppenthin between May 19 and June 5 in a rather big forest in the middle of the island (Almindingen) are adult birds and may be considered to be breeding specimens. They are exactly intermediate between *major* and *pinetorum*, one ♂ even having a rather slender and sharply pointed bill, resembling the type of bill found in W. Europe (and also in some Danish (Zealand) specimens) (fig. 12, no. 13, 14). Measurements of 4 breeding birds: wing ♂ 135, 138, 141; ♀ 141 mm. Culmen ♂ 28, 30, 30; ♀ 27 mm. One October specimen (♂) has a broken bill. wing 139 mm.

Three juvenile specimens (July, October) are undoubtedly migrant specimens from the north: they are typical *major* (listed above).

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[1] cf. Orn. Mon. Ber. 38, 1930, p. 82.

[2] Measured by Dr. C. Eijkman (Dordrecht).

Transitional Zones : II. *Poland.*
Material examined : Gorodischtsche (East) (6) ; Borowki (N.W.) (2). — (Brussels Mus. ; coll. Sillem-Van Marle).
The Polish populations seem to be neither true *major,* nor true *pinetorum*. By most authors (a.o. Schlegel, 1918 ; Domaniewski, 1925) they are referred to *major,* although it is stated that among them less typical birds with relatively small measurements occur (cf. also Zedlitz, 1920). The specimens from Gorodischtsche mostly approach *major* in the form of the bill, but more brownish undersurfaces occur even in worn plumage (18.III.1918). Wing lengths smaller than in typical *major* : ♂ 135—139, average (5) 137.6 ; ♀ 137 mm. Schlegel (1918) gives the following wing measurements of specimens from Gorodischtsche and Prypec : 9 ♂, 1 ♀ : 137—142, average 139.7 mm. Dementieff (1934) measures 42 Polish birds as follows : wing 132—141 mm. The specimens from Borowki, near Bydgoszcx (Bromberg), near the former German boundary only approach *major* in the generally lighter undersurface, which is creamy brown and not earthy brown as in German birds, and in the relatively long wing lengths (wing 139, 139 mm) ; bill relatively slender (fig. 12, no. 9, 10).

Transitional Zones : III. *Eastern Germany.*
Material examined : Reipzig near Frankfurt on Oder (coll. Hens) : 6 specimens collected by Stein, from 20.XI.1929 till 13.III.1930, during the winter following the extraordinary strong invasion of *major* in S. and S. W. direction. All 6 birds fully agree with *pinetorum* in their dark greyish brown coloration of the undersides, which is strikingly different from the light, often creamy tinged underside of *major*. Three of the 6 specimens, however, have almost true *major* bills (fig. 12, no. 11, 12), being stronger and more curved distally than in *pinetorum*. Wing ♂ 135, 136, 140 ; ♀ 134, 136, 137 mm. The specimens must be considered as intermediate between *major* and *pinetorum*. Unlike the Polish birds they agree more with *pinetorum* than with *major*, just like the specimens from Borowki, N.W. Poland. The result is in full agreement with Niethammer c.s. (1938), who states that intermediate *pinetorum-major* populations occur in „Westpreussen, Posen, Grenzmark, Mark Brandenburg, Schlesien (und sicher auch Hinterpommern)" (p. 13).

(Dendrocopos major "alpestris" (Reichenbach 1854 : Carinthia)).
Material examined : Switzerland (16). — (Basel Mus. ; Vogelwarte Sempach ; coll. Huber).
Measurements : Wing measurements appear to be larger than in German *pinetorum* :
Wing ♂ 132, 135, 136, 136, 137, 138, 139, 141 ; ♀ 133, 133, 134, 135, 135, 136, 137, 142 mm.
Culmen ♂ 26 27, 27.5, 27.5, 27.5, 27.5, 28, 29 ; ♀ 26, 26, 26, 26, 27, 27, 28, 30 mm.
Subspecific examination : The series as a whole almost agrees with the Scandinavian one, the specimens having a brightly coloured undersurface, which is only faintly tinged with yellowish or isabelline ; the lower abdomen and the under tailcoverts being as brightly coloured, and the form of the bill in most specimens (fig. 12, no. 7, 8) almost exactly agreeing with *major*; among them the most blunty and robust bill has been found (♀, 27.IV.1926, St. Moritz : coll. Sempach no. 1213). The form of the bill in the series varies between the most strongly characterized *major*-type and the *pinetorum*-type, the latter being only scarcely representated. The most slender bill is found in ♂, -VII.1927,

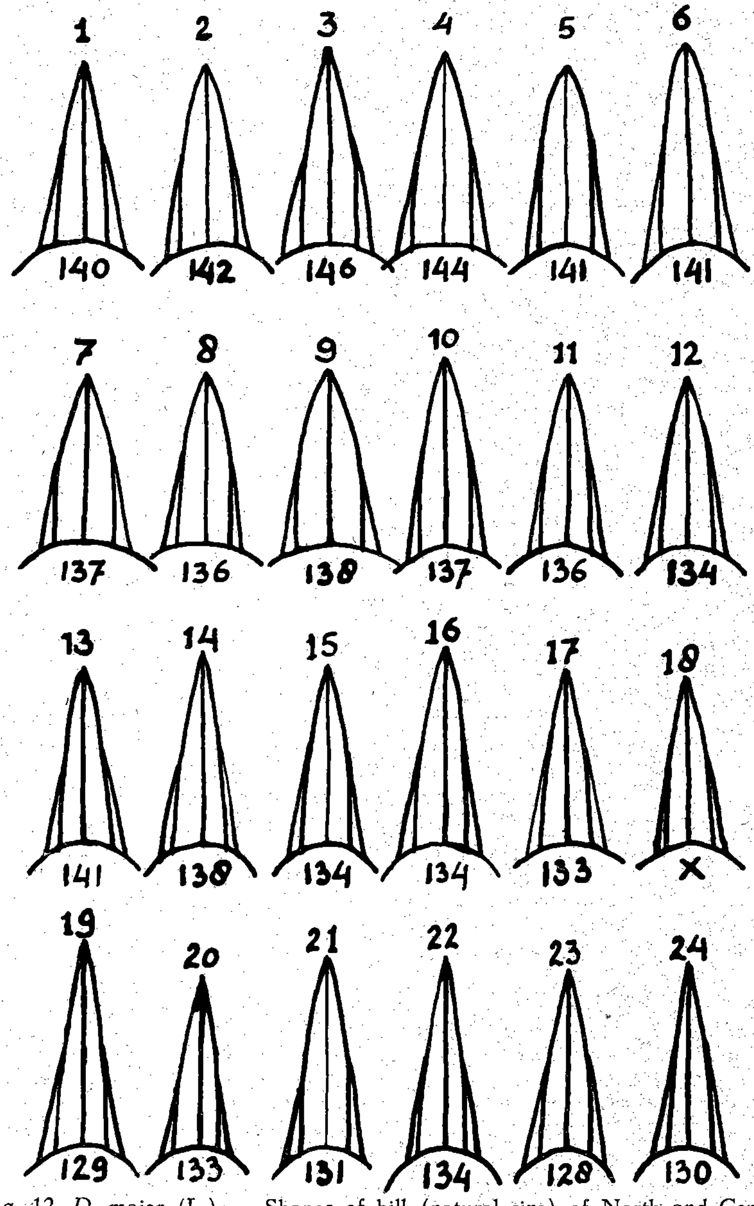

Fig. 12. *D. major* (L.) — Shapes of bill (natural size) of North and Central European populations, to show the broad blunted type in the race *major*, and the slender pointed types in West European birds, as also the intermediate forms The wing lengths of the individual birds are mentioned below each figure. **1** Tatysh, Upper Yenissei, Siberia ♂ April 14. **2** *Tunkun* Mts., Siberia ♀ April 6. **3** Uppsala, Sweden ♂ April 6. **4** Uppsala, Sweden ♂ Dec. 22. **5** Uppsala Sweden ♂ Nov. 9. **6** *Voss*, Norway ♂ Dec. 25. **7** St. Moritz, Switzerland ♀ April 27. **8** Grosswangen, Luzern, Switzerland ♀ Febr. 8. **9** Goro-

Erlach, Neuchâtel: wing 132 mm (*arduennus* influence ?). Two specimens collected near Basel (March 18, 1935; Sept. 26, 1946) have the underparts as dark brown as German *pinetorum*, their bills being also rather typical for that race. A specimen captured in Reiden, canton Luzern (May 4, 1943) also shows the typical *pinetorum* characters These specimens apparently represent the *pinetorum*-invasion into N. Switzerland, against the *major*-invasion coming from the east. A very dark red brown coloration, especially on the breast, throat, and forehead is found in a specimen from Schaffhausen (♀, -X-1925). It is probable that the name *praealpinus* (Von Burg, 1921) is based upon a similar specimen in which the phaeomelanine on the underside is extraordinarily developped. This character does not appear to be geographically localized since it is absent in all other Swiss specimens examined. I also found it in one Netherland specimen (♂ ad. 17.IX.1908, Langbroek, Utrecht: Amsterdam Mus.), which has been abusively referred to the "race" "*praealpinus*" by Snouckaert van Schauburg (1923), and in one Belgian specimen (♂ ad., 19.X.1927, Watermael: Brussels Mus.).

The name *alpestris* of Reichenbach apparently refers to the thick-billed form, for he gives the width of the bill of *alpestris* as 7½''', whereas 3 other German "species" all have widths of 7'''; for very typical *brevirostris* 8''' is stated. Johansen (1922) called attention to the fact that S. Bavarian Woodpeckers incline to have larger measurements and thicker bills than typical *pinetorum*, these characters conspicuously increasing in S. direction: in the neighbourhood of Munich all specimens examined by him proved to be true *pinetorum*; 40 km southward birds of both the *alpestris* and the *pinetorum* types occurred, whereas in Berchtesgaden only *alpestris* had been found. Two specimens from Hallein near Salzburg (coll. Hens) examined by the present author, however, have typical *pinetorum* bills! A *major*-like specimen from Berner Oberland is recorded by Floericke (1926): all characters typical for *major* being mentioned (wing 144 mm!). "*Alpestris*" should be treated as a synonym of *major*, or as a distinct, slightly smaller race.

The occurrence of a thick-billed form of *D. major* in the Alps explains the fact that Duse (1932) could record the frequent observation of birds of the *major*-type in N. Italy in early fall and winter 1930-31. These birds made the impression to migrate in S. and S.W. direction, and Duse thought, that they would represent the continuations of the remarkably strong invasion of *major* in the winter 1929—30, of which vanguards probably had been breeding in the cooler regions of the Alps, and of which young specimens were migrating farther south. It is probable that this invasion has been the result of a failed crop of pine-seeds in the coniferous mountain forests inhabited by "*alpestris*", and that both young and adult specimens went on searching for food in S. direction.

Range: Scarcely known, but at all events the mountain forests of the W. Alps and Swiss Jura. The species appears to be fairly common both in the plains and in the mountain forests ,where it is found up to the tree-line (Baumann, 1943).

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dischtsche, W. Poland ♂ Dec. 12. **10** Gorodischtsche, W. Poland ♀ March 18. **11** Frankfurt on Oder, E. Germany ♂ Febr. 2. **12** Frankfurt on Oder, E. Germany ♀ Nov. 25. **13** Bornholm Island. Baltic Sea ♀ May 19. **14** Bornholm Island, Baltic Sea ♂ June 5. **15** Zealand, Denmark ♀ May 19. **16** Zealand, Denmark ♀ June 6. **17** Leipzig, Germany ♀ Dec. 3. **18** Leipzig, Germany ♂ Sept. 11. **19** Voorschoten, Netherlands ♀ June 9. **20** Houthem, Netherlands ♀ March, 14. **21** Woensel, Netherlands ♂ May 16. **22** Weert, Netherlands ♂ March 30. **23** Hants, England ♀ April 18. **24** Kent, England ♂ Jan. 21.

Dendrocopos major italiae (Stresemann 1919: Bologna, Italy).
Material examined: Northern (7), central (1), and southern (1) Italy. -(Leiden Mus.; coll. Harrison; coll. Sillem-Van Marle).
Measurements:
Wing ♂ 123—129, average (4) 126.2; ♀ 124—134, average (5) 129.2 mm.
Culmen ♂ 25—28, average (4) 26.8; ♀ 24—28, average (5) 25.7 mm.
Range: Apenninic Peninsula, including Sicily. According to Arrigoni (1904) it is a common breeding bird.
Subspecific characters: This race has the slender pointed bill with straight contours as in *anglicus*. Undersurface distinctly tinged with creamy. It is distinguished by this character also in freshly moulted plumage, when specimens are only scarcely brighter coloured than *pinetorum*, or than Dutch specimens. In the course of the year the birds become light creamy or creamy white; as early as January they may be a'ready practically white (15.I.1927, ♂, Bari, S. Italy Leiden Mus.). I can find no distinct differences in the colour of the under tailcoverts and lower abdomen compared with *pinetorum* and *anglicus*. The red colour is also subject to fading in the course of the year, since a ♀ from May, 27, Venice (coll. Harrison) has very light almost carmine or orange red tipped feathers. General size smaller than in *pinetorum*. The resemblance between *italiae* and *anglicus*, stressed by Stresemann (1919), is only conspicuous when compared with *pinetorum*, and can easily be explained by the fact that *italiae* is historically and geographically nearer related to *anglicus* than to *pinetorum*.

Dendrocopos major arduennus (Kleinschmidt 1916: N. E. France).
By this name will be indicated a number of populations that cannot be named with the subspecific names *italiae* and *pinetorum*. These transitional populations are found in France, Belgium, and the Netherlands.
France.
Material examined: 13: Seine (1): Seine Inférieure (1); Maine-et-Loire (3); Haute-Garonne (1); Basses-Pyrenées (1); Hautes-Pyrenées (1); Aude (1); Rhône (3), -(coll. Harrison; coll. Mayaud; coll. Meinertzhagen).
Measurements:
Wing ♂ 132—135, average (5) 130.6; ♀ 128—132, average (7) 130.4 mm.
Culmen ♂ 25—30.5, average (6) 28.4; ♀ 25—30, average (7) 27.0 mm.
Range: The species is a common breeding bird in whole France including the Pyrenées, where it is mentioned by many authors to be common from sea-level up to the tree-line (cf. Mayaud, 1933).
Subspecific examination: Even freshly moulted specimens can be distinguished directly from comparable Dutch specimens by their more isabelline or light creamy undersurface, which extends up to the throat; in this respect they are clearly intermediate between a series of Italian and Dutch birds. Especially spring birds from France are conspicuous in a series from Dutch specimens from approximately the same date. By this character some birds can hardly be distinguished from Italian ones. A freshly moulted bird from Maine-et-Loire (Oct., 23; coll. Mayaud) has this character in an exaggerated stage, showing a conspicuous light reddish brown phaeomelanine pigmentation from the chin to the upper breast. A juvenile bird from the Rhône Dept. (Sept., 17; coll. Mayaud), however, is very conspicuous in the French series, exactly resembling German ones in the very dark dirty brown underside, and, in addition, in the rather broader bill. Perhaps this bird is a straggler. The bill is pointed and slender, but not as straight as in *anglicus*, the differences with *anglicus* being very slight. In most cases the bills closely resemble those of the compared Italian specimens,

although the latter are generally slightly shorter. Eight (89 %) specimens from France in the Paris Museum kindly examined for me by Dr. Berlioz, and 4 (80 %) in the Bordeaux Museum appear to have bills intermediate between the *pinetorum* and the *anglicus* types, but especially in the juvenile birds, they strongly incline to *anglicus* (compared with sketch drawings of typical bill shapes sent by me to the Paris and Bordeaux musea). A *pinetorum*-type of bill is present in a specimen from Blodelsheim (Haut Rhin; Paris Mus.) and in one from Beillant (Charente Maritime; Bordeaux Mus.), thus, indicating that the inclination to a stronger type of bill is present in the French populations (perhaps especially in the N.E.).

The resemblance between French specimens and those from the Balcans is especially noticeable in spring birds: freshly moulted Rumenian birds have a more pronounced reddish brown tinge on the throat and upper breast than comparable French birds, but, in the course of the season, this character becomes less distinct. In shape of bill the French birds almost exactly agree with the Rumenian ones. The resemblance is also noticed by Mayaud (1933) who states that a ♂ and a ♀ from Haute-Garonne could not be distinguished from Transylvanian ones, neither in coloration, nor in shape of bill. Nevertheless, he refers French populations to *pinetorum*. In later years Mayaud (1945) appears to be somewhat uncertain regarding the subspecific nomenclature of the French populations. Specimens from Lyonnais are stated to have the measurements and the shape of the bill as in *anglicus*, "mais leur coloration paraît plus pure, singulièrement le blanc des scapulaires" (p. 153). Domaniewski (1925, 1931) on the other hand has recognized the race *arduennus*, without having seen a sufficient material. His notes are of interest as he mentions a Nov. specimen from Montrésor which has a dark brown coloration exactly like that of *poelzami*.

Belgium.

Material examined: 64: Lower W. and S. W. parts (36); higher E. and S. E. parts (18); Luxembourg (3); without exact locality (7) - (Brussels Mus.; Leiden Mus.; coll. Van Havre).

Subspecific examination: The recent Belgian populations appear to be not uniform with regard to the shape of the bill; all transitional forms between sharply pointed *anglicus-like* bills and the much blunted *major*-type can be found, the latter without doubt occurring only in stragglers from the N. Specimens with *pinetorum*-like bills and large wing measurements are also referred to N. E. migrants!

All others may represent breeding birds. The different shapes of the bill can be classified into 4 groups, resembling those of *anglicus*, *„arduennus"*, *pinetorum*, and *major*. *Arduennus* represents a shape of bill intermediate between *pinetorum* and *anglicus*. With reference to 62 specimens examined the following division has been made:

Type-*major* - 6 specimens = 10 %; wing 136—143, average 139.5 mm.
-*pinetorum* - 13 „ = 21 %; „ 130—146, „ 137 mm.
-*„arduennus"* - 34 „ = 55 %; „ 127—136, „ 131 mm.
-*anglicus* - 9 „ = 14 %; „ 127—134, „ 130 mm.

In 8 breeding birds collected between April 10 and June 30 the following types have been found: *pinetorum* (1), *arduennus* (2), *anglicus* (5). Wing measurements 127—132, average 130 mm. It thus seems that the Belgian populations possess bills that are intermediate between those of *pinetorum* and *anglicus*. It is noteworthy, that an *anglicus*-type is correlated with a relatively small size, and that with the increase of thickness of the bill the increase of wing length is parallelized.

Concerning the colour of the underparts only slight differences between *pinetorum* could be established; in general they appear to be lighter and browner than *anglicus*. In freshly moulted plumage the underside is dark brown with a reddish tinge especially on the throat; in the course of the year this colour becomes lighter and more dirty grey; birds in breeding plumage have white or dirty creamy under parts.

No differences could be established between specimens collected in the higher S.E. part of the country (Luxembourg; Ardennes; Prov. of Namur) on the one hand, and those from the lower W. regions on the other hand.

Wing measurements of birds that are not apparent stragglers:

♂ 127—137, average (32) 131.8; ♀ 127—135, average (18) 131.0 mm.

These measurements show that the Belgian birds are at the average smaller than *pinetorum*.

Culmen ♂ ♀ 25—31.5, average (45) 28.1 mm (cf. Netherland measurements).

Not without hesitation I have applied the name *arduennus* to the Belgian populations of *D. major*, the "race" having been established on 2 specimens only. Nevertheless, Hartert (1921) gives a fairly correct interpretation of this scanty material: „Schnabel viel dünner als bei *pinetorum*, Flügel etwas länger als bei *anglicus*" (p. 2185). I do not think that *arduennus* should be used as a subspecific name; it only appears to be useful to me in indicating the intermediate populations between *pinetorum* and *anglicus*. The intermediate character of the Belgian breeding birds is clearly demonstrated by the fact that Van Havre (1928) has called them *pinetorum* whereas Verheyen (1941) has named them *anglicus*! The only 2 specimens upon which the name *arduennus* has been based has led Bacmeister & Kleinschmidt (1918) to make a wrong conclusion as regards the colour of the underparts, one specimen having a white, the other a brown breast. The authors considered a light underside to be correlated with a lengthened pointed bill and a preference for deciduous forests, whereas birds with a greyish brown underside should always possess a robust bill, adapted to a life in coniferous trees. As has been pointed out above, the colour of the underside in one race appears to be correlated with the season only!

Netherlands.

Material examined: 48 specimens collected *before 1890*; 100 specimens collected *after* 1890. — (Amsterdam Mus.; Leiden Mus.; Rotterdam Mus.; coll. Van Dedem; coll. Eijkman; coll. Hens; coll. Ten Kate; coll. Neijssel; coll. Sillem-Van Marle).

Subspecific examination: Of 100 specimens recently collected in all months of the year the following division has been made with reference to the shape of the bill (fig. 12, no. 19—22).

Type-*major*	- 8	specimens	= 8 %;	wing	137—143,	average	140 mm.
-*pinetorum*	- 33	,,	= 33 %;	,,	128—148,	,,	134 mm.
-„*arduennus*"	- 51	,,	= 51 %;	,,	128—136,	,,	132 mm.
-*anglicus*	- 8	,,	= 8 %;	,,	129—137,	,,	133 mm.

In 13 breeding birds collected between April 10 and July 15 only *arduennus* (10)- and *anglicus* (3) -like bills have been found. Wing measurements 128—133, average 131 mm. The measurements as a whole fairly well agree with those found in the Belgian material. Netherland specimens agree with Belgian ones in all characters, but a slightly more approach of the Belgian populations to *anglicus* appears to be present, as is also the case in *Garrulus glandarius* (cf. Voous, in press). Netherland specimens more than Belgian ones form the intermediate populations between *pinetorum* and *anglicus*; Belgian specimens also resemble French ones.

In the large series of Dutch birds the gradual fading of the colour of the underparts is apparent; autumn birds being as dark brown as British specimens, whereas late spring specimens are white or dirty white. The most brown specimens originate from the following dates: August (1), September (4), October (6), November (4) December (1). The pure white specimens from February (3), March (1), April (3), May (4). Summer birds often have very dirty underparts, apparently originating from close contacts with the trunks of the trees, the breast feathers being often stained with dark particles at their tips. It appears, however, that the general colour of the underparts is not subject to a high individual variability unless specimens from approximately the same date are compared.

Wing measurements of birds that are not apparent stragglers: ♂ 128—138, average (41) 132.2; ♀ 128—139, average (42) 133.0 mm.

Culmen ♂ ♀ 25—31, average (72) 28.0 mm (cf. Belgian measurements).

Those Netherland specimens collected *after* **1890**, that can be referred to migrant *major* are listed under that heading; it does not seem justified to try to ascertain the occurrence of German *pinetorum* in the Netherlands otherwise than by the capture of breeding birds that have been banded in Germany.

It is a noteworthy fact that of 48 Dutch specimens collected before 1890 the numerically proportion of specimens with *major-*, *pinetorum-*, *„arduennus"-*, and *anglicus*-types of bill is conspicuously different from that found in the recently collected series:

Type-*major*	- 16 specimens	= 33 %;	wing 131—148,	average 139 mm.
-pinetorum	- 20 „	= 42 %;	„ 129—145,	„ 139 mm.
-„arduennus"	- 10 „	= 21 %;	„ 130—138,	„ 133 mm.
-anglicus	- 2 „	= 4 %;	„ 132	„ 132 mm.

Only 4 of these specimens have been collected in the breeding season (April 10—July 15); 2 resemble *arduennus*, and 2 *anglicus* in the form of the bill. It thus appears that, although the character of the breeding birds in the previous century may have remained the same, northern migrants occurred far more frequently than in recent times; the large wing measurements found in *pinetorum*-like birds may also indicate a great proportion of northern stragglers. I refer to *major* all those specimens that have a blunted *major*-type of bill, as well as those specimens with a *pinetorum*-type of bill and which in addition have wing measurements reachting above 139 mm. This making the total number of *major*-specimens collected *before 1890*: 28 (= 58 %): wing 131—148, average 140 mm. I may add that 50 % of the total number of the specimens originating before 1890 have conspicuous white or creamy undersurfaces, whereas this number in the *recent series* is about 15 %, corresponding with the percentage of northern stragglers in the recent series (11 %). It appears to me that in the 19th century the breeding bird was far less common in W. Netherland (Holland) than it is now (indications in the literature are present) and that therefore the occasional northern stragglers have been collected more seriously.

Dendrocopos major anglicus (Hartert 1900: Horsham, Sussex).

Material examined: Kent (2); Hants (1). — (coll. Harrison; coll. Meinertzhagen).

Measurements: Wing ♂ 130; ♀ 128, 128 mm. Culmen ♂ 30; ♀ 26.5, 27 mm.

Range: England, Wales, and Scotland, in the latter country apparently extending its range. It appears to be locally distributed, and nowhere to be common. Not in Ireland.

Subspecific characters: In this race the slenderness of the bill in W. Europe reaches its culmination; it is sharpe and pointed and never has arched contours near the tip (fig. 12, no. 23—24). It can directly be distinguished from the *pinetorum*-type of bill. With *pinetorum* it has the dark coloured underside in common, although the general tinge appears to be slightly different, being of a somewhat darker grey tone than in *pinetorum*. As is also the case in large series of Dutch and Belgian specimens examined, the under surface is subject to a considerable deal of fading in the course of the year, becoming almost greyish, or dirty white in late spring specimens. Dr. J. Harrison (Sevenoaks) was so kind to examine the British specimens in his collection and communicated me (1946) that 8 of 9 autumn specimens had earthy brown undersides, whereas 8 specimen from May to July could be arranged as follows: cold earth (3); buffy white (2); white (3). The spring specimens examined by me (7 and 18 April) are darker and browner than a series of Dutch birds from approximately the same date. According to Ticehurst & Whistler (1933) there are no absolute differences in measurements between *anglicus* and *pinetorum* as was originally supposed by Hartert (1900, 1912): wing 127—137 mm. Nevertheless, the form of the bill is so typical for the race, that it does not seem justified to regard *anglicus* as "a very poor race" (Ticehurst & Whistler, 1933, p. 109). Although in the possession of a slender type of bill, which is totally different from that of *major*, *anglicus* appears to feed on the same way on pine-cone seeds as the Fennoscandinavian race, in those regions where these are available: Tracy (1924, 1938) found 7735 pine cones which had been emptied by one ♂ from Aug. 13—April 5. From this it appears that no direct relation exists between the shape of the bill and the way of feeding. Nesting holes have been recorded especially from broad-leaf trees (Tracy, 1938: birch 27; beach 2; conifer 6).

Dendrocopos major pinetorum (Brehm 1831: Germany; type locality here restricted to Leipzig).
Material examined: Germany (neighbourhood of Leipzig: 13; other localities: 3); W. Austria (2). — (Brussels Mus.; Leiden Mus.; coll. Hens).
Measurements:
Wing ♂ 134—137, average (10) 135.3; ♀ 132—139, average (6) 135.3 mm.
Culmen ♂ 26—31, average (12) 28.6; ♀ 26—28.5, average (6) 27.5 mm.
According to Niethammer (1938) measurements of 23 breeding birds from central Germany (especially Saxonia): wing 131—138 mm.
Range: Germany, westward at all events to the Rhine, where the characters of the race become less defined; Denmark, the Netherlands, and Belgium are inhabited by intermediate populations, whereas in France a subspecies is found which is distinct from *pinetorum*; in the S. the race penetrates into the region of "*alpestris*", having been found in N. Switzerland and Austria; apparently also in Bohemia, but S. of the Tatra Mountains the populations become intermediate between *pinetorum* and the Balcan race; in the east *pinetorum* slightly pass into *major* (Poland) as has been described above.
Subspecific characters: The race is characterized by the dark, more or less earthy brown coloration of the underparts, which in the freshly moulted plumage is more clear brown than in late winter and spring, when the whole undersurface becomes dirty ashy brown, originating from being stained with dust, which seems to be particularly obvious in centers of human industry, as e.g. the environments of Leipzig. This particularity is clearly expressed by Schlegel (1918) as follows: „Die deutschen Baumbewohner tragen auf ihrem Gewande recht deutlich die Visitenkarten des Landes der Industrie und Schornsteine zur Schau" (p. 335); the phenomenon can distinctly be observed in large series of passerine birds in the Brussels Mus., originating from the neighbourhood of Leipzig.

The bill is strong and the contours are slightly convex near the tip, the form as a whole is more elongated and less strong than in *major* (fig. 12, no. 17, 18). Size smaller.
Biotope: In central Europe the species is a denizen of both the deciduous and the coniferous forests. There does not exist any correlation between the shape of the bill and the kind of biotope inhabited (cf. *anglicus*!). Nesting holes are made especially in broadleaved trees (cf. Steinfatt, 1937: Willow 10. Lime 2).

Dendrocopos major subspec. Denmark.
Material examined: Zealand (21); Fynen (2); Jutland (1). — (Copenhagen Mus.).
Subspecific examination: The series containing 24 specimens shows many particularities. In the first place it is necessary to separate from it 5 specimens of *major*, which are apparent stragglers from the north, with wing measurements resp. of ♂ 139, 141, 143 and ♀ 140, 144 mm. The remaining series, among which additional stragglers *may* occur, is very heterogeneous, both regarding the shape of the bill and the coloration of the underparts.
In classifying the different types of bill of the whole series including the above mentioned *major*, the following scheme has been made (fig. 12, no. 15—16):

Type-*major*	- 8 specimens	= 33 %;	wing 135—144,	average	139.1 mm.
-*pinetorum*	- 10 ,,	= 42 %;	,, 135—143,	,,	137.6 mm.
-*,,arduennus"*	- 4 ,,	= 17 %;	,, 132—138,	,,	134.8 mm.
-*anglicus*	- 2 ,,	= 8 %;	,, 134 ,	,,	134 mm.

Apart from the 5 stragglers (*major*) the series shows a more pronounced predominancy of thicker bills and higher measurements than the Belgian and the Netherland ones. It is a noteworthy fact, however, that all 5 sure breeding birds (May 5—June 21) have sharpe pointed bills of the *anglicus* and *arduennus* types. With reference to the shape of the bill one may conclude that the Danish populations show resemblances with the western (*,,arduennus"*), central (*pinetorum*), and northern (*major*) populations. This variability in Danish birds is already noted by Schiöler (1922).
The colour of the underparts also demonstrates a high degree of individual variability. Most specimens show a peculiar greyish white coloration, which is nowhere to be found in other W. European populations, but among them dark brown specimens occur, irrespectively the time of the year: e.g. a ♂ from Oct. 28 with *anglicus*-like bill has a greyish white underside, whereas a ♀ from Jan. 21 with an almost *major*-like bill has a dark earthy brown underside. Thus, in the Danish populations no correlation seems to exist between the type of the bill and the colour of the underparts. Light creamy brown specimens — agreeing with *major* — have also been examined. Arranged following the date of collecting, the series shows no gradual fading, nor increase of whiteness, but these characters appear to be fully irregulary distributed.
In conclusion Danish birds are slightly intermediate between *pinetorum* and *major*, but only faintly approaching the latter in the shape of the bill and the colour of the underparts; besides, they show inclinations to *anglicus* in the shape of the bill only. After an examination of more than 50 Danish specimens Schiöler (1922) has named them *pinetorum*; his series, however, is said to differ greatly from *pinetorum* in generally missing the dark greyish brown colour of the underparts, which colour only scarcely is to be found. Löppenthin (1946) also refers the Danish breeding birds to *pinetorum*. In conspicuous contradiction to Schiöler (1922), however, he also refers *Bornholm* birds to *pinetorum*, a statement which is based on the examination of personally collected specimens (see above).

Owing to complicate geographic relations trinominal nomenclature is not adapted to name the Danish populations of *D. major* in a satisfactory way.

Wing measurements of birds that are not apparent stragglers: ♂ 135—139, average (8) 136.6 mm; ♀ 132—139, average (11) 136.2 mm.

Biotope: According to Jespersen (1946) the species is a "common breeder in all forest-covered parts of the country" and "has spread in the last half-century in Jutland as a result of the growing plantations" (p. 23). Instructive cases of the feeding of 2 or 3 specimens of Danish *major* on the seeds of pine-cones and on the fruits of *Juglans nigra* and *J. regia* are given by Lange (1937: Copenhagen): about 8500 emptied cones having been found.

Dendrocopos major candidus (Stresemann 1919: Bucarest, Rumenia).

Material examined: 9: Rumenia (Barza, Cernavoda, Constanza, Prov. of Dobrudsha; Ferbintzi, Prundu, Prov. of Muntenia); 1: Burgaria (Rila). — (coll. Harrison; coll. Sillem-Van Marle).

Measurements: Rumenia: wing ♂ 132, 133; ♀ 133, 134, 134, 137; average (7) 134.0 mm. Bulgaria: wing ♀ 138 mm. — Rumenia; culmen ♂ 29.5, 31.5; ♀ 26, 27, 28, 28, 29; average (7) 28.5 mm. Bulgaria: culmen ♀ 28 mm. — Wing of 12 Rumenian specimens examined by Stresemann (1919) 128—136, average 132.9 mm.

Range: Not exactly known, but at all events Rumenia, including the regions west to the Transylvanian Alps (Congreve, 1929), and (?) Bulgaria. The race *bulgariensis* (Gengler, 1920) apparently is based on a migratory specimen and has been discussed in the paragraph on *D. m. major*. In S.W. Russia and the Ukraine *candidus* is mentioned to be the breeding race (thin and pointed bill: Charlemagne, 1933: wing 136—137 mm; Dementieff, *fide* Grote, 1942); Domaniewski (1925) records *candidus* from Astrachan, but this may have been probably *tenuirostris*!

Subspecific characters: The Rumenian specimens vary underneath between a light buffy isabelline in fresh plumage to almost pure white in winter specimens, in this respect resembling more or less Italian birds. They may be distinguished from these by the isabelline tinge, which is apparent in all specimens. When arranged according to their dates a considerable amount of fading can be observed: the darkest undersurface is found in a specimen from Constanza (Nov. 21 ♀: almost reddish buff). The bill is rather sharpe and pointed, obviously distinct from the strong *pinetorum* type of bill, and resembling a slender *arduennus* type. Size averaging only slightly smaller than in *pinetorum*. The Bulgarian specimen exactly agrees with the small Rumenian series, and may thus be included into the present race.

Dendrocopos major subspec.

Material examined (Brussels Mus.; coll. Harrison):

1. Guta, S. of Tatra Mts., Slovakia,	♂ 19.X.1937,	wing 137,	culmen 28 mm.
2. ,, ,, ,,	♂ 25.IV.1938,	,, 136,	,, 29 mm.
3. Molnaszecsöd (Vas), Hungary	♂ 7.III.1928,	,, 135,	,, 30 mm.
4. ,, ,,	♀ 25.I.1933,	,, 132,	,, 26 mm.
5. Halogy (Vas), Hungary	♂ 12.II.1932,	,, 132,	,, 27 mm.

The freshly moulted specimen from Guta (on the River Waag in the Lesser Hungarian Plains) is underneath distinctly more reddish buff, inclining to isabelline, thus being hardly distinguishable from the Rumenian birds from the same date. The other specimen is much worn and dirty white underneath. The bills are of a slender *pinetorum* type. Two Hungarian specimens (nrs. 3, and 5) originating near the Austrian border in the Hungarian plains, have sharply pointed slender bills, exactly like those of the Rumenian ones; they have almost pure white undersurfaces, and in all respects agree with the Rumenian series rather than with *pinetorum*. The other specimen (4) has the thick wedge-shaped *major* type of bill combined with a dark brown undersurface. It is thought to be a straggler from the intermediate *major-pinetorum* populations, which are situated exactly north of the collecting place.

It seems to me that Hungarian specimens belong to *candidus*, rather than to *pinetorum*.

I do not know the status of the Yugoslavian and Albanian populations, but according to Ticehurst & Whistler (1929) the species appears to be scarce in Yugoslavia, whereas in Albania it is the rarest Woodpecker (Ticehurst & Whistler, 1932), being outnumbered both bij *leucotos* and *medius*. In Greece *D. major* appears to be absent, but Hartert (1900) mentions a specimen from Macedonia.

Dendrocopos major tenuirostris (Buturlin 1906: Kutais and Akhalzikh, Transcaucasia).

Material examined: Crimea (1) ♀, wing 138 mm. — (Dublin Mus.).

Measurements: According to Démentieff (1934):

Wing: Caucasus (40): 127.5—137 mm. Crimea (7): 130.5—136.5 mm.

Range: N. Caucasus (Kuban, Daghestan) and Transcaucasia (Kutais), also Crimea; northward gradually intergrading with the Russian *major*-like populations (Démentieff, 1934). Probably the name *kurae* (Laubmann, 1915: Kura Valley, Gouv Elisabethpol) refers to transitional birds between *tenuirostris* and *poelzami* (cf. also Dementieff, 1934) and does not apply to migrants from northern *major*-like populations, as is suggested by Hartert-Steinbacher (1935). The description of the "race" *kurae*, however, is somewhat confused. No specimens of *kurae* could be examined by the author.

Subspecific characters: Topo-typical specimens could not be examined by the author, so he must refer to the critical remarks about this race given by Dementieff (1934) and Hartert-Steinbacher (1935) "In der Färbung wie *pinetorum*, also unten etwas bräunlicher und mehr erdfarben als die Spechte des angrenzenden Russlands. Der Schnabel ist aber schlanker, die Flügelmasse sind nicht kleiner" (Hartert-Steinbacher, 1935, p. 365). The specimen from Crimea examined has a very worn plumage and a dirty white underside, and must probably be referred to the breeding race, which according to Dementieff (1934) and Stegmann (*fide* Hartert-Steinbacher, 1935) is *tenuirostris*. If I understand well, the name *tenuirostris*, which should indicate the possession of a slender type of bill, has been given in comparison with the Russian *major* populations; so it is clear that in the Crimea specimen I found a *pinetorum*-like bill, which, however, is by no means more slender than e.g. in *candidus*, as the above mentioned notes by Hartert-Steinbacher (1935) would suggest. Thus, it becomes clear, why Laubmann (1915) treats *tenuirostris* as a synonym of *pinetorum*.

Dendrocopos major paphlagoniae (Kummerlöwe & Niethammer 1935: Ilgaz-Dagh, Paphlagonia, Asia Minor).

Material examined: none.

Measurements: Wing according to Kummerlöwe & Niethammer (1935): ♂ 135, 138, 139, 141; ♀ 134 mm. Culmen ♂ 29, 32, 33, 34; ♀ 31 mm.

Range: Certainly known from the type-locality only. Hartert (1900),

however, mentioned already the existence of true *D. major* in Asia Minor, but it was not until 1935 that trustworthy specimens were obtained. The race inhabits the same region as *D. syriacus,* from which it appears to be ecologically separated: *major* is said to be a mountain bird (Pine and Fir forests), whereas *syriacus* should be more a bird of the plains, the separation, however, being not exclusive. In the type-locality *paphlagoniae* seems to be common.
Subspecific characters: Kummerlöwe & Niethammer (1935) compared this race with *pinetorum,* from which it can be distinguished by the bill being slender and more pointed, this character also being apparent in comparison with *tenuirostris* and *poelzami.* Measurements apparently slightly larger than in *tenuirostris* and *candidus*! *Paphlagoniae* may be considered either to be an isolated offspring of the Balcan populations, with which it has the pointed shape of the bill in common, or the vanguard of the *tenuirostris* populations, penetrating into Asia Minor out of their original Caucasian refuge.

Dendrocopos major harterti (Arrigoni 1902: Macomer, W. Sardinia).
Material examined: 15: Sardinia (Arzana, Bonorva, Ilbano, Lanusei, Macomer, Ogliastra, Villagrande). -(Brussels Mus.; coll. Harrison; coll. Hens; coll. Meinertzhagen; coll. Sillem-Van Marle).
Measurements:
Wing ♂ 132—139, average (7) 134.6; ♀ 129—139, average (8) 133.4 mm.
Culmen ♂ 25.5—30, average (7) 28; ♀ 25—29, average (8) 27 mm.
Range: Sardinia.
Subspecific characters: Bill pointed, though somewhat stronger than in *anglicus*; more slender than in *hispanus*; larger and more robust than in *italiae.* Undersurface much like *hispanus,* in fresh plumage very dark coffee brown; it is, however, subject to considerable fading, becoming light creamy brown in spring (April 23, Macomer). In spring plumage some specimens resemble *italiae* in the colour of the underside, but these can be distinguished from that race by the still more or less distinct brownish tinge, which is missing in *italiae.* Moreover, the brown colour is distinctly different from that found in central and west European subspecies. The red on the undersurface is very dark and bright, and the outer tailfeathers are more strongly and more regularly barred with black and white than in all other European races except *hispanus* and *parroti.* The increase of melanine on the tailfeathers is clearly demonstrated in the third pair, in which the white is absent or only scarcely represented at the tip of the feathers. The white patches on the wing quills are also relatively small.

Dendrocopos major parroti (Hartert 1911: Corsica).
Material examined: 2: Corsica (Evisa Vizzavona). -(coll. Meinertzhagen).
Measurements: Wing ♂ 137, 141; culmen ♂ 30, 30 mm.
Range: Corsica.
Subspecific characters: The specimens examined almost fully agree with those from Sardinia; they have, however, a slightly larger and more robust bill. Hartert (1912) gives the following measurements of the culmen: *harterti*: 25—28, once 30; *parroti*: 30—33.5 mm. The specimens can be distinguished from the only one available *hispanus,* by having a slightly lighter coloured undersurface, which is less tinged with reddish brown, and by the slightly more slender bill.
Biotope: The race is according to Jourdain (1912) common in the coniferous zone between 600 and 1200 m, but it appears to be far from numerous in the lower cork-oaks and olive-growths.

Dendrocopos major canariensis (Koenig 1889: Tenerife, Canarian Islands).
Material examined: 11: Tenerife (collected by Thanner). -(Copenhagen Mus.; Dublin Mus.; Leiden Mus.; coll. Meinertzhagen; coll. Sillem-Van Marle).
Measurements:
Wing ♂ 131—137, average (6) 133.7; ♀ 132—135, average (5) 133.2 mm.
Culmen ♂ 26.5—30, average (6) 28.4; ♀ 26—28.5 average (5) 27.4 mm.
Range: Tenerife, Canarian Islands.
Subspecific characters: This race can hardly be distinguished from the Sardinian race *harterti* but still it is different in the less extension of white in the lateral tailfeathers, in which the regular black bars are as wide as, or broader than, the white interspaces, and by the parallel phenomenon of relative diminution of white in the proximal wing quills. The lower flanks are partly white in both races, and the forehead in *canariensis* may be either whitish or tinged with buffy, as is the case in all S. W. European specimens. No red cervical collar! Bill slender and rather sharply pointed.
Biotope: The race appears to be confined to the heavy mountainous forests of *Pinus canariensis* between 1200 and 1800 m, which is the same region as is inhabited by the rare *Fringilla teydea* (Koenig, 1890; Bannerman, 1920).

Dendrocopos major thanneri (Le Roi 1911: Gran Canaria, Canarian Islands).
Material examined: 4: Mogan, Gran Canaria. -(Leiden Mus.; coll. Sillem-Van Marle).
Measurements: Wing ♂ 131, 135; ♀ 131, 138 mm. Culmen ♂ 30, 30; ♀ 27, 27 mm.
Range: Gran Canaria, Canarian Islands.
Subspecific characters: At once distinguishable from *canariensis* by the much lighter coloration underneath, which in the specimens examined is isabelline buff. Otherwise exactly like *canariensis*. The general colour of the underparts closely resembles those of the Balcan specimens, having the same pronounced isabelline tinge. In the late spring specimens before me, the breast feathers are stained with dark patches, apparently originating from the resinous substances of the pine trees in which they live.
Biotope: The race is equally confined to the pine forests, but averaging at lower altitude than the Tenerife race (900—1200 m) (Bannerman, 1920).

Dendrocopos major hispanus (Schlüter 1908: Sevilla, Spain).
Material examined: 3: Portugal (Cercedilla (North), collected by Witherby, coll. Meinertzhagen: ♂ wing 141.5, culmen 29 mm; — Cintra (South), Leiden Mus: ♂ wing 127, culmen 27 mm; — Coimbra (Central), Leiden Mus.).
Range: Iberian Peninsula south of the Pyrenees; local distribution apparently unknown.
Subspecific characters: A very dark brown coloured race, the undersurface being darker and browner than in *anglicus*. Bill pointed and robust. In the quills of wing and tail a general increase of melanine is apparent. The outermost two pairs of tailfeathers are broadly barred with black and the third pair has much less white at the tip than in central and W. European specimens. A red crescent on the breast may be absent or present, or only slightly indicated (Schlüter, 1908). The differences in size between the two adult specimens examined is noteworthy.
Biotope: The race occurs in fair numbers in cork woods and olive plantations in Portugal (Tait, 1924); in Spain it is also observed in pine forests: Anda-

lucian Sierras (*Abies pinsapo* forests: Lynes, 1912), Sierra de Guadarrama, and Sierra de Gredos (Witherby 1928); it is found nesting in pine trees and feeding on the seeds of pine cones, wedged in trunks (Witherby, 1928).

Dendrocopos major lynesi (Harrison 1944: Azrou, Middle Atlas, Central Morocco, 4800 ft.).
Material examined: 2: Azrou, Middle Atlas (*cotype*); Taddert, High Atlas (coll. Meinertzhagen); besides 1 without locality (Brussels Mus.).
Measurements: Wing ♂ 135; ♀ 131, 134 mm. Culmen ♂ 28.5; ♀ 26, 26.5 mm. Wing according to Harrison (1944) 129—136, average (14) 131.7 mm.
Range: Middle and High Atlas of Morocco.
Subspecific characters: This race is but poorly distinguishable from *hispanus*, the coloration underneath perhaps being somewhat more coffee brown, exactly matching the Sardinian specimens, and the lateral tailfeathers being somewhat more regularly transversely banded; otherwise I can find no differences. The red breast collar is either present or absent, but apparently always relatively faintly developped, at all events averaging less than in *mauritanus*, in this respect resembling *hispanus*. Compared with *mauritanus* the present race is according to Harrison (1944) distinctly darker underneath, varying from a rather strong smoky brown to sandy brown or even buffy white. Measurements larger than in *mauritanus*.
Biotope: The race is according to Chaworth Musters (1939) and Meinertzhagen (1940) common in the *Ilex* woods up to about 2100 m, and is recorded to be exceedingly tame.

Dendrocopos major mauritanus (Brehm 1855: Morocco; restricted by Harrison (1944) to the lowlands).
Material examined: none.
Measurements: Wing according to Harrison (1944) 120—127, average (17) 123.8 mm.
Range: Coastal lowlands of N. Morocco.
Subspecific characters: This race seems to be hard to characterize, owing to the existence of transitional specimens between *hispanus* on the one hand and *numidus* on the other hand. The red breast band may be either present or absent, but it is never intermingled with black, as is the case in *numidus*. The general colour of the underparts is usually much paler than in *hispanus*, apparently somewhat intermediate between *hispanus* and *numidus*; according to Harrison (1944) it is "mostly pale buffy white" (p. 62). The form of bill apparently is the same as is found in *lynesi* and *hispanus*.

Dendrocopos major poelzami (Bogdanow 1879: Lenkoran).
Material examined: 2: Lenkoran. (Brussels Mus.; Leiden Mus.).
Measurements: Wing ♀ 123, 123 mm. Culmen ♀ 27.5, 28.5 mm. According to Démentieff (1934) wing (17) 120.5—128 mm.
Range: S. Caspian Mountains, eastwards from Astarabad in Persia, westwards to the plains of Lenkoran.
Subspecific examination: The race is characterized by the very dark clear brown underside and the bright red undertailcoverts and lower abdomen. The increase of (phaeo-)melanine is also expressed in the brown tinge of the earcoverts and of the patch on the sides of the neck, which in other races is more or less pure white, as also in the proximal scapulars, which in one specimen (Leiden Mus.) are not white but slightly tinged with brown. The bill is pointed and sharpe. Size relatively small.

Biotope : *Poelzami* appears to be common in the characteristic almost true arcto-tertiary deciduous mountain forests (*Quercus, Carpinus, Fagus, Ulmus, Pterocarya, Juglans*) from the plains up to the tree-line (Radde, 1884 ; Stresemann, 1928).

Dendrocopos major numidus (Malherbe 1842 : Oran, Algeria).
Material examined : Tunesia (6) ; Algeria (7) ; Morocco (3) ; without exact locality (2). -(Brussels Mus. ; Leiden Mus. ; coll. Meinertzhagen ; coll. Sillem-Van Marle).
Measurements :
Wing ♂ 124—131, average (7) 128.0 ; ♀ 127—130, average (9) 128.4 mm.
Culmen ♀ 30—34, average (7) 31.9 ; ♀ 27—30, average (8) 28.6 mm.
Range : Tunesia ; Algeria, as far west at least to the Merada Mountains in extreme E. Morocco (♂, ♀, juv. June 20—July 10, 1943, coll. Meinertzhagen).
Subspecific characters : Directly distinguished from *mauritanus* : (1) the breast collar is always present and, though variable in extent, usually well developped. It is conspicuously intermingled with black, the latter colour originating from the black bases of the red-tipped feathers ; (2) the underside appears to be somewhat lighter, less tinged with brown, and (3) the bill is much longer and of a very slender shape, being the longest bill of the species found in Europe. — A juvenile specimen in the Leiden Mus. has apart from the brownish black breast band with only a few red tips, a conspicuously striped underside, becoming almost transversely barred on the thighs and lower flanks, thus, showing resemblances with the juvenile plumage of *D. syriacus* !
Biotope : In N. Africa the species is said to be a denizen of oak-forests only, apparently never having been found in coniferous (Aleppo-) forests (cf. Bannerman, 1927).

VIII **Dendrocopos syriacus** (Hemprich & Ehrenberg).

This *D. major*-like form (with 4 subspecies) has been given specific rank owing to the fact that it is found side by side with races of *D. major* both in S. E. Europe and Transcaucasia. *Syriacus* shows a number of taxonomic differences by which it can be distinguished from *major* (cf. Stresemann, 1920) : general coloration dull brownish black, not glossy blue black as in *major* ; underparts slightly streaked, especially on the lower flanks and thighs, in some cases inclining to cross bars ; lateral rectrices black, or with a few white spots only ; no black postauricular band ; greater extension of white on forehead and red on hind neck ; nasal tufts greyish white, not black as in *major*. Shape of bill slender and pointed. In the juvenile dress a broad black-and-red gorget is usually present ("Blutspecht"), besides, the dull greyish underparts are very heavily striped ; in this respect juvenile birds of *syriacus* much resemble those of *numidus* !

Dendrocopos syriacus syriacus (Hemprich & Ehrenberg 1883: Libanon, Syria).
Material examined : Asia Minor (4 ; Smyrna) ; Syria (4 ; Damascus) ; Palestine (3 ; Jaffa) ; Mesopotamia (2 ; Nineveh). -(Brussels Mus. ; Dublin Mus. ; Leiden Mus. ; coll. Meinertzhagen, coll. Sillem-Van Marle).
Measurements :
Wing ♂ 126, 128, 128 ; ♀ 126, 129, 130, 133 mm.
Culmen ♂ 30, 31, 31.5 ; ♀ 28, 28, 29, 31 mm.
Range : Asia Minor, Syria, Palestine (breeding near Jerusalem : Sladen,

1919), Mesopotamia, W. Persia (Zagross Mts: Paludan, 1938), and probably S. Caspian Mts. (Sarudny, 1911).
Subspecific characters: Black shaft streaks on flanks and thighs only faintly developped; no conspicuous cross bars.
Biotope: The species inhabits deciduous forests of several kind, especially oaks in park-like land-scapes, gardens and trees in cultivated areas: Ankara: numerous in the gardens, nests found in poplars (Kummerlöwe & Niethammer, 1935); Aleppo: numerous in the gardens, nests found in mulberry trees (Clarke, 1924). In Asia Minor the species is found at lower altitudes than *major*, but in Persia it is observed at ca 1200 m (Zagross Mts: Paludan, 1938), whereas Witherby (1903: Fars) found nests at ca 1000, and ca 2000 m.

Dendrocopos syriacus balcanicus (Gengler & Stresemann 1919: Macedonia, Servia, Bulgaria).
Material examined: 1: ♀, Verchez, Bulgaria; wing 133, culmen 28 mm; lateral tailfeathers with a small white subapical spot on the outer web only. (coll. Harrison).
Range and Biotope: After the species had been discovered in S. E. Europe by Stresemann & Gengler in 1919, it seems that it is busy extending its range with a surprising rapidity. It is known from Bulgaria (Klein, 1925; Harrison & Pateff, 1939), Macedonia, and Servia, but also from Rumenia (Dobrudsha) and from the other side of the Transylvanian Alps, even breeding in the region between the rivers Theiss and Donau (Schenk, 1939; Stresemann, 1943). In all these countries it occurs side by with *D. major candidus*, which, however, appears to be scarce in Servia, Macedonia, and W. Bulgaria. It is a most noteworthy fact, that the ecological differences between *balcanicus* and *candidus* are so sharply defined that *balcanicus* is able to penetrate into the region of *candidus* without pushing away this native species: *candidus* is confined to true forest regions, often being found in the mountains, whereas *syriacus* seems to prefer gardens and trees in cultivated areas, which represent a much more available biotope than that of *candidus* (Stresemann, 1943). Nevertheless, in Sofia *balcanicus* and *candidus* have been observed during the winter in the same tree, but from the Rhodope Mountains (S. W. Bulgaria) apparently only *candidus* is known (Harrison & Pateff, 1933); the same may be true with reference to the dense coniferous forests of the Alibotush Mountains (S. W. Bulgaria) between 1400 and 1900 m alt. (Scharnke & Wolf, 1938). Further progress of the penetration of *balcanicus* into E. Europe is to be expected.
From the present knowledge on the distribution of *balcanicus* in S. E. Europe it is not difficult to decide to give *balcanicus* full specific rank (Gengler, 1920) in spite of the extensive speculations made by Stresemann (1920) in order to maintain *balcanicus* as a subspecies of *major*. Stresemann changed his opinions in 1925 already, when Klein (1925) found *candidus* and *balcanicus* in equal numbers in Bulgaria, apparently without hybridizing at an important scale. The descriptions of the only two known hybrids between *candidus* and *balcanicus* (Veles, Bulgaria, wing 133 mm: Stresemann, 1920; Overbász, Hungaria, wing 134 mm: Pateff, 1939) much resemble each other, the birds apparently being only slightly different from *candidus*. The presence of slight traces of cross barring on the lower flanks and thighs and the absence of a black postauricular band in the Hungarian and the faint development of it in the Macedonian specimen appear to be the only traces of the supposed hybrid origin of these specimens.

Dendrocopos syriacus transcaucasicus Buturlin 1910 : S. Caucasus.
Material examined : none.
Range : Transcaucasia, in the regions of Tiflis and Elisabethpol, where it occurs side by side with *D. major "kurae"*. According to Radde (1884) both species appear to be equally numerous in the neigbourhood of Tiflis, although he could obtain 12 specimens of *major* and only 4 of *syriacus*. The validity of the race *transcaucasicus* has been recently doubted by Démentieff (1934). It is possible that the greater amount of white on the lateral tailfeathers is the result of interbreeding with *major* !
Subspecific characters : Only differs from *syriacus* in the presence of 2 or 3 white cross bars on the lateral tailfeathers (Hartert, 1912).

Dendrocopos syriacus milleri Sarudny 1908 : Mt. Kuh-i-Tuftan, S. E. Persia.
Material examined : none.
Range : Only known from the type-locality, where it has been obtained in *Pistacea-* and *Populus*-forests.
Subspecific characters : Only distinguished from *syriacus* by larger size and probably more slender shape of bill. According to Sarudny (1909) wing of 3 ♂ ♂ 132—139 mm, whereas W. Persian ♂ ♂ measure 124—131, average (9) 127,2 mm.

IX **Dendrocopos assimilis** (Blyth 1849 : Rawalpindi).

Synonym (cf. Stresemann, 1921 A) : *Picus scindeanus* Horsfield & Moore 1858 : Shikarpore, Sind.
Material examined : 2 : Munchar, Sind ; Peshawar, Punjab. -(coll. Meinertzhagen).
Measurements: wing ♂ 113 ; ♀ 119 mm.
Range : Beloetschistan, Sind, and W. Punjab, eastward to about Jhelum district (Ticehurst, 1923), north to Peshawar : fairly common near Quetta (Meinertzhagen, 1920), Rawalpindi, and in the Salt Range (Whistler, 1916, and 1922).
Biotope and Discussion : In its relative small range *assimilis* appears to replace *syriacus*, with which it has never been found in the same country : *syriacus* does not go farther east than to the volcanoe Kuh-i-Tuftan in Persian Beloetschistan. In the East (Sind) the range of *assimilis* borders that of *Leiopicus mahrattensis*. *Assimilis* and *mahrattensis* are the only species of Woodpecker found in Sind (Ticehurst, 1923), where they apparently live in a rather strong interspecific competition owing to the fact that they inhabit the same type of biotope : low jungle and thorn scrub usually in low altitudes (Meinertzhagen, *in litt.*, 1946) ; each species being numerous in those places only where the other is scarce or absent. *Assimilis* has been found breeding especially in Tamarisks (Sind : 14 of 23 nesting holes : Ticehurst, 1923) ; in Quetta Whitehead (1909) found it usually breeding in mulberry trees.
Assimilis is so close to the *major* group, that it has been specifically united with it by Hartert (1900), although separated from it again in 1912. Démentieff (1934) also found evidence in favour of the specific uniting with *major*, together with *syriacus* and *himalayensis*.
Judging from its range and the close taxonomic similarities with *syriacus*, *assimilis* appears to be a remnant of the same populations from which also *syriacus* has originated. As in *syriacus* there is no postauricular stripe, and the underparts are white or creamy ; a red breast band, however, does not appear to be present neither in juvenile nor in adult specimens, although red tips to the breast feathers have been observed in several rare occasions (Hartert, 1912) ; young

birds show faintly streaked underparts and cross bars on the flanks, as in the adults of *syriacus*. Although inhabiting an *Asiatic* range *assimilis*, nevertheless, is of a *secundary European* origin since it apparently represents the distal form of the chain of *syriacus* populations that historically have originated from each other, and that have been driven away from Europe by successive Asiatic invaders (*major poelzami*; *major candidus*; *major tenuirostris*). With the exception of *medius*, *assimilis* is the most antique European form of the group, having retained a wholly red crown in the adult male. It has been isolated from the former *syriacus* populations by the northward extension of the Persian Gulf, which has left pleistocene deposits in E. Persia, west of the recent range of *assimilis*.

As is a common phenomenon in those forms that have been driven away far from their main center of dispersal, *assimilis* is the smallest European member of the *major* group: wing 116—126 mm (Hartert, 1912).

5. ABERRANT SPECIES.

I am still in doubt concerning the relationship of the aberrant species *D. arizonae* (Hargitt) and *"Desertipicus" dorae* (Bates & Kinnear). Unlike all other American members of the genus *Dendrocopos*, *arizonae* shows cross barring on the lateral tailfeathers only, the whole uppersurface being uniform earthy brown, only the quillfeathers showing the characteristic white blotches. In this respect *arizonae* stands taxonomically quite isolated, unless *Desertipicus dorae* is also regarded as a form of *Dendrocopos*. Judging from the description of *dorae* (Kinnear & Bates, 1935) it is most likely that in resembles *arizonae* in its external features: *dorae* is described by Kinnear (*in litt.*, 1946) as "a uniform brown bird with — in the male — a red nape and — in both sexes — some red on the abdomen". After a direct comparison in the British Museum Kinnear informs me as follows (*in litt.*, 1947): "The two Woodpeckers *D. dorae* and *D. arizonae* have a superficial resemblance but *dorae* has no white on the sides of head and neck nor is the underside spotted, while in *D. arizonae* the scarlet spot on the abdomen is absent". The monotypic genus *Desertipicus* has been based by Kinnear & Bates (1935) upon the absence of the characteristic malar stripe, and any white on scapulars and back. A malar stripe is present in *arizonae* but a uniform brown coloration of the upper surface is found in both *arizonae* and dorae. The malar stripe is also quite obsolete in a typical member of *Dendrocopos* as *D. medius*, although traces of its presence in this species can still be detected. Nevertheless, if *arizonae* is still treated as a species of *Dendrocopos*, no arguments exist justifying the maintainance of *"Desertipicus"*. Peters (*in litt.*, 1946) also has his doubts concerning the validity of this genus, although he has not personally seen it either, but Kinnear (*in litt.*, 1946) still prefers to keep it as a monotypic genus. At all events, both the areas of *arizonae* and *dorae* are situated on the very outskirts of the holarctic region, although apparently in biotopes that cannot be directly compared. Besides *dorae* appears to inhabit a biotope that represents the very limits of the ecological possibilities suitable to a woodpecker! They may be considered to be the offspring of a former generally distributed form, although they are apparently not directly related with each other: in *dorae* the under tailcoverts and the lower abdomen are tinged with red, whereas the red coloration is absent in *arizonae*, as in all North American species of *Dendrocopos*!

X **Dendrocopos dorae** (Bates & Kinnear, 1935: Ukadh, Taif-Mecca Road, Arabia).
Material examined: none.
Measurements: According to Bates & Kinnear (1935): wing ♂ 113, 115 mm; 4 ♀ 108—112 mm; culmen ♂ 24, 25 mm; 4 ♀ 20—22 mm.
Range and biotope: Arabia: the only woodpecker! Collected at widely separated localities in the Taif area east of Mecca (Ukadh, Farha, Ashaira, Rabba (near Abha), along Wadi Ranqua). According to *Philby*, the discoverer of the species, it is a bird of the higher elevations of the Arabian plateau, collected between 550—2450 m; it is almost without exceptions found in the mountain wadis where *Acacia* trees are numerous. They often may be observed cross wise sitting on the branches like a normal perching bird (cf. Bates & Philby, 1937; Bates, 1937).
Discussion of relationship and history. As members of the *D. major* group only inhabit those regions that most closely border the isolated, almost *eremian* range of *dorae* (Arabia), I am inclined to consider *dorae* as a tertiary relict of the *major* group in the time that the uppersurface was still uniform, not possessing the white shoulder patches. A uniform upperside is also present in *himalayensis*, which I have treated as a tertiary inhabitant of its present Cashmere range too! The apparent dominant phaeomelanine pigmentation, causing the general brown colour may be interpreted as the result of a climatic adaptation of *dorae*.

XI **Dendrocopos arizonae** (Hargitt 1886: Santa Rita Mountains, Arizona).
Material examined: 3: Santa Rita Mts., Arizona; Chihuahua, Mexico. — (Leiden Mus.; coll. Sillem-Van Marle).
Measurements: Arizona: wing ♂ 122, ♀ 112; culmen ♂ 29, ♀ 25 mm. Chihuahua: wing ♂ 113; culmen ♂ 24.5 mm.
Range and subspecies: S.W. New Mexico, S. Arizona, W. Mexico, south through the states of Sinaloa, Durango, and Zacatecas, to Colima (Ridway, 1914).
The southern populations have been recognized as a separate race (*fraterculus* (Ridgway 1887): Colima, S.W. Mexico) on account of smaller size and by "averaging more heavily spotted beneath, and with white spots on outer webs of primaries smaller (sometimes obsolete)" (Ridway, 1914, p. 263).
Discussion of relationship and history. It is a noteworthy fact that the present range of *arizonae* coincides with the distribution of the glacial sonoran forest refugium, as indicated by Reinig (1937). In its W. Mexican area, which mainly consists of desert plateaus with mountain ridges *arizonae* inhabits the broad-leaved mountain forests, in which representatives of the arcto-tertiary forest vegetation prevail, exhibiting a remarkable great number of species. From the S. Arizonan and N.W. Mexican mountains (Santa Rita Mts. Huachuca Mts., Chiricahua Mts.) Harshberger (1911) mentions the occurrence of 40 non-coniferous trees, among which no less than 8 species of *Quercus*! From the desert mountain ranges and dry canyons of Chihuahua only 2 coniferous and 4 non-coniferous trees are mentioned, among the latter 1 species of *Fraxinus* and 3 of *Quercus* occur! Generally speaking Mexico and Central America possess a great number of endemic Oak species which is the result of a repeated southward migration into a protected mild area, caused by successive ice ages, as also by species formation caused by local isolation.
Arizonae is described by all authors to be generally a bird of the mountains, being found at altitudes of 1300—2450 m (Bent, 1939); besides, its partiality to oaks is repeatedly mentioned (Swarth, 1929; Pearson, 1932). It is also said to occur in forests in which are found: Giant Sycamore, ashe, maple,

black walnut, locust (Bent, 1939). The species appears to be scarce in its whole range, often travelling in small flocks of 5—15 specimens.

Judging from the above discussed distribution of *arizonae* and its correlation with one of the southernmost situated glacial forest refugia, it appears that *D. arizonae* is an old form. From a taxonomical point of view it has no direct relatives in the nearctic fauna, but a close exterior similarity apparently exists with *dorae*, as has been discussed above. Still, I doubt whether *arizonae* can be considered to represent the only member of the extensive *D. major* group found in the New World, or whether it is an aberrant form of some not yet recognized group of *Dendrocopos*-like woodpeckers, which once occurred in North America. I incline to take the first mentioned opinion based upon the consideration that no other nearctic members of *Dendrocopos* are known possessing a uniform (neither white, nor transversely barred) upperside, a character, which is an exclusive feature of the *major* group. Nevertheless, I realize that *arizonae* differs from the *major* group in the following respects: (1) lack of red on lower abdomen or under tailcoverts, (2) underside broadly spotted or squamated caused by the presence of a dark brown apical spot to each feather. The absence of white shoulder-patches does not appear to me to be a criterium for excluding *arizonae* out of the *major* group, as has been pointed out in the chapter on *dorae*.

Independently from any decision taken in the dilemma regarding the relationship of *D. arizonae*, Eurasia may be considered to be the original home of the *D. major* group, America having been peopled in some preglacial time, and not afterwards, as is indicated by the absence in North America of all other members of the genus with uniform brown or black upperparts (hindneck to central rectrices, excluding scapulars), which in Eurasia are represented in so many forms. Faint indications of white bars on rump and scapulars have been found by Swarth (*fide* Bent, 1939) in some Arizonan specimens. These traces may be caused by narrow white edgings to some of the feathers, a phenomenon that I also found in the only 1 specimen of *D. major tscherskii*, which I was able to examine.

VI DENDROCOPOS LEUCOTOS (BECHSTEIN).

THE HISTORY OF DENDROCOPOS LEUCOTOS (Bechstein).

D. leucotos has not so wide a range as *D. major*, but still it occurs from the borders of the Pacific to almost those of the Atlantic Ocean, being absent in the Central Asiatic mountains (Tian Shan) and in the Himalayas.

The most important fact that may spread some light upon the history of its postglacial distribution is the resemblance of Manchurian specimens (*"ussuriensis"*) with those from E. and N.E. Europe (*leucotos*). This resemblance may be called an identity since neither Stegmann (1930 and 1936), nor Kozlova (1932), nor Hartert-Steinbacher (1935) have succeeded in discovering useful distinguishing characters between *"ussuriensis"* and *leucotos*. Nevertheless, it seems that Stegmann (1936) could not decide to refer the E. Asiatic populations to *leucotos*. As all E. Asiatic birds appear to be of one general type, which, indeed, shows a certain amount of individual variability, inclining to be slightly more white on upperside and lateral rectrices in Kamchatka, still Stegmann (l.c.) uses the name *voznessenskii* (Buturlin 1907: Kamchatka) for them. As no sufficient material was available to recognize possible very slight constant differences, both *voznessenskii* (Kamchatka), *ussu-*

riensis (Sidemi, S. Ussuria), and *saghalinensis* (Sakhalin) are treated here as synonyms of *leucotos*. Stegmann (1936), however, could not detect differences between specimens from Transbaicalia and from Kamchatka.
Siberian populations, however, incline to produce a certain amount of generally more white specimens, conspicuously on both upper- and underparts, besides, showing reduction of black streaks on the underside and of black bars on tertials and lateral tailfeathers. In some cases even specimens possessing white patches on the central rectrices occur, which is a unique exception in the species (Stegmann, 1930). The purest white specimens of this type (*uralensis*) are found, according to Stegmann (1936) in almost uniform populations in the S. Ural mountains, Transuralia, Tara, Tobolsk, and the region where the rivers Irtysch and Ob meet; besides, in the forest-oases of the S.W. Siberian steppes. In these regions no heavily striped birds are said to occur, but going in eastern as well as in western directions heavily striped birds occur more frequently (e.g. Altai), whereas light birds become gradually rarer, being totally absent in N. Europe and Poland on the one hand, and Manchuria on the other hand. Finally, the pure whitebacked form *leucotos* is in Europe most common in Russia (although rare in many central regions: Grote, 1926; "south to about 49° 30′ N.L. in Poltawa gov. and on the lower Wolga": Kozlova, in litt., 1946), Fennoscandinavia (rather common in Norway: Kolthoff & Jägerskiöld, 1898), Baltic States, and Poland, becoming rare in Bohemia and the Carpathian mountains, and extremely rare in Central Germany (several records; eastwards to the Drachenfels on Rhine: 22.VI.1905, cf. Niethammer, 1938); breeding in S. Germany, and probably occurring exceptionally in Switzerland (Bieri, 1945), and N. Italy (Arrigoni, 1929). It has never been recorded from Denmark, Netherlands, France, Great Britain, whereas one doubtful record is known from Belgium (Aubel near Liege, XI 1840: Van Havre, 1928). Consequently one may suggest, that *leucotos* postglacially has spread from the Manchurian glacial forest refugium, through the taiga of Siberia into E. Europe, where it has extended its range even farther westward than *D. m. major*. It also has spread along the Asiatic coast in northern direction into Sakhalin Island and Kamchatka, and via Hokkaido also into the southernmost island of the Kuriles chain (Kunashiri, not common: Bergman, 1931). In the course of postglacial times, differences in the plumage of the Siberian birds took place, the feathers becoming longer and softer, especially on the back, whereas the eumelanine pigmentation became gradually more reduced on tertials and lateral rectrices; the whole evolution resulting in the origin of a characteristic Siberian bird with a white appearance and with a soft and downy plumage. Based upon the recent distribution, it is supposed by the author, that the transformation from *leucotos* into *uralensis* is of a postglacial date. An argument in favour of this theory is furnished by the fact, that the E. Asiatic *leucotos* populations have a rather disconnected area, being found in what Kozlova (1932) called isolated colonies: Minussinsk, Altai, Kentei, Amur (Lesser Khingan Mts.), S. Ussuria. *Uralensis* is found north and northwest of some of these regions, its eastern boundaries going as far as approximately to Irkutsk. Thus, in Minussinsk, Altai, and Kentei Mts., the original Manchurian birds have retained their characters, whereas the northern populations have become changed. The same type of distribution is found in *Garrulus glandarius*: the race *bambergi* being found in Manchuria and in the E. Tian Shan (Korla); the Siberian race *brandti* occurring north and northwest of it (Voous, 1945).
D. leucotos is by far not the only bird-species from which it has been considered to have spread postglacially out of Manchuria through the whole of Siberia into E. Europe. Reinig (1938) supposed it for *Cractes infaustus*, which postgla-

cially has reached N. Scandinavia, as also for *Dryocopus martius*, which in recent years has spread so conspicuously into W. Europe: „die östliche Herkunft dieses Vogels steht fest und wohl ebenso sicher ist, dass das mandschurische Refugium der Ausgangsort für die postglaziale Arealerweiterung nach Westen und Norden gewesen ist" (Reinig, 1938, p. 82). I also supposed it with reference to *Garrulus g. bambergi* (Voous, 1945). *Cractes* and *Dryocopus* apparently have spread in conjunction with the typical dense coniferous taiga, but *Garrulus* and *D. leucotos* appear to have prefered the birch zone of the taiga.

All authors agree that *leucotos* is but very rarely found in coniferous forests, prefering open broad-leaved forests with many dead trees. In its Siberian range *D. leucotos* „fehlt im richtigen Nadelwalde ganz. Er kommt ja in der Taigazone vor, doch bewohnt er hier immer nur die mehr mit Laubhölzern bestandenen Flussauen und den Waldrand. Für die Birkenwaldzone ist er sehr charakteristisch. In lichteren Kiefernbeständen, die mit Birken und Espen gemischt sind, ist er auch zu finden. In der Waldsteppe nicht selten und sogar im Wüstengebiet mit Saxaul-Bewachsung" (H. Johansen *in litt.* 1946). In the Amur region the species inhabits the broad-leaved forests on the mountain slopes and along the streams (Stegmann, 1930); in E. Finland Pynnönen (1939) found it in extensive broad-leaved woods only, two nesting holes being situated in a sound poplar and one in a decayed birch; Hortling (1929) describes it as inhabiting the Ahorn-forest-zone in S. Finland, north to the Oak-zone, this being the region, where *Parus caeruleus* and *Picus canus* are characteristic; in the Bialowies virgin forest it is a common breeding bird in marshy deciduous woods, being locally even commoner than *D. major* (Tischler, 1943); finally in the Bavarian Alps the species has been observed breeding in those parts of the mixed forest (mainly *Abies alba* and *Picea excelsa*), where beech and maple prevails: a nesting hole was situated in *Abies alba* (Verthein, 1935), another in a dead *Fagus* (Franz, 1937). In all these forests dead trees and decayed stumps have to occur in abundancy to make the biotope suitable to *D. leucotos*. In Switzerland the species is probably extremely rare. Although only mentioned by Meylan & Haller (1946) in the hypothetical list of Swiss birds, it appears to me that a visual observation by Bieri (1945; besides, additional remarks *in litteris* 1946: ♂, 28.VIII.1945, St. Immer valley, Berner Jura) is trustworthy. In the Leiden Museum 2 mounted specimens are preserved with the indications "Suisse" (Temminck collection), but this may be a mistake for "Silesie", since in Temminck's *"Manuel d'Ornithologie"* (1820, p. 396), to which is referred, only this locality is mentioned: in a bad handwriting "Suisse" and „Silesie" have the same orthographic configuration. Nevertheless, in its penetration into the Alps, the postglacial extension of *D. leucotos* agrees with that of *D. m. major*!

Not only birds (*D. leucotos, Dryocopos martius, Cractes infaustus, Garrulus g. bambergi*) are thought to have spread postglacially from Manchuria into Europe. Reinig (1937) mentions a number of species of Fishes, and Insects (among which *Bombus hypnorum, Zygaena lonicera*) that probably originate from the Amur region „aber auch heute ist der Zuström östlicher Formen im nördlichen Europa noch nicht abgeschlossen" (Reinig, 1937, p. 86).

The survival in a S.E. mediterranean refugium during the last glacial period must be supposed with reference to the subspecies *lilfordi*, which differs conspicuously from *leucotos* in having the whole back transversely barred with black. It inhabits S.E. Europe, northward to Bulgaria and probably to the Dobrudsha (Stresemann, 1920A) and Dalmatia; it occurs doubtfully in the Peleponnesus (Niethammer, 1943), but abundantly in the Mamuras forest in Albania (Ticehurst & Whistler, 1932); inhabiting also Asia Minor (very sporadically: Braun, 1908; Kummerlöwe & Niethammer, 1935: northern mountains: Ilgaz Dagh, 1900 m) and the western Caucasus (Dementieff, 1934). *Lilfordi* has a much more restricted area than e.g. *D. syriacus* and the S.E. populations of *D. medius*, being apparently absent in the S. Caspian and the Iranian regions and in Syria, apparently also in Crimea (Gladkow *in litt.* 1946). It is said to have occurred a few times as a straggler into Italy (Arrigoni, 1904), but doubtful records exist in the literature of its occurrence in Corsica and in the Pyrenees. It is mentioned by Legendre (1929) to have been captured in the Pyrenees on several occasions during the 19th century. For the first time apparent breeding birds have been taken near Urdos in the spring of 1851 by Loche (1852), but the species is only recently rediscovered by Danis (1937) in the western Pyrenees (♂ ad., Guillers near Bedous, Basses Pyrenees). The description given by Danis (1937) fully agrees with the subspecific characters of *lilfordi*. The specimen, which is now in the Paris Museum, has been examined by Berlioz, who gives the following account: "Malheureusement, capturé en pleine mue cet oiseau est en assez mauvais état: néansmoins ses charactères apparents semblent le rapprocher beaucoup de ceux de la forme *lilfordi*" (*in litt.*, 1946). In the Brussels Museum I was able to examine two Pyrenees specimens (♂, ♀) without data in the collection of De Selys Longchamps. Both these old specimens resemble *lilfordi*, although the back, which is not in a very good condition, shows only traces of black cross bars. The same may be said of two specimens from Corsica in the collection of De Selys Longchamps (Brussels Museum), which also appear to incline to *lilfordi* rather than to *leucotos*. These specimens, which according to the labels are collected by Isui Jonston (8.IX.1842) and Wellby (6.VI.1843) respectively, are not the only specimens known in collections, since Dr. W. Kuenzi wrote me (1946) that in the Natural History Museum of Bern two specimens are preserved apparently with no other data than "Korsika". In the second half of the 19th and in the 20th century nobody has met with this species in Corsica (cf. Arrigoni, 1904): its occurrence in that island has been indicated by Salvadori only (*fide* Arrigoni, 1904). So the species may be either exterminated there, or be extremely rare (most probably). Its occurrence in that remote island furnishes an additional argument in favour of the suggestion that *D. leucotos* in S.E. Europe is represented in a few relict populations only.

It thus appears, that during the last interglacial period *lilfordi* had a wide European distribution, having retreated to both the S.E. and S.W. refugional forest areas. Only in the eastern region it has maintained itself sufficiently to form a wel pronounced subspecies, but in S.W. Europe it has almost become extinct, leaving only relict populations in the Pyrenees and in Corsica. The fact, that the Pyrenees and Corsica specimens examined show the subspecific characters of *lilfordi* in an incomplete stage only, indicates, that they belong to relict populations in which the same potential subspecific characters have not developed as strongly as has been the case in the S.E. populations. In this respect it is noteworthy, that, judging from the description of the N. Chinese form (*sinicus*: Pekin) given by Hartert (1912), *lilfordi* appears to show close similarities to N. Chinese populations, indicating the relative higher age of *lilfordi* and *sinicus*, compared with *leucotos* and *uralensis*. A pure white back and rump, as indicated by the specific name *leucotos*, are not the typical characters of the species, as these are only found in the youngest races *leucotos* and *uralensis*. Even young birds of these races possess distinct dull black edges to most white feathers of the upper parts!

It is very probable that — at all events during the last glacial epoch — the presence of both *D. medius* and *D. leucotos* in the S.E. European forests have excluded the occurrence of *D. major* in these regions, since *leucotos* and *major* inhabit approximately the same kind of biotope, whereas their feeding habits resemble each other also. In the Mamuras forest, north of Albania, Ticehurst & Whistler (1932) found that *lilfordi* was feeding mostly on relative large wood-boring larvae of beetles and moths, which the birds cut with their heavy bills out of the mostly rotten tree stumps and beween logs in the bark. Equally in the S. German mountains 59—79% of the food brought by the parents to their nestlings appeared to consist of wood-boring insects (*Cerambycidae*) (Franz, 1937). Judging from these records and from the heavy shape of the bill found in all races, it seems that *D. leucotos* represents the strongest type of Woodpecker of the genus.

From the fact that *D. leucotos* ranges in Japan south to the northern Riu Kiu Islands (*owstoni*: Amami Oshima), one may conclude that the distribution of the species dates back to tertiary times. The chain of the Japanese volcanic islands may have been separated from the continent in late pliocene times: tertiary fluviatile deposits found on the boundaries of the island blocks 720 m beneath sea-level contained remnants of the plio-pleistocene *Stegodon*-fauna (Schaffer, 1941). *D. kizuki* and *D. l. owstoni* are the only members of the genus *Dendrocopos* that are found in the Riu Kiu Islands; *kizuki* represents one of those pigmy forms that practically have been driven away from the continent into remote island groups, whereas *leucotos* probably is an element of the late tertiary fauna of which the peculiar Woodpecker *Sapheopipo noguchii* (Seebohm: Okinawa Oshima), and also the Jays *Lalocitta lidti* (Bonaparte: Amami Oshima) and *Garrulus lanceolatus* Vigors (N.W. Himalayas) are the remnants. The fact, that *owstoni* is very conspicuously different from the palaearctic forms of the species, though being somewhat approached by the S. Chinese and Formosan races, represents a clear evidence in favour of the significance of a long lasting geographic isolation within a small area and under peculiar climatic conditions. The taxonomic differences between the races *owstoni* on the one hand and *uralensis* on the other hand are among the strongest geographic alterations found within one bird species: *owstoni* being almost totally darkened by the superfluous development of eumelanine, resulting even in the nearly total reduction of white on the back (typical subtropical island form), whereas *uralensis* has obtained the peculiar white siberian plumage, caused by the gradual decrease of eumelanine pigmentation. The influence of the warm humid climate (subtropics) is also apparent in the S. Chinese and Formosan birds: these, however, are by far not so obscured as *owstoni*.

In S. China and in Formosa the relict character of the *D. leucotos* populations is demonstrated by the fact that the birds are inhabitants of the difficultly accessible steep mountain regions only, where, however, they appear to be locally not uncommon. Nevertheless, according to La Touche (1931: Fokien) the species "may be reckoned among the rarer Woodpeckers of China" (p. 19). In Formosa it has been obtained in the Racu Racu Mountains (up to 2100 m) and on Ho Ho Mount (up to 1500 m) (Ogilvie Grant & La Touche, 1907), whereas in Amami Oshima the species is also an inhabitant of the mountainous parts of the island (Kuroda, 1925), where Cycads, Tree-ferns, Giant Bamboose, and *Ficus* occur (Jahn, 1942). In Japan the species appears to be a ubiquist: in S. Hondo, Shikoku, and Kiushiu inhabiting the subtropical evergreen forests in the plains, as well as in the mountains (*Quercus, Camellia, Cinnamomum, Acer, Magnolia, Castanea*), whereas in Central Hondo it is found in the antique deciduous forests, as well as in the coniferous mountain forests;

in Hokkaido it usually inhabits planted Oak-woods, and other broad-leaved forests (*Quercus, Ulmus, Acer, Juglans, Betula,* etc.) (Jahn, 1942).
The genesis through island isolation of a conspicuously darkened form (Formosa, Amami) has not been correlated in *D. leucotos* with the origin of pigmy forms, in spite of the small ranges inhabited: the birds of Amami Oshima belong to the largest E. Asiatic forms (wing 148—157 mm, against 145—152 mm in E. Asiatic *leucotos*); the Formosa race (*insularis*: wing 132—139 mm), however, is distinctly smaller than the very similar Chinese form (*fohkiensis*).
Although subspecific differences exist between the Manchurian and Hokkaido, and the Hondo forms of *D. leucotos*, indicating that at least the Hondo population is older than the last glacial epoch, yet, no other indications of the pleistocene history of *D. leucotos* in E. Asia can be detected in its recent distribution.

XII **Dendrocopos leucotos** (Bechstein).

Dendrocopos leucotos lilfordi (Sharpe & Dreser 1871: Epirus, Greece).

Probable synonyms (cf. Démentieff, 1934A): *Dryobates leucotos caucasius* Tschchikwischwili 1928: W. Caucasus. *Dryobates lilfordi ponticus* Buturlin 1929: Batum, N. Caucasus.
Material examined: Constantinople (1); Pyrenees (2); Corsica (2). — (Brussels Mus.; coll. Meinertzhagen).
Measurements:
Constantinople: wing ♀ 147; culmen ♀ 37 mm.
Pyrenees: wing ♂ 141; ♀ 145; culmen ♂ 36; ♀ 32.5 mm.
Corsica: wing ♂ 144; ♀ 143; culmen ♂ 36; ♀ 34 mm.
Range: See "*History of D. leucotos*".
Subspecific characters: Upper back and rump white, transversely barred with black; under parts more boldly streaked than in *leucotos*, inclining to faint cross bars on the lower flanks and thighs. Ground colour of under side slightly tinged yellowish. The black earstripe, connecting the black moustachial streak with the black occiput, is not characteristic of this race, as is suggested by Hartert (1912), since it may be found in other races also (I found it in several Central European specimens (a.o. Silesia), and in specimens respectively from Zarizyn on River Volga, Amur region, Hokkaido, and Hondo).

Dendrocopos leucotos leucotos (Bechstein 1803: Silesia).
Probable synonyms:
Dryobates leucotos voznessenskii Buturlin 1907: Kamchatka.
Dendrocopus leuconotus ussuriensis Buturlin 1907: Sidemi, S. Ussuria.
Dryobates leucotos coreensis Clark 1907: Fusan, Corea.
Dryobates leucotos saghalinensis Yamashina 1931: Sakhalin Island.
Material examined: I. *Europe*: Silesia (3); Poland (2); Bohemian Forest (3: Frauenau); Hungary (1: Borsod); Sweden (1); Norway (2: Voss, Lier). — (Brussels Mus.; Copenhagen Mus.; Dublin Mus.; Leiden Mus.; coll. Meinertzhagen).
II. *Asia*: Altai (4); Amur (3); Vladivostok (1). The specimens from Katon Karagai, Altai, are somewhat intermediate. — (Brussels Mus.; Copenhagen Mus.; Dublin Mus.; coll. Sillem-Van Marle).
Measurements:
Europe: wing ♂ 139—151, average (8) 145.4; ♀ 143, 146 mm.

Altai: wing ♂ 151, 151, 152; ♀ 145 mm.
Manchuria: wing ♂ 146; ♀ 146, 147, 148 mm.
Schlegel (1918) gives the following measurements of specimens from the Bavarian Alps:
wing ♂ 140—144, average (6) 142; ♀ 138, 141, 142 mm.
culmen ♂ 34—41, average (6) 38; ♀ 36, 37, 38 mm.
Europe: culmen ♂ 34—38, average (8) 36.2; ♀ 34, 36 mm.
Altai: culmen ♂ 39, 39.5, 40; ♀ 38 mm.
Manchuria: culmen ♂ 37; ♀ 34, 35.5, 36 mm.
Range: discontinuous(!): see *"History of D. leucotos"*.
Subspecific characters: The pure white back and rump, and the abundancy of white on scapulars and tertials, as well as the irregularly black barred lateral tailfeathers in which white usually prevails, furnish sufficient distinguishing characters of this race. A remarkable individual variability in the length and strength of the bill is found in the european populations, the meaning of which I am not able to detect.

Dendrocopos leucotos uralensis (Malherbe 1861: Ural Mts.).
Material examined: Stalingrad on Volga (1); Gouv. Tomsk (1); Tarbagatai (1); Kara Irtysch (2). — (coll. Hens; coll. Sillem-Van Marle).
Measurements:
Wing ♂ 145, 146, 147, 148; ♀ 150 mm.
Culmen ♂ 36, 37, 38, 41; ♀ 36 mm.
Range: W. Siberia and Ural Mountains; situated between the Asiatic and European ranges of *leucotos*. See "History of *D. leucotos*".
Subspecific characters: Typical specimens can directly be distinguished from *leucotos* by their conspicuously white upperside, including scapulars and tertials, the white feathers of the back being also longer and broader, and by the reduction of black bars on the lateral tailfeathers, which incline to be pure white at the ends; the underparts have only few and very narrow black streaks, which are concentrated on the sides of the breast, they may even be practically absent.

Japan.

From the Japanese Islands a number of subtile races have been described, particularly by Japanese authors. The Hokkaido birds resemble the Manchurian ones, from which they are but slightly different. All Japanese birds incline to have creamy to isabelline or even light buff (not white) light parts; rather strongly streaked underparts with a slight, but apparent, rosy wash; a general reduction of the light parts throughout the body, including the presence of narrow black bars on the back and broad bars on the lateral tailfeathers; brown ear-coverts; also strong bills. The degree of development of these characters furnishes the subspecific distinctions between the respective island races.

Material examined: Hokkaido (2); Tokyo, Hondo (1); besides, 5 specimens labelled "Japan". — (Leiden Mus.; coll. Sillem-Van Marle).
The following descriptions are of importance:
D. l. subcirris (Stejneger 1886: Hokkaido).
D. l. yamashinae (Bergman 1931: Kunashiri, S. Kuriles).
D. l. stejnegeri (Kuroda 1921: Shinano Prov., C. Hondo).
D. l. tookaidonis (Momiyama 1927: Pacific side C. Hondo).
D. l. namiyei (Stejneger 1886: Yamato, S. W. Hondo).
D. l. kurodae (Götz 1926: Yamato Prov., S. W. Hondo).

D. l. uchidae (Momiyama 1927: Kiushiu).
D. l. takahashii (Kuroda & Mori 1920: Dagelet Island).

Dendrocopos leucotos sinicus (Buturlin 1907: Pekin).
Material examined: none.
Range: China (except S.): exact range unknown.
Subspecific characters: Said to resemble those of *lilfordi* (cf. Hartert, 1912).

Dendrocopos leucotos fohkiensis (Buturlin 1908: Fokien).
Material examined: none.
Range: S E. China: exact range unknown.
Subspecific characters: As in *insularis*, but larger.

Dendrocopos leucotos insularis (Gould 1862: Formosa).
Material examined: 10: Formosa. — (Leiden Mus.; coll. Meinertzhagen).
Measurements:
Wing ♂ 132—139, average (6) 135.9; ♀ 132—138, average (4) 134.2 mm.
Culmen ♂ 31—38, average (6) 35.7; ♀ 33—35, average (4) 33.8 mm.
Range: Formosa.
Subspecific characters: Lower back and rump white, with narrow black cross bars; scapulars black with only a few white markings; underside very heavily streaked, especially in the breast region; ground colour light yellowish buff.

Dendrocopos leucotos owstoni (Ogawa 1905: Amami, N. Riu Kiu Islands).
Material examined: 1: Amami, ♀, collected by Allan Owston: wing 157, culmen 36.5 mm. — (coll. Meinertzhagen).
Measurements:
Wing according to Momiyama (1926): 27 ♂♂ 149—147; 13 ♀♀ 148—157.5 mm.
Range: Amami Island, Riu Kiu.
Subspecific characters: A very dark bird: back and rump black, with white edgings to a few feathers only; mantle, scapulars and wingcoverts black, of the latter only a few have small white markings; under parts very dark yellowish red, heavily and broadly streaked black; on the breastsides the dark bands almost reach each other in the median line; throat and earcoverts dark brown; undertailcoverts red, with faint brown shaft stripes.

VII NORTH AMERICAN WHITE-BACKED WOODPECKERS.

1. INTRODUCTION AND RELATIONSHIP.

In North America the *Hairy* (*villosus*) and the *Downy* (*pubescens*) Woodpeckers ecologically replace the European *Greater* (*major*) and *Lesser* (*minor*) *Pied* Woodpeckers. It seems that their mutually ecological proportions are the same, since *villosus* and *major* are found in forests of whatever kind, and in places wherever big trees occur, feeding on the trunks or the taller branches, whereas *pubescens* and *minor* especially occur in more open deciduous or mixed woods, gardens, and orchards, searching for food along the smaller branches and the thin twigs, and only rarely occurring in clear coniferous forests or dense forests of any kind. The relative proportions of size are approximately the same as found in the European species (average wing measurements):

Netherlands (♂♀: personal measurements):
major: wing 132.2; culmen 28.0 mm.
minor: wing 88.5; culmen 16.5 mm.

Eastern United States (♂ ♀ : Ridgway, 1914) :
villosus : wing 120.4 ; culmen 29.2 mm.
pubescens : wing 94.1 ; culmen 16.4 mm.

It has been shown that the genetic relations between *major* and *minor* are not very close ; the conspicuous taxonomic differences between *villosus* and *pubescens*, however, prove their close genetic relation, but their history is obscured by the fact that the species live side by side in an extensive range. Even *D. pubescens* is not found in any region, where *villosus* does not occur! Taxonomically *pubescens* may be characterized as the minor edition of *villosus*, both species especially have in common the broad black eye stripe, the white median dorsal stripe, and the uniform (unstriped) underside, even in juvenile plumage. Apart from the relatively smaller and feeble bill of *pubescens* differences exist in the colour pattern of the lateral rectrices only :

villosus : lateral pair of rectrices uniform white ; outermost but one with a broad uniform white tip, but usually with a black patch at the base of the inner web.

pubescens : lateral rectrices broadly barred with black and white.

These differences, however, do not appear to be principal ones, since in one of the Bahaman races of *villosus* (*piger*) "one or more black spots on inner webs of two lateral pairs of normal rectrices" are stated to occur regularly (Ridgway, 1914, p. 209), and an additional island race (*picoideus* : Queen Charlotte Islands, British Columbia) has been characterized by having "the lateral rectrices sometimes spotted or broadly barred with black" (Ridgway, 1914, p. 220), besides, a few cross bars have been found by me on two outermost pairs of tailfeathers in a ♀ from Costa Rica (*extimus* : Leiden Mus.). In northern specimens of *pubescens* the black bars are much reduced in size, becoming nearly obsolete in some specimens of the race *nelsoni* (Ridgway, 1914). The proportional differences between *villosus* and *pubescens*, which are conspicuous in northern and temporate birds, become less defined when the southern races of both species are compared (average measurements of ♂ : Ridgway, 1914) :

v. extimus (mountain zone Costa Rica) : wing 102.8 ; culmen 24.9 ; tail 58.6 mm.
p. gairdneri (coastal humid zone of California) : wing 95.1 ; culmen 16.4 ; tail 58.1 mm.

Relative small measurements of culmen, tarsus, and middle toe in a subspecies of *villosus* are also found in the race *parvulus* from north-central Salvador of which the following measurements are of interest (average of 3 adult males : Dickey & Van Rossem, 1929, p. 220) :

v. parvulus (mountain zone of Salvador) : wing 103.3 ; culmen 21.4 ; tail 59.3 mm.

Besides, *v. extimus* and *p. gairdneri* have the following characters in common, which make them almost indistinguishable from each other on terms of distinct species : (1) a dark uniform drab brown underside from upper throat to under tailcoverts ; (2) light parts on sides of head and on back washed with brown ; (3) reduction of number and size of white spots on wing quills. It thus appears that differences between the two species become obsolete in southern glacial forest refugia of the continent. In consequence one may consider the separation between *villosus* and *pubescens* to be of a post-tertiary age, caused by glacial isolation. The recent distribution of these species, however, furnishes no further indications with reference to the exact glacial history of the species. The hypothesis receives additional evidence in the presence of a very locally distributed form (*stricklandi*) in the mountains of S. Mexico, which shows close taxonomic resemblances with *villosus-pubescens*, agreeing with the southern races in general measurements, and in the reduction of the white spotting of the wing quills; besides, having a broad black eyestripe, and regularly barred lateral tailfeathers. Nevertheless, *stricklandi* possesses a few characters which give it a somewhat aberrant character: (1) white dorsal stripe narrowly barred with black; (2) underside whitish, regularly streaked and spotted with blackish; (3) dark sooty black, not pure black dark parts of upperside.

The black barring in *stricklandi* may be an original character ,since it is found in almost all members of the geologically relatively old *"Ladder-backed"* group, and since the medial dorsal white stripe in *villosus* and *pubescens* usually is intermingled with black feathers, even showing indications of black bars in specimens of *pubescens gairdneri* examined. In addition black bars, spots, and streaks on the white back are racial characters of *D. villosus picoideus* from the Queen Charlotte Islands (not examined; Ridgway, 1914). Streaked underparts are found neither in *villosus*, nor in *pubescens*, but I saw streaks on the sides of the chest in adult specimens of *D. v. villosus* and *D. v. auduboni*, and especially in *D. v. extimus*. In the Bahaman races (*maynardi, piger*) of *villosus*, the presence of black streaks on the sides of the breast are even used as racial characters, whereas in the Queen Charlotte Islands race (*picoideus*) even "the sides sometimes are streaked and the flanks barred or transversely spotted with black" (Ridgway, 1914, p. 220). Besides, streaked underparts are found in most species of *Dendrocopos*; if they are absent in the adult, they can usually be found in the juvenile. Thus, the aberrant characters of *stricklandi* have been reduced to original characters of the *villosus-pubescens* group, whereas there are clear evidences that the conspicuous white dorsal stripe and the uniform underside of the latter possibly have been derived respectively from an "ordinary" transversely barred upperside, and from a streaked, and on the flanks slightly barred underside.

The habitat of *stricklandi* is confined to the pine woods on the mountain slopes of S. E. Mexico (Vera Cruz, Puebla, Mexico, Morelos), especially on the high volcanoes (Orizaba, Popocatapetl, Ixtaccihuatl) where the species has been found in altitudes from 2400—3350 m (Ridgway, 1914). In these lower mountain zones the forests are of the broad-leaved type, consisting mainly of a number of holarctic tree species (*Quercus, Tilia, Alnus*), but at higher altitudes pines become more abundant. On Mt. Orizaba (4600 m) " the summit rises above a forest of Pines which begins with *Pinus leiophylla* at 2000 m and at 2700 m consists of *Pinus montezumae var. macrophylla, P. teocote* and *P. pseudostrobus*" (Harsberger, 1911, p. 652). *D. stricklandi* has remained a rare bird in collections. Owing to the considerable cutting off and thinning out of its original pine forests, even in its habitat, the species apparently has become gradually rarer (cf. Sutton & Burleigh, 1940). The conspicuous great number of holarctic forest elements in these Central American regions may be explained by the influence of the glacial periods and the fact that the northern and temporate forest associations have found suitable localities to maintain themselves in a tropical climate. *D. stricklandi* equally is considered here to be a *relict* of the tertiary North American Woodpecker fauna, which has found a remote refuge in the S. E. Mexican mountain pine forests. From these preglacial populations the early glacial *villosus-pubescens* populations have derived. The aberrent taxonomic characters found in *stricklandi* may thus be the remnants of the taxonomic characters of the preglacial populations.

2. POSTGLACIAL HISTORY OF D. VILLOSUS AND D. PUBESCENS.

It is a most noteworthy fact that the recent distributional phenomena of *D. villosus* and *D. pubescens* are so strikingly alike that they can best be treated combined. The respective distribution of their races are the results of the same history, which has been induced by the influences of the successive glacial periods. The result of the postglacial history of *villosus* and *pubescens* is indicated by the fact that within the limits of the U.S.A., Canada and British Columbia both species taxonomically can be divided into *two groups*, inhabiting the *eastern*, resp. the *western* part of the continent. These groups differ from each other mainly on account of the reduction of size and number of the white spotting on the wing feathers in the western populations, usually resulting in the total absence of white spots on the (lesser and median) upper wing-coverts, and the generally much darker appearance of the wings, as compared with eastern birds (fig. 13). These two groups, which in the case of *villosus* already have been described by Jenkins (1906), have been referred by Stejneger (1906) to represent different glacially isolated populations, which have spread postglacially all over the wooded parts of North America (fig. 14, 15). The separation into distinct eastern and western forest refugia have been again recently clearly indicated by Reinig (1937); more detailed discussions are given here in the chapter on the distribution and the history of *D. borealis* and *X. albolarvatus*, in which clear evidence is given concerning the exact localisation of these refuges. It is a most noteworthy fact that the apparent centers of postglacial distribution of *villosus* and *pubescens* correlate with the main great *forest refugia* (fig. 17): (a) S. E. of the Alleghanies; (b) coastal range of California, Oregon, and Washington. In addition, the present ranges of the eastern and western groups closely correlate with the extension of the deciduous forest vegetation on the one hand, and the coniferous forests of the Pacific coast on the other hand.

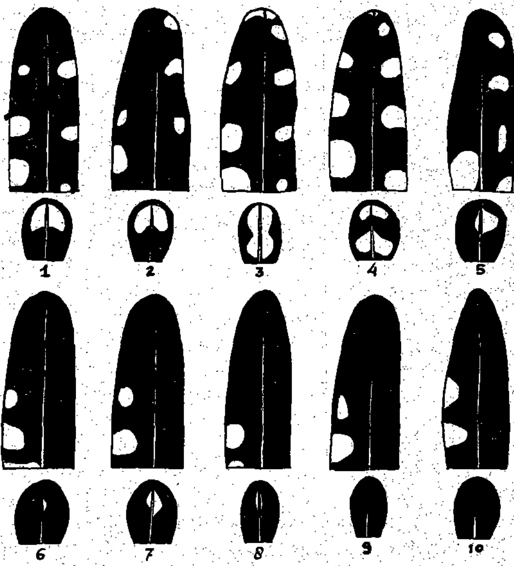

Fig. 13. *D. villosus* (L.) — Left inner tertials and smaller upper wingcoverts of adult specimens showing the relative less amount of white in the pacific western races. A. Eastern races: 1 Kissimmee, Florida (*audubonii*); 2 Fairfax, Virginia (*audubonii*!); 3 Locust Grove, New York (*villosus*); 4 Fort Keogh, Montana (*septentrionalis*). B. Intermediate: 5 Jasperhouse, Alberta (*monticola*). C. Western races: 6 Fort Teion, California (*orius*); 7 Sitka, Baranoff Island (*sitkensis*); 8 "Mexico" (*jardini*); 9 "Guatemala" (*sanctorum*); 10 Volcanoe de Turrialba, Costa Rica (*extimus*).

The eastern forest vegetation has postglacially spread over the greater part of North America east of the Rockies, extending its range as far N.W. as to N. and N.W. Alaska: *villosus septentrionalis* occurring southward from centra S. Alaska middle Yukon, and central Mackenzie; *pubescens nelsoni* occuring soutward from N.W. Alaska (coasts of Kotzebue and Norton Sounds in the Behring Strait) and southward from S. W. Mackenzie Both are undoubtedly nothing, but somewhat enlarged representatives of the S. E. populations, besides, in relation to their cold habitats showing a certain amount of reduction of eumelanine pigmentation, resulting in the conspicuous extension of the white patches on the wingfeathers, and the pure white underside. These forms are markedly different from the dark coloured S. Alaskan forms (*v. sitkensis*; *p. leucurus*: S. Alaska and N. British Columbia), which may be considered to belong to the original inhabitants of the coastal coniferous forest refugium. The *villosus* and *pubescens* populations which postglacially spread from the S. E. deciduous forests (Florida, Georgia, Carolinas) furnish suitable examples in support of the rule of Bergmann, since they gradually become larger in N. and N.W. direction. This phenomenon has led to the recognition of a smaller S. E. race (*v. audubonii*; *p. pubescens*), an intermediate one (*v. villosus*; *p. medianus*), and a larger N. and N.W. one (*v. septentrionalis*; *p. nelsoni*), the limits of their respective ranges being of course subject to various arbitrary decisions. Along the whole pacific coast of North America, north to Fairweather Bay (*villosus*) and Kenai Peninsula (*pubescens*) dark coloured populations occur in a narrow coastal zone only, apparently originating from the Pacific refuge. From the fact that central and northern Alaska, however, is inhabited by eastern invaders, neither the distribution of *villosus*, nor that of *pubescens* indicate the presence of glacial forest refugia in Alaska. However the recent glacial situation in Alaska is not favourable for exact geologic indications of the pleistocene distribution of ice and forests. Cooper (1942) describes the situation of the glaciers in the Prince William Sound Region as follows: "Everywhere in the line of possible ice advance the mature vegetation of the fiord walls terminates abruptly. Between this boundary and the glacial front lies a "barren" zone, usually very narrow; or else the ice is actually invading the ancient forest or tundra. The same sharp limit is evident throughout coastal Alaska wherever glaciers enter the zone of forest. At Glacier Bay and other localities in southeastern Alaska there has been ice-recession for a period up to two centuries, but nowhere has the sharpness of the ancient forest line been blurred" (p. 20—21). In conclusion, in pleistocene glacial times coniferous forests may have maintained themselves perhaps immediately bordering the glaciers, as still at present is the case. There fore, according to Cain (*in litt.*, 1946) we "can believe that the data indicate (as accepted by biologists, geographers, and geologists) that there were refugia in Alaska during the Pleistocene". Apparently as a result of the very humid coastal climate the races inhabiting the coastal regions with copious rainfall of Washington, Oregon, and N. California, west of the Cascade Mountains, show a remarkable tendency to strong melanine pigmentation on the lower surface (*v. harrisi*; *p. gairdneri*): rule of Gloger. The same result of the influence of a humid climate is found in the Bahama Islands races: according to Todd & Worthington (1911) 10 specimens of *D. v. maynardi* originating from New Providence, all "have a slight brownish wash on the breast, approaching some of the Pacific coast forms of this species in this respect" (p. 420).

Originating from the pacific refuge, coniferous forests postglacially spread over the mountain slopes of the Rockies, apparently immediately followed by the Woodpecker populations: at present the Rockies are inhabited by unmistakable western representatives of *villosus* (*monticola*) and *pubescens* (*leucurus*), which taxonomically are in conspicuous contrast to the bordering eastern populations. *D. p. leucurus* from the Transition and Canadian zones of W. North America, east of E. Montana and W. Nebraska, however, demonstrates slight influences of the contact with the heavily spotted eastern form (*nelsoni*) in showing a certain amount of variability in the absence of white spots on the wingcoverts

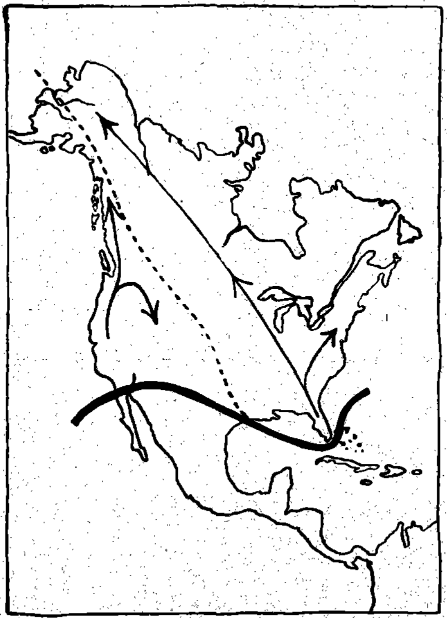

Fig. 14. *D. pubescens* (L.) — 4 atlantic, and 4 pacific races.

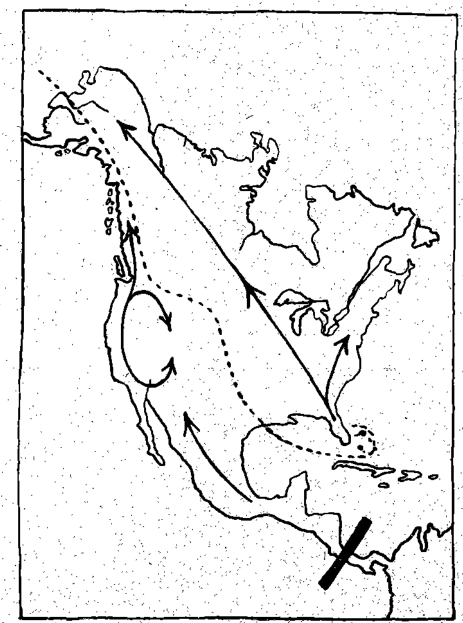

Fig. 15. *D. villosus* (L.) — 6 atlantic, 10 pacific, 5 Central American races.

Fig. 14 and 15. *American White-backed Woodpeckers.* The broad black line indicates the southern limit of the respective ranges. The northern limit approximately corresponds with the arctic tree-line. The dotted line indicates the boundary between the dark western (pacific) races (small, and relatively less white spots on the wings), and the light eastern (atlantic) races (broad and relatively more white spots on the wings). The arrows indicate the postglacial dispersal out of the atlantic, pacific, and Central American refugia.

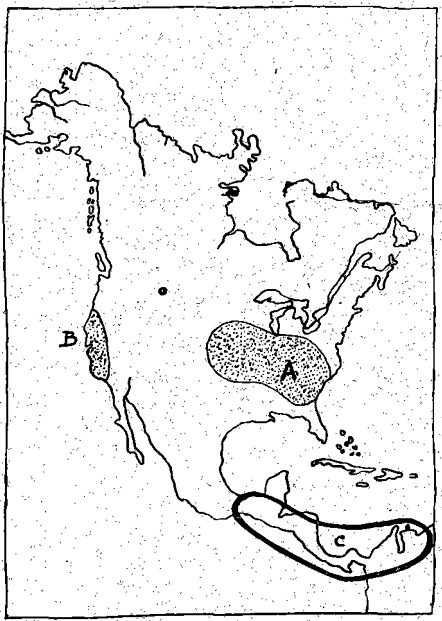

Fig. 16. Map showing the discontinuous distribution of *Hippocastanaceae* in North America, after Pax (1928, Karte 8). A: 4 atlantic species of *Aesculus*: *glabra, octandra, parviflora, pavia*; *B*: 1 pacific species of *Aesculus*: *california*; C: genus *Billia*, which is closely related to *Aesculus*. The black spot in S. British Columbia represents a tertiary record of *Aesculus*, indicating the preglacial continuous range of the deciduous forest vegetation.

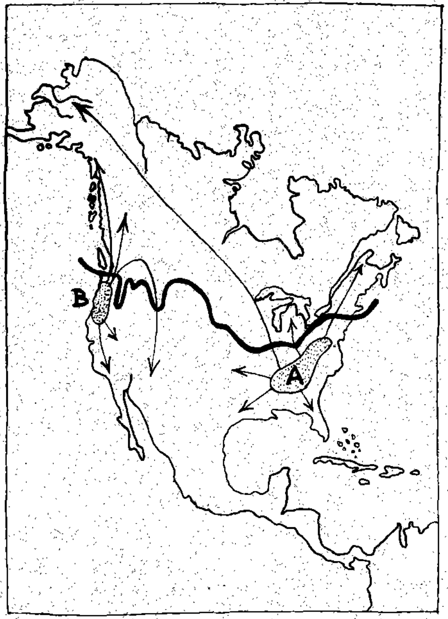

Fig. 17. Postglacial plant migration in North America (indicated by the arrows), after Harshberger (1911, fig. 4). The broad black line indicates the southern limit of the land-ice during the last (Wisconsin) glacial period. The dotted areas represent: A (atlantic) postglacial dispersal center of deciduous vegetation; B (pacific) postglacial center of coniferous forests.

(not personally seen; cf. Ridgway, 1914) whereas Jenkins (1906) mentions 3 specimens of *D. villosus* from the regions between the Rockies and the Cascade Mountains, which show characters of both *septentrionalis* and *harrisi*; finally Weydemeyer (1928) describes the intergradation between *septentrionalis* (east) and *monticola* (west) in Lincoln Co., Montana, in spite of the ecological difference that exists between these two races: *septentrionalis* inhabiting the Canadian, Hudsonian, and Alpine-arctic zones, whereas *monticola* is found at lower elevations, especially in the Transition life zone. A specimen from Fort Keogh, Montana, examined by me, surely belongs to *septentrionalis* (April 7; ♂ ad. wing 139 mm), whereas Oberholser (1911) suggests that breeding specimens of that region belong to *monticola* and not to *septentrionalis*, which are suggested to be migrants or winter birds.

From the absence of *pubescens* south of the glacial forest refugia within the borders of the U.S.A., contrary to the presence of several races of *villosus* in the Mexican and Central American mountain forests, which represent the southernmost situated refugia of the arcto-tertiary forest vegetation, one may conclude that *villosus* is the older form and that *pubescens* has split up from it by isolation in some glacial period. This hypothesis is confirmed by the great similarity that exists between the southern races of *villosus* with *pubescens*, as has been shown above. The small dark coloured forms of *villosus* even go farther south (W. Panama) than the holarctic forest elements as *Liquidambar, Morus, Ostrea* and *Carpinus* which reach their southern limit in Guatemala whereas *Tilia* and *Ulmus* do not go farther south than to extreme S. Mexico (Harsberger 1911). The Central American area is strongly confined to the deciduous mountain forests of higher altitudes. In Salvador *D. villosus* has been found in the cloud forest of the "Upper Tropical Zone (2440—2750 m) and in no case was one noted in the Sonoran Zone" (Dickey & Van Rossem, 1929). The small size and the markedly brown underside of the Central American races of *D. villosus* as compared with the North American races, have been cited by Rensch (1933) as a very instructive case in favour of the climatic zoogeographic rules of Bergmann and of Gloger.

In conclusion it appears that 3 groups of subspecies can be recognized which refer to 3 separate North American forest refugia: (1) atlantic (S. E. United States); (2) pacific (N. W. United States); (3) southern (S. Mexico and Central America). The presence of 3 glacial forest refugia is clearly demonstrated in the recent distribution of *Hippocastaneaceae* in North and Central America (fig. 16): 4 species inhabiting the United States (*Aesculus glabra, octandra, parviflora, pavia*). 1 species (*A. californica*) inhabiting the Californian coastal region, and a closely allied genus (*Billia*) inhabiting S. Mexico, and Central America, south to N. Columbia (Pax, 1928).

(1) atlantic races:
D. pubescens: *pubescens, medianus, nelsoni, microleucus.*
D. villosus: *audubonii, villosus, septentrionalis, terraenovae, piger, maynardi.*
(2) pacific races:
D. pubescens: *glacialis, gairdneri, turati, leucurus.*
D. villosus: *sitkensis, picoideus, harrisi, orius, hyloscopus, scrippsae, monticola, leucothorectis, icastus, intermedius.*
(3) southern races:
D. pubescens: none.
D. villosus: *jardinii, sanctorum, parvulus, extimus. fumeus.*

Owing to lack of material the author has not made a subspecific examination; he may refer to Ridgway (1914), Oberholser (1911), Dickey & Van Rossem (1929), and to the A. O. U. Checklist (4th ed. 1931).

XIII **Dendrocopos stricklandi** (Malherbe 1845: Mexico).

Material examined: 1: "Mexico", ♀, wing 112; culmen 18 mm. — (Leiden Mus.).
Range: Upper pine forests on the S.E. mountains of Mexico up to about 3400 m: Vera Cruz, Puebla, Mexico, Morebs (Ridgway, 1914).

XIV **Dendrocopos pubescens** (Linnaeus 1766: Carolina).

Material examined: "North America" (5); Georgia (1); Alabama (1); N. Carolina (2); Virginia (2); New York (8); Massachusets (4); Ohio (2); Wisconsin (1); N. Dacota (2); Alberta (1); Victoria, Brit. Columbia (2); Vancouver Island (1); California (3). — (Amsterdam Mus.; Brussels Mus.; Leiden Mus.; coll. Sillem-Van Marle).
Range (fig. 14): wooded parts of North America, from Alaska in the West, and Newfoundland in the East, south to Texas, New Mexico, Arizona, and California, north of the desert ranges.

XV **Dendrocopos villosus** (Linnaeus 1766: New Jersey).

Material examined: "North America" (2); Florida (2); S. Carolina (1); Virginia (3); New York (6); Michigan (2); Wisconsin (2); Alberta (1); Montana (1); Sitka, Baranoff Island (2); California (7); San Diego (2); "Mexico" (2); Guatemala (1); Costa Rica (3). — Amsterdam Mus.; Brussels Mus.; Leiden Mus.; coll. Meinertzhagen).
Range (fig. 15): wooded parts of North America, including Bahama Islands, from Alaska in the West, and New Foundland in the East, through the mountain forests of Mexico and Central America, south to Costa Rica und W. Panama.

VIII XENOPICUS ALBOLARVATUS (Cassin 1850: Georgetown, Oregon Valley, California).

Material examined: 2: California. — (Leiden Mus.).
Range: Coastal mountains of W. North America, from S. British Columbia, to S. California (Cuyamaca Mts., San Diego Co.), eastwards into W. Idaho, and Nevada.
Specific characters: This species resembles the genus *Dendrocopos*, but the broad white blotching of the wing quills, one of the predominating characters of *Dendrocopos*, is lacking. Instead of this, the primaries have partially white outer and inner webs (fig. 18); all other feathers, including secondaries, tertials, scapulars, tailfeathers, wing- and tailcoverts, are glossy black, a character that is nowhere found in the genus *Dendrocopos*. The white head and neck, which in the male has a striated red occiput, is an additional aberrant unique character. Young males, however, have a red, or salmon orange crown from forehead to occiput (Chapman,1928), whereas in young females only a few red feathers are present on the median portion of the occiput (Ridgway, 1914).
In spite of the fact that in the *A.O.U. Checklist* 1931, 4th ed. the species unexpectedly has been put into *Dryobates* (cf. Grinnell, 1932), and of a few suggestions by Peters (*in litt.*, 1946) in favour of this treatment, I much hesitate to do so, although I clearly recognize, that there are hardly more than subjective reasons to take a decision in a question which refers to the labile characterizing — in some cases — of the systematic genus. In a recent letter (1946), however, Peters informs me that "*Xenopicus* is said to have a tongue which is less extensible than in the other, North American at least, representatives of the genus *Dendrocopos*. In this respect *Xenopicus* is more nearly allied to *Sphyrapicus*" (!). Nevertheless, I should not like to deny the genetic relation-

ship that probably exists between the monotypic genus *Xenopicus* (Baird 1858: type by monotypy *Leuconerpes albolarvatus* Cassin) and *Dendrocopos*. *Subspecific characters*: No subspecific examination could be done, owing to lack of material. A southern race (*gravirostris* Grinnell 1902: Los Angeles, California) has been separated from the northern typical one on account of a larger bill (cf. Ridgway, 1914).

Fig. 18. *X. albolarvatus* (Cass.) — Showing the aberrant pattern of the primaries, compared with typical members of *Dendrocopos*: 1 *X. a. albolarvatus*: ♂ Fort Brook, N. California. 2 *D. v. villosus*: ♂ Kalamaroo, Michigan; 3 *D.m. major*: ♂ Uppsala, Sweden.

Biotope and history: The species is confined to coniferous forests, which are abundant on the mountain slopes of its habitat. Pine seeds constitute the most important food of the species; besides, it has been observed feeding on ants and other insects on the trunks of Sequoias, Sugar Pines, and Douglas Firs (Bent, 1939). In some winters the species descends in considerable numbers into the plains; these migrations may be correlated with the failure of the pine seeds crop: in the winter 1901—1902 hundreds of specimens have been observed in Nevada Co. (Richards, 1924). These invasions may be compared with those exhibited by the equally pine seeds eating *D. major major* from N. Europe.

The range of *Xenopicus* covers almost strictly the area, which apparently was a forest refugium (Reinig, 1937) since "in the northwestern states (Wash., Oregon, Idaho, northern Calif.) the glaciation was of the mountain type for the most parts allowing abundant refugia" (Cain, *in litt.*, 1946). The glacial forest vegetation of this refuge apparently mainly consisted of coniferous trees of which especially the Lodgepole Pine (*Pinus contorta*) has acted as a glacial and a postglacial pioneer species. In E. Washington *P. contorta* retreated not farther southward in the Wisconsin Glacial period, than into Columbia Basin, "and persisted as the predominant arboreal species until well into postglacial time" (Hansen, 1944, p. 86). "The predominance of coniferous vegetation (in these regions) is remarkable and paradoxic. The Pacific coast is the sole refuge of the most characteristic and wide-spread types of miocene coniferae, the Sequoias. Any attempted explanation of this extreme paucity at present of broad-leaved trees, which existed in the form of Magnolias, Beeches, Chestnuts, Elms, and Gums Liquidambar down to the beginning of the glacial period as shown by remains in the auriferous gravels of the west, bristles with difficulties. Much may be attributed to glaciation; something to the tremendous outpours of lava; much to the narowness of the forestbelt, to the want of a summer rain, and to the most unequal and precarious distribution of that of winter" (Harshberger, 1911, p. 261).

Judging from the recent small area and the limited biotope of *X. albolarvatus*, the species may be considered to be a relict of tertiary times, as are the Sequoias and the various other species of conifers in which it likes to live. It probably has split from the general *Dendrocopos* populations, from which it now taxonomically sufficiently differs to warrant *generic separation*.

Note. Shortly after closing this manuscript Mr. J. L. Peters enabled me to cite the following paragraph out of a letter of Dr. A. M. Miller (1946): "These specimens show that the tip of the tongue apparatus in *Xenopicus* extends forward around the skull to the nasal hinge at the base of the bill. It does not extend on and coil into the orbit as it does in several of our specimens of *Dryobates villosus*. One example of *Dryobates pubescens* has the tongue bones extending only as far as the *Xenopicus*. Others are a little longer and begin to coil into the orbit. The same is true for examples of *Dryobates scalaris* and *Dryobates nuttallii*. In *Sphyrapicus* these skeletal parts stop at the summit of the head". "In short, it seems to me that the white-headed woodpecker in the development of the tongue approaches and perhaps equals the minimum development in *Dryobates*".

IX LADDER-BACKED WOODPECKERS.

1. INTRODUCTION.

With *"Ladder-backed" Woodpeckers* will be indicated those species in which the black-and-white cross barring on the upperparts reaches its highest degree of development. Back, rump, and scapulars are always distinctly transversely barred, but specific variability exists in the barring of the hindneck, interscapu-

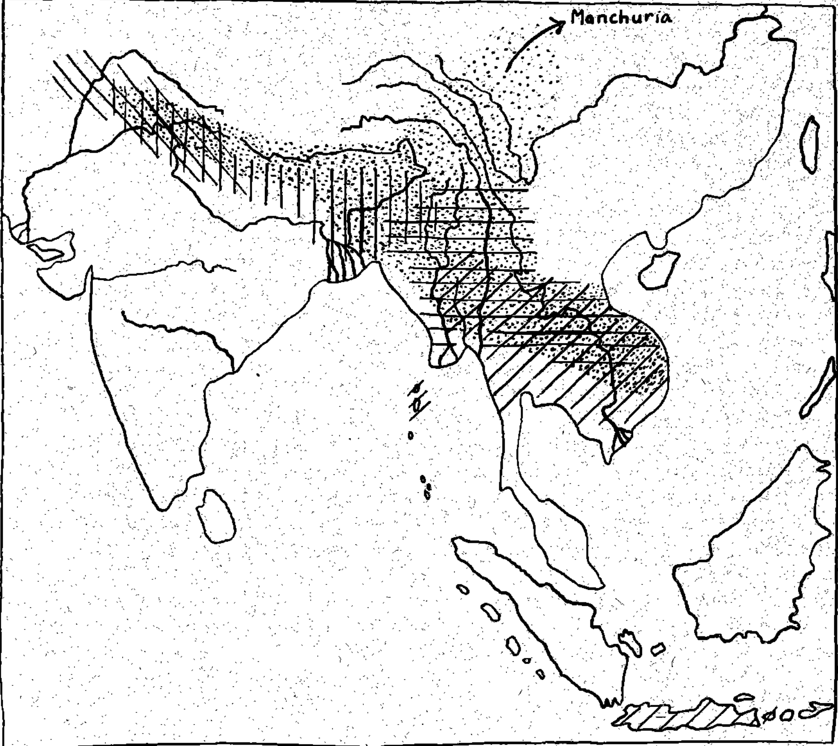

Fig. 19. *Ladder-backed Woodpeckers* — Range in Asia. / / / *analis*. ≡≡≡ *atratus*. ||||||||| *macei*. \\\ *brunnifrons*. ∴∴∴ *hyperythrus*. Note the overcrowding of species of this group in the Burmese region, as also the discontinuous range of *D. analis*.

lary region, upper tailcoverts, and central rectrices. Arranged in a series, especially with the upperside above, several species of the group can hardly be distinguished from each other (*atratus* ♀, *macei* ♀, *scalaris* ♀, *borealis* ♀) (fig. 20,21). The following species will be treated here belonging to this group: *analis, atratus, macei, brunnifrons, scalaris, nuttallii, borealis, ligniarius, mixtus*; also *hyperythrus*.

The distribution of the Ladder-backed Woodpeckers comprizes: S. E. Asia, from the Himalayas, Upper Burma and Indo China to Java, also inhabiting the Andamans (*analis*), but absent in Malacca south of Tenasserim, Sumatra, and Borneo (!) (*analis, atratus, macei, brunnifrons*); the coastal region of California (*nuttallii*); Sonoran regions (*scalaris*); S. E. North America (*borealis*); temperate and subtropical zones of S. and S. W. America (*ligniarius, mixtus*); thus, showing a very disjunct distribution on the continents surrounding the Pacific. These regions are remarkable, since they include those regions that are supposed to be the center of origin of much recent plant- and animal-life (S. E. Asia; fig. 19); besides, they represent those areas that are known as recent refugia of the arcto-tertiary flora, which has maintained itself in the Chinese regions, but which otherwise shows a conspicuous discontinuity in its distribution: far the greater majority of the remaining ones is found in the Californian region and in S. E. North America. E. Asiatic-North American disjunctions are known in the distribution of different plantspecies. In respect to the Woodpeckers a few examples concerning trees are of a special interest:

(1) in the genus *Acer* the section *Palmata* inhabits (a) China, Corea, S. Ussuria, Hondo, Hokkaido, and (b) Pacific North America (British Columbia, Washington, Oregon) (Pax, 1927);

(2) in the same genus the section *Macrantha* inhabits (a) Burma, China, Corea, Manchuria, Hondo, and (b) Atlantic North America (S. E. Canada, Alleghanies) (Pax, 1927);

(3) the genus *Magnolia* has a wide E. Asiatic and Australasian distribution and is found in North America on the eastside only (Florida, Mexico, and Central America to N.W. Columbia; E. Cuba, Haiti, Portorico) (Pax, 1928);

(4) the distribution of the genus *Aesculus* shows conspicuous discontinuities: in Asia and America species are found in (a) Hindu Kush and Himalayas (*indica*), Lower Burma (*punduana*), W. China (*Wilsoni*), three isolated populations in Tonkin and along the Chinese coast (*chinensis*); Hondo (turbinata), and Hokkaido (*dissimilis*); (b) California (*californica*), E. North America (*glabra, octandra, parviflora, pavia*, a.o.) (Pax, 1928).

All areas inhabited by this Woodpecker group have not been covered with pleistocene land-ice; in North America they represent exactly the glacial forest refugia, including the Sonoran regions, mentioned by Reinig (1937). The South American forms may be early pleistocene invaders from the northern continent, which have penetrated into these regions through the andine temperate zones.

Thus, in spite of the highly discontinuous ranges, I feel justified to consider all members of the group to be genetically related, the group apparently having had a former wider continuous distribution in S. E. and E. Asia, whence it has spread into North America in preglacial times. The details of the supposed history of each species — as far as indicated by its recent distribution (!) — will be discussed separately.

2. DISCUSSION OF TAXONOMIC CHARACTERS.

I. The **degree of transversely banding** (fig. 20, 21) of the upperparts shows a certain amount of specific variability. I will try to express this variability quantitatively in giving one figure when each of the mentioned parts is barred: hindneck; upper interscapulary region; lower interscapulary region; scapulars; upper wingcoverts; back; rump; upper tailcoverts; central rectrices; lateral rectrices. If all those regions show cross barring, the species gets a 10, if only one region is not banded, but uniform black, e.g. hindneck only, the species gets a 9, etc. According to this proceeding the following result has been reached:

ligniarius: 10
mixtus: 10
analis: 9
scalaris: 8
nuttallii: 7.5
borealis: 7
macei: 5.5
atratus: 5
brunnifrons: 4

Following this result the geographically outermost sections of the group show the closest resemblances (*analis-ligniarius*, *mixtus*). This is in agreement with the fact, that the discontinuous distribution of *analis* indicates a species of high age, as is shown elsewhere.

II. The extension of the **red colour on the head** of the adult male is also subject to specific variation within this group. When it is tried to give a quantitative basis to this character, 1 figure will be given for a red forehead only, 2 for a red upper head and crown, 1 for a red occiput, and 1 for a red hindneck. Thus *atratus* and *macei*, having a total red cap from forehead to hindneck, will get a 5, whereas e.g. *nuttallii* with only a red occiput and hindneck gets a 2. Special calculation is necessary in the case of *borealis*, which has a very small and often concealed red patch on each side of the occiput (¼), and for *mixtus*, which has a broad red patch on each side of the occiput (½), as well as for *brunnifrons*, which on the crown has the yellow component only of the lipochromous coloration (1½). The following *estimated* calculation can be made:

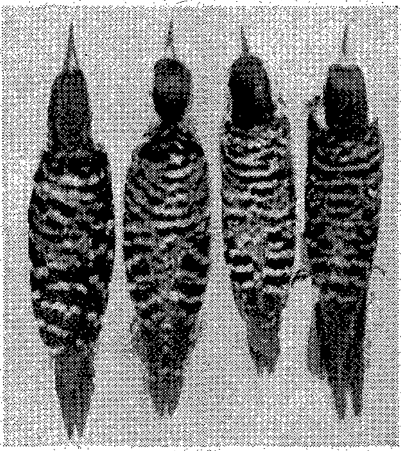

Fig. 20. *Ladder-backed Woodpeckers* — Dorsal surfaces of S.E. Asiatic and North American species to show the remarkable resemblances. From left to right: *macei*: Chakrata, Simla Hill States; *analis*: Bangkok, Siam; *scalaris*: Tucson, Arizona; *borealis*: N. Carolina. (J. Agterberg, phot.).

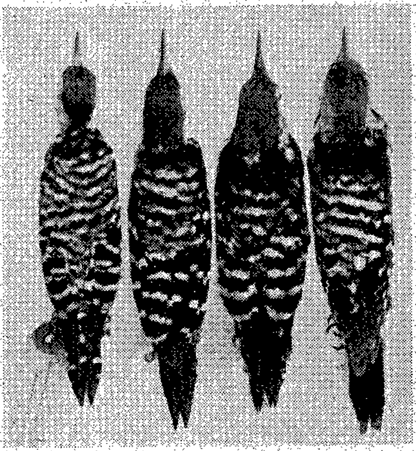

Fig. 21. *Ladder-backed Woodpeckers* — Dorsal surfaces of S. Asiatic species to show the remarkable resemblances. From left to right: *analis*: Bangkok, Siam; *macei*: Chakrata, Simla Hill States; *atratus*: Maymyo, Burma; *brunnifrons*: Cashmere. (J. Agterberg, phot.).

macei: 5
atratus: 5
scalaris: 4
analis: 3
nuttallii: 2
brunnifrons: 1½
ligniarius: 1
mixtus: ½
borealis: ¼

Following this result the South American forms belong to the most differentiated ones, the red being much reduced in the adult stage, although again fully developed in the juvenile specimens, which possess broad red tips to all feathers of forehead and crown. *Ligniarius* and *mixtus*, although closely related to the S. E. Asiatic species of the group have developed the male secundary sexual character along the usual way of reduction, whereas in *atratus* and *macei* the original stage has retained. In this way, an additional argument is formed in favour of the view, that S. E. Asia is the original center of distribution of the group, whereas South America has been peopled secundarily. The adults of *analis* and *nuttallii* together, have retained the complementary parts of the original red cap: *analis*: forehead and upper head (3); *nuttallii*: occiput and hindneck (2). Nevertheless, the juvenile *nuttallii* — at all events the male — has the same extension of red as the adult *analis*, whereas the juvenile *analis* ♂ has a red forehead only! The isolated position of *borealis*, which in this character resembles the *canicapillus* group, is discussed separately.

III. The back stripe through the eye shows the following specific variation (+ is present; — is absent; ± is very slightly developed):

analis: —
macei: —
atratus: —
brunnifrons: —
ligniarius: ±
mixtus: ±
borealis: ±
nuttallii: +
scalaris: +

(In *ligniarius* and *mixtus* the brownish earcoverts give the impression that these species have a brownish eyestripe).

It appears that the black eye-stripe is mainly developed in the North American forms, but that it is principally absent in the South American species. This leads to the conclusion that the South American forms once more have retained an original character, also found in the S. E. Asiatic forms, from which they may have derived.

IV. The character of red lipochrome pigmentation on the under tailcoverts, crissum, and lower abdomen is distributed as follows (+ is red present; — is red absent):

analis: +
macei: +
atratus: +
brunnifrons: +
borealis: —
nuttallii: —
scalaris: —
ligniarius: —
mixtus: —

Following this, the red pigmentation is a conspicuous Old World character, not to be found in the New World members of the group. As it appears that the extension of lipochromes on lower tailcoverts, etc. is a character of many supposed original members of the genus *Dendrocopos*, an additional argument is obtained in favour of the view, that the South American forms of *Dendrocopos* originate from S. E. Asia.

The theory that the Ladder-backed Woodpeckers have originated from S. E. Asia is founded on several arguments, referring to biogeography and taxonomy; their spreading into the nearctic region is supposed dating back to preglacial times.

3. THE INTERRELATIONSHIP OF THE ASIATIC LADDER-BACKED WOODPECKERS.

I. *Macei* and *atratus*.

Macei and *atratus* are referred to one species by various authors, among which Stanford & Ticehurst (1939) have brought forward the most impressive evidence. According to Stuart Baker (1927, 1934), who will give both *macei* and *atratus* full specific rank, the forms are found side by side in the Khasia and the Cachar Hills, and in Manipur, without producing intermediates.

Stanford & Ticehurst (1939), however, state that *macei* and *atratus* are mutually exclusive: indeed, both were found by Hume in Manipur, but *macei* in the "basin" and *atratus* in the "eastern hills", whereas in the Khasia and Cachar Hills only *macei* should occur. Besides, the *macei*-specimens from Manipur examined by Stanford & Ticehurst (1939) are said to have broad streaks on the underparts, thus, resembling to some extent *atratus*! Not only from a taxonomical point of view *macei* and *atratus* are closely related, for also their call much resemble each other: *macei* having "a curious squeaking voice, which distinguishes it easily from all except the next species of Woodpecker" (= *atratus*) (Stuart Baker, 1927, p. 41); besides they equally largely feed on ants, which they take on the trees as well as on the ground, which is an exceptional practice in the genus: *macei*: Stuart Baker (1927); *atratus*: Delacour & Jabouille (1931).

Stuart Baker (1927) mentions that *macei* is a bird of the "open or semi-open country in the plains and lower valleys running into the mountains" (p. 41) and several other authors have recorded its occurrence at lower elevations in the valleys and the foothills of the mountains:

Kangra District, Punjab (Whistler, 1926 A): 600—1700 m.
Rotung, Assam (Roonwal, 1939): 450 m.
Kobo, N. E. Assam (Roonwal, 1939): 120 m.
Assam (plains) (Stuart Baker, 1934): 200—300 m.
Assam (hills) (Stuart Baker, 1934): up to 1200 m.
Sankrametta, E. Ghats (Whistler & Kinnear, 1934): 1050 m.

Atratus occurs at higher elevations, being found on the level of the plains and in the mountains (Chin Hills: "eigentlich erst in der Hochgebirgszone zu Hause", Stresemann & Heinrich, 1940, p. 235):

Chin Hills (Mount Victoria) (Stresemann & Heinrich, 1940): 1400—2800 m.
Southern Shan Sates (Bingham, 1903): 1700—2300 m.
Mt. Chieng Dao, N. Siam (De Schauensee, 1934 A): 1200—1500 m.
Khun Tan Mts., N. Siam (Riley, 1938): 600—1200 m.
N. Siam (Deignan, 1945): 1200—1500 m (summits).

In relation to the altitudinal divergency *atratus* appears to prefer open coniferous forests with a clear underground and moss-covered trees (Mt. Victoria, Stresemann & Heinrich, 1940), or open forests of pine or oak (N. Siam, Deignan, 1945), whereas *macei* inhabits equally open well wooded countries and thin deciduous tree jungle (Stuart Baker, 1934), which all represent suitable localities to ants.

It is said that the nests of both *macei* and *atratus* have been found in sound wood only (Stuart Baker, 1934).

In conclusion it appears, that the stated occurrence of *macei* and *atratus* side by side in the same region is the result of their ecological divergency in their mian areas: *atratus* in the E. (N. Siam, Indo China) and S. E. (Arakan Yomas), *macei* in the W. and N.W. (Himalayas). So the nomenclatural dilemma, whether they are conspecific or not, has been reduced to the problem, whether ecological distinct forms that possess a zone of contact at their boundaries without meeting each other, must be treated as conspecific in nomenclature or must be kept separate. In this work no solution will be given. As both the ecologically distinct forms from *D. major*, *D. leucopterus* and *D. syriacus* have been treated as distinct species, it will be — provisionally — done with *macei* and *atratus* also. The limits of species recognition, however, can be traced, based on personal appreciation only.

II. *Macei* and *analis.*

The difference between *macei* and *atratus* in their altitudinal distribution may not be an argument to separate these taxonomically closely allied forms, as Deignan (1945) has done in uniting *macei* specifically with *analis,* which is the second Ladder-backed lowland form of Farther India, keeping *atratus* separate. Taxonomically *analis* is close to *macei-atratus,* but in the possession of transversely barred upper tailcoverts and central rectrices it stands apart; thus, *atratus* resembling *macei* much more conspicuously than *analis.* Besides, there is no close contact between the areas of *macei* and *analis,* such as in found in those of *macei* and *atratus.* On account of its peculiar disconnected range and its taxonomic relations to the South American forms (*ligniarius, mixtus*), the distribution of *analis* may be considered to be of a high age. By a former geographic isolation *macei-atratus* has become separated from the generally distributed E. Asiatic Ladderbacked populations, but in the present ranges of the E. Asiatic Ladderbacked species, I fail to detect the historical relation that doubtlessly exists between *analis* on the one hand and *macei-atratus* on the other hand.

Deignan (1945) united *analis* with *macei* mainly on account of the fact, that both are lowland species; but I think this is an inadequate reason. Indeed, *analis* seems to avoid forest or heavy jungle of any kind "not ascending the hills to any height" (Stuart Baker, 1927), preferring well wooded cultivated regions, fruit gardens and coconut grooves. Only a supposed W. Javan race (*montis* Robinson & Kloss, 1923 A) inhabits mountainous areas up to 1800 m (Tjibodas, Pangerango, Papandajan) but in the same region a doubtfully distinguishable lowland form (*analis*) occurs. According to Stuart Baker (1927) the species has not been recorded feeding on the ground (*contra macei* and *atratus*), but Delacour & Jabouille (1931) mention to have seen it quite often on the ground (Indo China).

III. *Macei* and *brunnifrons.*

D. macei has a close western relative in *D. brunnifrons* (= *auriceps* (Vigors)!), which mainly differs from *macei* in the peculiar head coloration, both in the male and in the female. In the male a carmine red coloration is present on the hindneck only, gradually fading through orange and golden yellow into a dark umber brown on crown and forehead. This unusual type of coloration is also found in *D. mahrattensis.* It seems that an exceptional separation between the yellow and red carotinoid components of the common red lipochrome has taken place, which in the laboratory can be obtained artificially with the help of a chromatographic absorbtion method in which a solution of the lipochrome in petrol is used (cf. Völker, 1939; red lipochromes of *D. major, Picus viridis,* and *P. canus* used). In the female the umber brown coloration is probably the result of the intermixture of some yellow lipochrome with the ordinary melanine pigmentation. Thus, no principal differences exist between *macei* and *brunnifrons* based upon the divergencies in head coloration.

The range of *brunnifrons* correlates to some extent with that of *D. himalayensis* and *Garrulus lanceolatus,* since *brunnifrons* is found in the W. Himalayas only, being especially common in Garhwal, Simla States, and S. Cashmere, but extending its range even into Afghanistan. It is a common bird in the western foothills of the Himalayas, in the Punjab (Kangra District, Whistler, 1926) and in Rawalpindi (Murree, Whistler, 1930), but like *himalayensis* it has never been found in Ladakh. In its eastern range *brunnifrons* occurs side by side with *macei* (Murree, Simla States, Garhwal, Kumaon), but as it prefers higher altitudes than *macei,* the species probably do not meet frequently. Ac-

cording to Whistler (1926 A) the altitudinal range of *brunnifrons* in the Kangra District (Punjab) is situated between that of *himalayensis* and *macei*!
Simla States (coll. Van der Sleen and Meinertzhagen): 2100—2250 m. Kangra District, Punjab (Whistler, 1926 A): 1200—2100 m.
Murree, Rawalpindi (Whistler, 1930): up to 2300 m.
Sind Valley, Cashmere (coll. Meinertzhagen): 1700 m.
Chitral (Whitehead, 1909): 1200—3000 m.
According to Stuart Baker (1934) *brunnifrons* prefers mixed Oak-forest, but it has also been found in Pine-, Cedar-, and other kinds of forest.
Judging from its geographic distribution, *brunnifrons* may be considered to be a member of the original Cashmere fauna, which dates back to late tertiary times. It is supposed that *D. himalayensis* and *Garrulus lanceolatus* are elements of this fauna also. *Garrulus* and *D. himalayensis*, however, may be considered to be autochthonous palearctic birds of the Cashmere region during the time, that this part of the eurasiatic block became folded and uplifted, having become separated from Eurasia afterwards by a part of the Tethys Sea, which has left marine tertiary deposits to the north of it (Wadia, 1939). *Brunnifrons*, on the contrary, has invaded this region from the east, since it is a member of that group, that in tertiary times appears to have had a wide E. Asiatic range. Recent animal- and plant-distribution indicates that the Cashmere region has remained isolated from the E. Himalayas for a considerable time, but I have failed to detect exact geographic evidence of it. At all events, the Cashmere form of Ladderbacked Woodpecker has succeeded in obtaining a different secundary sexual character, by which at present it can be distinguished from the other forms. An additional Ladder-backed species has penetrated into the N.W. again (*macei*), but apparently in relatively recent time, as it has gone not farther westward than to Murree, N.E. Rawalpindi (Whistler, 1930, not personally seen!), becoming rare throughout the whole western part of its range, whereas *brunnifrons* appears to be one of the most common Woodpeckers of the N.W. Himalayas (Stuart Baker, 1934).
In conclusion, it appears, that genetic relations exist between *brunnifrons* and the other Ladder-backed members of the group; its specific distinction being the result of geographic isolation. Besides, further evidence is given of the — at least — tertiary presence of the Ladder-backed group in E. Asia, which furnishes an additional argument in favour of the hypothesis that these Woodpeckers are of a eurasiatic and not of an American origin.

XVI **Dendrocopos analis** (Bonaparte 1850: E. Java).

Material examined: Siam (11); Andamans (2); Java (73); Bali (5). — (Amsterdam Mus.; Basel Mus.; Copenhagen Mus.; Leiden Mus.; coll. F. C. van Heurn).
Measurements:
Wing: Siam ♂ 94—103, average (10) 99.2; ♀ 100 mm
Java ♂ 90—97, average (34) 93.6; ♀ 90—98, average (35) 93.6 mm
Bali ♂ 94, 100, 100; ♀ 96, 97 mm.
Andamans ♂ 96, 97 mm.
Range: D. analis has a very disjunct range in S. E. Asia (fig. 22), as it is absent in Malacca, south of Tenasserim (ca. 12° N.L., Riley, 1938), Sumatra (cf. Stresemann, 1921 B; also Nias Island, W. off Sumatra, cf. Chasen, 1935), and Borneo, whereas it is very locally (!) found in Burma, north to Tounghoo (Stuart Baker, 1927) (plains of Kyundaw, east of Chin Hills: Stresemann & Heinrich, 1940; Arakan Yomas: Ticehurst, 1933), in Siam (Bangkok (S. Central), Meklong (West) Koh Lak (West, near Penin-

sular Siam: Robinson & Kloss, 1922), Chieng Mai (North): Deignan, 1945), being absent in Cochin China and fairly common in S. Annam (Delacour & Jabouille, 1931 and 1940); besides, occurring in the Andamans, Java, Madura (Stresemann, 1913), and Bali Islands. The Andamans are of a tertiary age, and so may be its land fauna, including *D. analis*. Apparently caused by its longlasting island isolation *D. analis andamanensis* has become considerably different from the mainland form, but still showing clear taxonomic resemblances with *analis* (cf. Stresemann, 1921 B). In Java the species belongs to the most common Wodpeckers, which can be found in the trees near native villages and in cultivated areas, wherever there are trees (Bernstein, 1859; Vorderman, 1899). In the intermediate Sundaic zone (Malacca, Sumatra, Borneo) where *analis* is missing, it is apparently exterminated as is probably the case in more species that are present in Java but absent in Sumatra. Its extermination may be caused by the interspecific competition with some species that has reached Sumatra and Borneo from the continent perhaps during one of the following pleistocene invasions, which are correlated with the successive states of the Sunda plat, being intermittently land or sea. In this respect it is very remarkable that a strict geographic vicariation is found between the species *D. analis* and *Meiglyptes tukki* (Lesson) (fig. 22). The latter being a Woodpecker of approximately the same size as *analis* (wing about 94—119 mm) and inhabiting the same type of biotope: in its whole range it is a common bird in the jungle of the lowland, also visiting cultivated regions, plantations, and gardens (Stresemann, 1921 B; Robinson, 1939). The range of *M. tukki* is exactly that part in the range of *D. analis*, that is not inhabited by *analis*, and that separates the two disjunct areas of this species: the extreme south of Tenasserim, and Peninsular Siam; Malacca; Penang, and Singapore Islands; Sumatra, Billiton, Borneo, Bangey Island; N. Natuna Islands; Nias, and Banjak Islands off the W. coast of Sumatra. In conclusion it is probable that the presence of *M. tukki* has caused the extermination of *D. analis* in the region inhabited by *tukki*. *M. tukki* has several close relatives inhabiting mountainous regions of S. E. Asia, incl. Java.

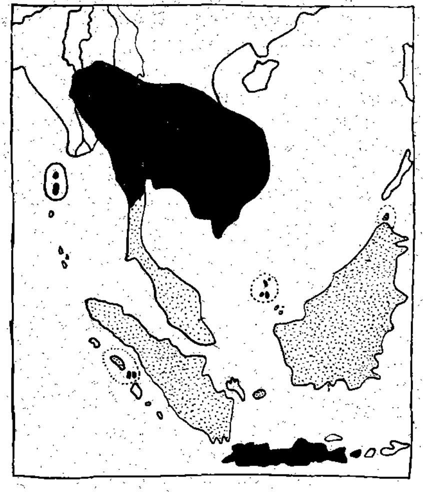

Fig. 22. *D. analis* (Bp.) — Map showing the discontinuous range of *D. analis* and the geographic vicariation with *Meiglyptes tukki* (Less.).
■ *D. analis*. ░ *M. tukki*.

Subspecific examination:

Various authors disagree in recognizing distinct continental and Javanese subspecies. I have come to the following result. Subspecific characters refer to the general colour of the underside, the degree of striping of the underside, and the average measurements.

Siamese birds (*longipennis*) almost have a white ground colour, especially on the throat; the black stripes on the breast are bold and more or less rounded to spots, and the lower flanks and thighs are faintly, but distinctly transversely barred. Wing-measurements according to Stresemann (1913):

Burma ♂, ♀ 93—104, average (8) 96.9 mm.
Siam ♂ 96—102, average (5) 98.6 mm.
Cochin China and Annam ♂, ♀ 92—102, average (16) 96.7 mm.

Javanese specimens are conspicuously differently coloured: the underparts are distinctly tinged yellowish and the throat is dirty white. The dark streaks on the underside are narrower, not inclining to rounded spots on the breast, whereas the cross barring on the flanks is obsolete. These characters are most striking in the W. Javan mountain birds (*montis*), in which even the throat has a distinct yellowish tinge. I fail to detect, however, constant differences in specimens from the mountain regions compared with those from the lowlands (*analis*), but if a series of mountain birds originating from Bandoeng, and the volcanoes Salak (2), Pangerango (1), Gedeh (3), and from Bandjaran (1), and Tjibeureum (1) is compared with a series from Batavia (8), Buitenzorg (22), Semarang (1), Tirtasari (3), Soerakarta (3), and Soerabaja (3), the differences are quite clear. Nevertheless, there are only few specimens, that can be identified on account of its plumage characters only, without the help of the indications on the label. So the name *montis* cannot stand as a valuable race in nomenclature, although its existence must be kept in mind.

Bali birds generally miss the yellowish tinge on the underparts, especially on the throat. Besides, the underside is more heavily streaked and slightly cross barred. Only in a series they are distinct from the Javanese lowland from, but important differences are reached not until mountain specimens are compared: Bali specimens and "*montis*" are clearly distinct in every specimen. Hesse (1912 A) already called attention to the fact that Balinese and Siamese specimens resemble each other closely, thus uniting them subspecifically (*longipennis*). It appears, however ,that Bali birds are somewhat intermediate between *longipennis* and *analis*, both in coloration and average measurements. The degree of development of the discussed taxonomic characters do not correlate in this case with geographic distribution: slight differences exist — only visible in series — between populations of the successive regions: Farther India, Bali, Java (lowland), Java (mountains).

Therefore, from a nomenclatural point of view I should recommend uniting Javanese and Balinese birds under one name, in spite of the fact that clear differences exist between "*montis*" and Bali specimens. Continental birds differ sufficiently from Sunda birds in plumage and average measurements to warrant subspecific distinction (in accordance with Stuart Baker, 1926; *contra* Stresemann, 1940).

Andaman birds differ from the others in having bold rounded black spots throughout the whole lower surface, and grey instead of black bases to the red feathers of the crown; the abdomen is tinged with brown instead of with yellowish; chin and throat are faintly spotted with black; and the under tailcoverts have a deep red colour.

In conclusion, the following races are recognized:

D. a. longipennis (Hesse 1912: Bangkok, Siam).
D. a. analis (Bonaparte 1850: E. Java).
synonym: *D. a. montis* (Robinson & Kloss 1923 A: Mt. Tjibodas, W. Java).
D. a. andamanensis (Blyth 1859: Andamans).

XVII **Dendrocopos atratus** (Blyth 1849: Tenasserim).

Material examined: Phu Kobo, near Xieng Khouang, Laos, ♂ wing 117; culmen 27 mm. — (Leiden Mus.). Maymyo, Burma, ♂ wing 113; culmen 28 mm. — (coll. Meinertzhagen).
Measurements: De Schauensee (1934 A) gives the following measurements of N. Siam birds:
Wing ♂ 110.5—118.5, average (10) 115.4 mm.
Wing ♀ 117—120, average (5) 118.5 mm.
Range: Khasia Hills, Manipur, Burma (Chin Hills: Stresemann & Heinrich, 1940); Arakan Yomas (Ticehurst, 1933)), S.W. Yunnan (Rothschild, 1926), Shan States, N. Siam (Khun Tan Mts: De Schauensee, 1934 A; Riley, 1938), Laos (Delacour & Greenway, 1940); south to Tenasserim.
Specific characters: see under *D. macei.*

XVIII **Dendrocopos macei** (Vieillot 1818: Bengal).

Material examined: Assam (3); Bengal (2; Calcutta); Simla Hill States (2, Chakrata); "Himalaya" (6). — (Amsterdam Mus.; Basel Mus.; Dublin Mus.; Leiden Mus.; coll. Meinertzhagen).
Range: N. Burma (Myitkyina: Stanford & Ticehurst, 1939), Manipur, Khasia and Garo Hills, Chittagong, Bengal (Roonwal, 1939), Bhutan (Ludlow & Kinnear, 1944), Sikkim, Nepal, W. Himalaya, west to extreme N. E. of Rawalpindi (Murree: Ticehurst, 1930).
Specific characters: The species differs from *atratus* in being much less streaked on the underside; the ground colour being tinged with fulvous, and not with a slight olive wash as in *atratus*; the fulvous coloration extending up to the chin and on the earcoverts; on the upperside the white cross barring extends to the lower hind neck, and the red on the occiput and hindneck is slightly more restricted.
Measurements and subspecific characters: According to Ticehurst (1928) W. Himalayan specimens (*westermani*) should have longer wings and longer bills than E. Himalayan and Burmese ones (*macei*):
macei: ♂ wing 100—109, once 113; culmen 22—26 mm.
westermani: ♂ wing 113—118; culmen 27—30 mm.
The type of *westermani* (Blyth 1870: type-locality N.W. Himalayas: Ticehurst, 1928), without exact locality ("Himalaya"), is still in the Amsterdam Museum: No. 1940, ♂ wing 114, culmen 26.5 mm. The following measurements are found in the specimens examined:
Assam: wing ♂ 106; ♀ 101, 108; culmen 23, 23.5, 24 mm.
Bengal: wing ♀ 97, 102; culmen 22, 23 mm.
Simla Hill States: wing ♂ 106; ♀ 106; culmen 24.5, 27 mm.
"Himalaya": wing ♂ 109, 111, 114, 115; ♀ 99, 113; culmen 21, 25, 26, 26.5, 28, 29 mm.
Whistler & Kinnear (1934) recognize *westermani* on account of the more conspicuous development of an indistinct and broken gorget of black spots in *westermani* (which I can confirm), and the greater wing measurements: E. Himalaya: 8 ♂♂ 103.5—110; Calcutta: 3 ♂♂ 101.5—106; W. Himalaya: 5 ♂♂ 114—120 mm. As it seems that western specimens incline to higher measurements, the recognition of an extreme western race appears justified to those authors that like it to recognize faintly characterized subspecies. *Westermani* is not accepted by Stuart Baker (1934). As a matter of fact no definite boundary exists between the ranges of *macei* and *westermani.*

XIX **Dendrocopos brunnifrons** (Gould 1831: N.W. Himalaya).

Synonym: *Picus auriceps* Vigors 1831: Simla (cf. Hartert—Steinbacher, 1935, p. 368).
Material examined: Simla Hill States (9); Cashmere (3); Nepal (1); Darjeeling (2: Leiden Mus.; purchased from G. A. Frank, natural history dealer, 1868: probably *error*!). (Amsterdam Mus.; Dublin Mus.; Leiden Mus.; coll. Meinertzhagen; coll. Sillem-Van Marle).
Measurements:
Wing ♂ 113—121, average (10) 116.5; culmen ♂ 22.5—25 mm.
Wing ♀ 110—120, average (5) 115.6; culmen ♀ 20—24.5 mm.
Range: N.W. Himalayas, from W. Afghan Mountains through Chitral (Whitehead, 1909), S. Cashmere, Murree, Simla Hill States, and Himalayan Foothills (Punjab: Whistler, 1926 A), to Garhwal, and Nepal (Stuart Baker, 1927).
Specific characters: see above.

4 NORTH-AMERICAN LADDER-BACKED WOODPECKERS.

XX **Dendrocopos borealis** (Vieillot 1887: U.S. America; type-locality settled by Wetmore 1941: Mt. Pleasant, opposite Charleston, S. Carolina).

Material examined: N. Carolina (2); Florida (2); "North America" (3). — (Leiden Mus.; coll. Sillem-Van Marle).
Range (fig. 23): S. E. States of North America, from E. Texas, Oklahoma, Arkansas, Tennessee, and North Carolina, south to Florida. Occasionally in Kentucky, and Virginia. The race *hylonomus* (Wetmore) inhabits central and southern Florida only. "*D. borealis* is gradually becoming less widely distributed, and less common in the southern Gulf states and Texas as the virgin forest is being cut. It is a bird that does not inhabit second growth woodlands. I think it would be too much to say that it has become rare as yet in Texas, as we have numerous records up through 1939. There are probably more recent records but our files are not complete beyond then" (Friedmann, *in litt.*, 1946).
Subspecific characters and measurements:
Ridgway (1914) already mentioned the fact that specimens from Florida show smaller measurements than those from the northern areas, but not earlier than 1941 Wetmore separated the southern from the northern populations under the name *hylonomus* (Kissimmee, Florida). This race has been accepted in the 20th supplement to the *American Ornithologists' Union Checklist of North American Birds* (Auk 62, 1945, p. 433). Measurements according to Wetmore (1941, p. 498) are:
borealis: wing 30 ♂♂ 116—123.5; 32 ♀♀ 116—123.5 mm.
hylonomus: wing 29 ♂♂ 110—117; 18 ♀♀ 113.5—116.5 mm.
The scanty material examined by the present writer confirms these results:
N. Carolina (Rockingham; Southport) wing ♂ 121; ♀ 122 mm.
Florida (Miami, Tarpon Springs) wing ♂ 114; ♀ 117 mm.
No other subspecific differences are described.
Biotope: According to Murphey (1939) the species shows a definite preference for open pine forests (*Pinus palustris*; *P. ellioti*; *P. taeda*) being especially associated to live trees, both for nesting purposes and for food. They are mostly seen in small flocks in the very tops of the tallest trees, feeding in the tip ends of the branches, like a Chikadee. Wayne (1906) who states to have examined more than 100 nesting holes of this species, says that the nest is dug out almost without exception in a live pine; the eggs are never laid "until the pine gum pours freely from beneath and around the hole, and in order to accelerate the flow the birds puncture the bark to the "skin" of the tree thereby cau-

sing the gum to exude freely" (Wayne, 1906, p. 62). In S. Carolina the species is often observed feeding in corn fields, perching on the infected ears and extracting the worms that live within them (Dingle, 1926; Ward, 1930). *Specific characters and history:* Apart from the secundary sexual characters in the male, *D. borealis* shows close similarities to the species *scalaris* and *nuttallii*, from which it can be distinguished by possessing a very short, but sharply defined black stripe through the eye. The male has two small often concealed red patches on the sides of the occiput only, by which it differs from all other members of the group. Nevertheless, in the juvenile ♂ the whole center of the crown is said to be red; in the juvenile ♀, however, no red is present on the crown (Chapman, 1929).

D. borealis is the only member of Ladder-backed Woodpecker that lives in the S.E. United States, in those regions that represent the glacial refugium of the arcto-tertiary forest flora. Although closely related to *scalaris* and *nuttallii*, *borealis* cannot be considered to be a recent (pleistocene) member of the group, owing to the above mentioned taxonomic differences. S.E. America is a distinct glacial forest refugium, separated from the Pacific one, as also from the Mexican one, by a broad zone of löss, indicating a deforestated stage at some time (Reinig, 1937). In the Atlantic refugium many arcto-tertiary plant-species, with a formerly much wider distribution, have survived here only, whereas they appear to have become extinct elsewhere in North America (fig. 16, 17), being also missing in the Californian refugional area: a.o. *Tilia, Robinia, Gleditschia, Gymnocladus, Liquidambar, Viburnum, Ilex, Catalpa, Diospyros, Sassafras, Benzoin, Carya, Morus, Ulmus, Fagus, Castanea, Carpinus, Betula, Magnolia, Liriodendron* (Harshberger, 1911, p. 200). Nevertheless, other arcto-tertiary plant-elements have maintained themselves both in the E. and in the W. refugium, among which *Aesculus, Acer, Rhamnus, Staphylea, Rhus, Cercis, Prunus, Pirus, Crataegus, Amelanchier, Calycanthus, Philadelphus, Ribes, Cornus, Sambucus, Viburnum, Symphoricarpos, Lonicera, Cephalanthus, Styrax, Fraxinus, Platanus* (Harshberger, 1911, p. 200). Cain (1943) has enumerated the arborescent

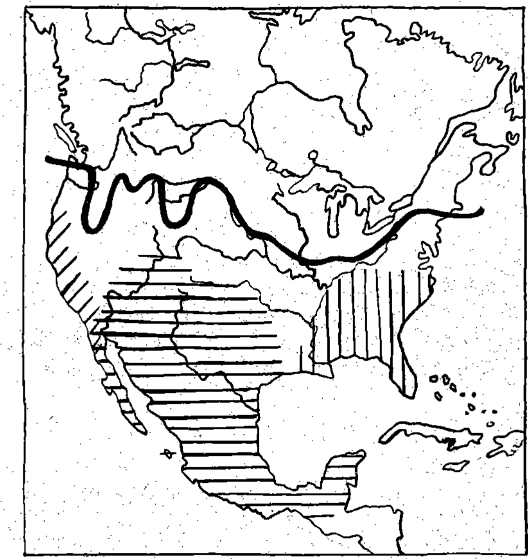

Fig. 23. *Ladder-baked Woodpeckers* — Range in North Amerika. ||||||| *borealis*. //// *nuttallii* ═══ *scalaris*. The broad black line approximately indicates the last (Wisconsin) stage of pleistocene glaciation. The ranges indicate the localization of the atlantic and pacific glacial forest refugia, as well as the fact that *D scalaris* has been driven away into more or less poorly vegetated Mexican regions.

genera found in the Great Smoky Mountains National Park, Alleghanies, and reviewed their known occurrence as fossils in the S.E. United States during Cretaceous and Tertiary times. He comes to the conclusion that totally 93% of the 67 recent tree -and shrub genera have been found in the same region in pre-pleistocene times. From this it appears, that the S.E. flora contains rather antique elements of a wide general distribution, possessing close recent relatives in China and Japan. From this I conclude that *borealis* is an old member of the group, having been isolated in the same region since the close of the tertiary and the advancement of the first glacial period. Its close association to the Longleaf Pine (*Pinus palustris*) has given it a rather remarkable coastal-plains distribution of a geologically recent date ; in the interior it goes up to the mountain pine-forests, but it does seem to be common there.

XXI **Dendrocopos nuttallii** (Gambel 1843 : Los Angeles).

Material examined: 7 (Placerita Canyon, Los Angeles Co. ; "California"). — (Brussels Mus. ; Leiden Mus. ; coll. Sillem-Van Marle).

Measurements :

Wing ♂ 100, 103, 106, 106 ; ♀ 102, 104, 104 mm.

Culmen ♂ 21, 22, 22, 23 ; ♀ 20, 21.5, 23 mm.

Range (fig. 23) : The arid regions of S. Oregon and California, west of the Sierra Nevada ; also N. Lower California. The species "breaks across the mountain divide to the south to follow the Mohave River in to the desert at Victorville" (Miller, 1934, p. 252) ; besides, it has been found in winter east of the Nevada Mountains in Owens Valley, at the W. side of the Owens Lake, Inyo Co., California (Miller, 1934), whereas Peters (1936) found it in summer near Phoenix, Arizona.

Specific characters : Very closely resembling *D. scalaris*, but distinguished by the very broad black eye-stripe and the scantily barred lateral tailfeathers. Nasal tufts not dirty white or brownish, but clear white, contrasting with the black forehead. Male with a broad red patch on occiput and hindneck only ; a number of feathers of the crown have white spots. An apparent slightly different subspecies (*longirostrata*) has been described from San Felipe, N. E. Lower California (Huey, 1927).

Biotope ; discussion : According to Bent (1939) the species inhabits different kinds of biotope, usually in arid regions : Oak-groves (Live Oak ; White Oak), and deciduous trees along streams, low bushes, often chaparral ; but apparently very rarely in pine timber, orchards and stands of Giant Cactus. Nevertheless, Richards (1924 : Grass Valley District) observed it occasionally in coniferous forests, and Huey (1927) found it near San Felipe, N.E. Lower California as apparent breeding birds in a thick growth of "Garrumbullo" Cactus (*Lophocereus*). Its aversion to coniferous forests is remarkable, since the tree-flora of the inhabited country is characterized by an overwhelming number of conifers, originating from the northern woods, many of them even dating back to miocene times. The chaparral formation in S. California, however, including a great number of sonoran plant-elements, besides, possessing many species of Oak, may be supposed to be the original biotope of *nuttallii*. In its choice of biotope *nuttallii* starts to resemble scalaris, to which it is also taxonomically closely related. Their respective ranges come together at several points (S. E. California ; N. Lower California), but their breeding ranges do not appear to overlap, although odd specimens of *nuttallii* have been found within the region of *scalaris* (Arizona : Peters, 1936).

In conclusion, it is probable, that *nuttallii* represents nothing else but the slightly transformed populations of *scalaris*, which either has maintained a small part of the originally wide North American range of Ladder-backed Woodpeckers, or have penetrated secundarily together with the sonoran chaparral plant-elements, into S.E. California. At all events there will be less to disregard the specific union of *nuttallii* with *D. scalaris*. However, the fact, that in *D. scalaris* apparently environmental causes only have induced a number of slightly different wholly equivalent races, does not make it desirable to include into that species a race of another historical value. For this reason, *nuttallii* will be treated here as a distinct species.

XXII **Dendrocopos scalaris** (Wagler 1829: Mexico = Vera Cruz).

Material examined: 8 (Texas; Tucson, Arizona; S. Bernardino; Yuma; "Mexico"; Cumpas, Sonora; Mt. Orizaba, Vera Cruz; Yucatan). — (Brussels Mus; Leiden Mus.; coll. Meinertzhagen; coll. Sillem-Van Marle).
Range: (cf. Oberholser, 1912, pl. 12) (fig. 23) Western desert regions of the United States, from extreme S. Utah, Nevada, California, through Arizona, New Mexico, and Lower California; also extreme S.E. Colorado, through Texas, Mexico, south to Chiapas, Yucatan, and British Honduras.
Subspecific characters: Systematic reviews have been given by Oberholser (1912), and Ridgway (1914); besides, new races have been described by Van Rossem (1942). Subspecific distinctions are based upon (1) size; (2) relative broadness of black and white barring of upperparts and lateral rectrices; (3) general colour of underparts (buffy to light creamy, or almost white); (4) degree of spotting or streaking of underparts, especially on chest and lower flanks.
The geographic variation of the measurements in *D. scalaris* furnishes an example in favour of the Rule of Bergmann: the northern populations being conspicuously larger than the southern ones. The following measurements are extracted from Ridgway (1914): wing ♂ (mm):
Arizona, New Mexico, Sonora, Chihuahua (*cactophilus*): 99—107.5.
Texas Tamaulipas, Nuevo Léon (*symplectus*): 98—107.
San Luis Potosi, Guanajuato, Hidalgo, Mexico (*bairdi*): 102—107.5.
Jalisco, Tepic (*centrophilus*): 100—104.5.
Guerrero, Oaxaca (*azelus*): 92.
Vera Cruz (*ridgwayi*): 88—92.5.
Chiapas (*percus*): 94—99.
Yucatan (*parvus*): 87—92.
British Honduras (*leucoptilurus*): 85—88.5.
Biotope and history.
The species resembles very closely the other species of the group (fig. 20): the male may be distinguished from the other American males by the white subapical spots to the red feathers of the crown, whereas the female differs from the other females by having the lateral tailfeathers regularly and equally barred with black and white.
Taxonomically *scalaris* is closely related to all other members of the group, but it differs in having a conspicuously different habitat: it is a typical bird of the scanty growths of chaparral and cactus deserts, rarely occurring in true forest regions; its distribution being principally a more or less pronounced sonoran (*senu lato*) one. In these hot and dry regions it is about the only species of Woodpecker found. It is, however, never found breeding in the Giant Cactus (*Cereus giganteus*) like *Centurus uropygialis uropygialis* Baird, although it is quite familiar to heavy stands of Cardón (*Pachycereus calvus*), a kind of single stalked giant Cactus, in which it has been found drilling its nesting hole very

near the top of the plant (Central Lower California: Bancroft, 1930). In regions where these are present, *scalaris* also inhabits Oak-groves (Life Oak-zone, Monterrey, Nuevo León: Sutton & Burleigh, 1939): besides, it has been observed in the marginal timber along streams, in canyons, and in parks and tree yards in towns (Pearson, 1932). Nesting holes are recorded from different kinds of desert plants: *Cactus* (especially in *Cholla* Cactus), *Prosopis*, *Yucca*, *Agave*, and many others; occasionally in various other suitable localities, like fence posts, telegraph poles, etc. (Bent, 1939). Like other members of the group (*analis*, *macei*, *atratus*) the species has been recorded feeding on the ground (Arizona: Bendire, *fide* Bent, 1939).

D. scalaris apparently has been driven away from its original forest home into poorly vegetated dry areas in the southern part of the continent by glacial periods and the simultaneous advancements of successive Woodpecker populations. There are more species of Woodpeckers that have found a glacial refuge in Mexico and Central America (*arizonae*; *stricklandi*; *villosus subsp.*), but these have maintained themselves in mountain forests formed by the many species of esecially Oak and Pine, which are also fugitives from the north. The original kind of habitat of *scalaris* is demonstrated by observations in the Colorado Valley, where it has been found inhabiting the willows along the lagoons, but being absent there, where *D. pubescens turati* is found (Bent, 1939), the latter thus acting as a stronger competitor in the original forest home.

5. THE INTERRELATIONSHIP OF THE SOUTH AMERICAN LADDER-BACKED WOODPECKERS.

The range of the two species of Ladder-backed Woodpeckers in South America (*ligniarius*, *mixtus*) does not appear to be exactly known. This is especially noteworthy in the case of *D.* (*mixtus*) *cancellatus*, which appears to be extremely rare in collections, and which up to now is only known from a few scattered localities in S. and S.W. Brazil. The only specimens I know of (except the types which probably still are in the Berlin Museum: Wagler, 1829) are preserved in the American Museum of Natural History in New York (Chapada, Matto Grosso, Brazil: Zimmer, *in litt.*, 1946) and in the Museum of Comparative Zoology at Harvard College, Cambridge (Miranda, Matto Grosso, Brazil: Peters, *in litt.*, 1946). Nevertheless, judging from the original description and information by Peters, I am convinced that *cancellatus* is nothing but a subspecies of *mixtus*, "from which it differs chiefly in being less boldly streaked underneath, and in being slightly whiter on the back, that is, the white bars are equal to or wider than the black bars. I can detect no essential difference in the markings of the tailfeathers or tertials" (Peters, *in litt.*, 1946). (cf. fig. 24).

The very few specimens of South American Ladder-backed species (in total 8!) that I was able to examine show so many similarities with the other representatives, especially with *D. analis*, that it appears justified to treat them as the most distal populations of he original S.E. Asiatic Ladder-backed group. They are among the most strongly barred species of the group, both on the upper and underparts! Whereas in S.E. Asia the Ladder-backed species mainly occur in tropic and subtropic areas, it is remarkable that the South American species are wanting in the tropics, mainly occurring in temporate (and subtropic) regions. From this type of distribution it is suggested that they are pliocene or early pleistocene invaders into Neogaea, originating from the North American populations. The true Woodpecker-like behaviour and the marked resemblance in appearance and life-habits, especially with the Californian *D. nuttallii* should be remembered in this respect (Wetmore, 1926).

The separation into two systematic species appears justified, since in West Patagonia both species are said to occur side by side (Chubut, Neuquen, Rio Negro, Cordoba, La Rioja: *Lista Sist. Av. Argent.*, 1938). However, I am not sure, whether in these regions the two species meet each other with or without hybridizing. Besides, *mixtus* seems to be a bird of lower countries, inhabiting the scanty willows that border the Rio Negro and its tributaries, the Neuquen and Limay (Wetmore, 1926), whereas *ligniarius* really descends from the eastern slopes of the Andes into Argentine. In W. Bolivia *ligniarius* is known from the mountain regions east to the Province of Santa Cruz, whereas *cancellatus* has been collected in the neighbouring Matto Grosso (Chapada) and *malleator* is recorded north to Tarija in S. Bolivia (*Lista Sist. Av. Argent.*, 1938). Nevertheless, there is a distinct western form (*ligniarius*) which is characteristic of the temporate ever-green *Nothofagus* forest-association, even occurring in Chiloë and Clothilde Islands, and in the Antarctic Beech virgin forests of S. Chile, "sparingly even to the Straits of Magellan" (Hellmayr, 1932), whereas a second form (*mixtus*) inhabits the drier, partly monsoon forest-associations of the Paraguayan and Argentine Chaco, and S. and S.W. Brazil, often breeding in the dry branches of the Ceibo-tree, *Erythrina cristagalli* (Hartert & Venturi, 1909).

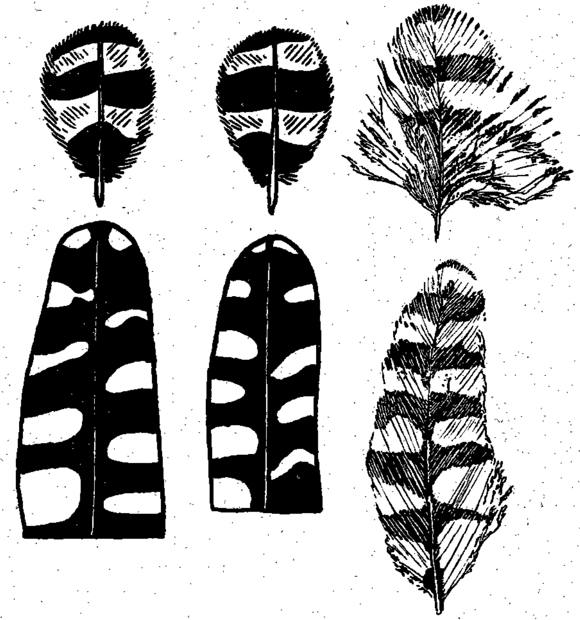

Fig. 24. *Ladder-backed Woodpeckers* — South America: upper row: back feathers; lower row: 2nd innermost tertials. From left to right: *D. ligniarius*, *D.m. mixtus* en *D.m. cancellatus*. The drawings of *cancellatus* are kindly made by Mr. William H. Drury, Jr., Biol. Lab., Harvard Coll., Cambridge, Mass., from a specimen in the Mus. of Comp. Zool.

D. ligniarius and *D. mixtus* are taxonomically very closely related. Principal differences exist only in the different extension in the adult male of the red coloration on the occiput, which in *ligniarius* comprises the whole occiput, while in *mixtus* the red patch is separated into a right and a left one.

The specific separation probably dates back to the pleistocene transgression of a part of South America, causing an oceanic penetration into the region of the Rio de la Plata, which again separated the Brazilian and the Patagonian parts of the continent. In the Patagonian island *ligniarius* developed, whereas *mixtus* was isolated either in the S. Brazilian island or in the temporarily connecting archipelago between the two parts of the continent. Not before recent times the two species, which originally formed a continuous chain of populations, met in Central West Patagonia.

XXIII **Dendrocopos ligniarus** (Molina 1782: Chile).

Material examined: 6 (Chile: Santiago). — (Brussels Mus.; Leiden Mus.).
Measurements: wing: ♂: 95.97, 99, 108; ♀ 95, 96 mm.
culmen: ♂ 24, 24.5, 24.5, 24.5; ♀ 20, 22 mm.
Range: S.W. part of Bolivia (Dept. Santa Cruz; Dept. Cochabamba: Bond & De Schauensee, 1943); Argentina (W. Patagonia: Chubut, Neuquen, Rio Negro, Cordoba. La Rioja: *List Sist. Av. Argent.*, 1938); Chile, south to the Straits of Magellan (Caredo Bay), including Chiloë Island, and Guiatecas Islands (Clothilde I.) (Hellmayr, 1932).

XXIV **Dendrocopos mixtus** (Boddaert).

Dendrocopos mixtus malleator (Wetmore 1922: Las Palmas, Chaco, Argentina)
Material examined: none.
Range: "N. Argentina from the Territory of Chaco (Las Palmas) and Tucuman (Tapia), north in the Chaco to northern Paraguay (Puerto Pinasco)" (Wetmore, 1922); also S. Bolivia (Tarija: *Lista Sist. Av. Argent.*, 1938; Villa Montes: Bond & De Schauensee, 1943).

Dendrocopos mixtus mixtus (Boddaert 1783: Buenos Aires, Argentina).
Material examined: none.
Range: N. Argentina (Buenos Aires; Entre Rios: *Lista Sist. Av. Argent.*, 1938).

Dendrocopos mixtus berlepschi (Hellmayr 1915: Mangrullo, Neuquen, W. Patagonia).
Material examined: none.
Range: Central West Patagonia (Mendozo, Neuquen, Rio Negro, La Pampa, San Luis: *Lista Sist. Av. Argent.*, 1938).

Dendrocopos mixtus cancellatus (Wagler 1829: Mexico = Sao Paulo, S. Brazil: Hargitt, 1890).
Material examined: none.
Range: S. and S.W. Brazil (Matto Grosso, Goyaz, Sao Paulo, Minas Geraes: Naumburg, 1930).

6. ABERANT FORM OF LADDER-BACKED GROUP.

XXV **Dendrocopos hyperythrus** (Vigors 1831: Nepal).

Material examined: Burma (Maymyo: 2); Sikkim (2); Darjeeling (1); Chakrata (W. Garhwal; 2); — (Dublin Mus.; Leiden Mus.; coll. Meinertzhagen).
Range: All mountain regions of Farther India, including Lower Laos, S. Annam (Delacour & Jabouille, 1940), N. Siam (Williamson, 1916; Deignan, 1945), Shan States, Burma, Assam, Cachin Hills, Chin Hills; — E. Bengal, Tippera, Chittagong — Yunnan (Rothschild, 1921), Sechuan, E. Tibet (Ludlow & Kinnear, 1944), Bhutan (Ludlow & Kinnear, 1937). Sikkim, Darjeeling, Nepal, Garhwal, N.W. Himalayas, where it is found in Cashmere, and W. Tibet; — S. Manchuria.
Manchurian migrants are found in Chihli (La Touche, 1920), Shantung (common), and several other parts of China (Hupeh; Shanghai; La Touche,

1931—34; Kwangsi: Yen, 1933), and in Corea (Yamashina, 1932). Records of the species in N.E. Tonkin (Delacour & Jabouille, 1939) perhaps also refer to the Manchurian race.

Discussion: The species differs from typical members of *Dendrocopos* firstly by the absence of a distinct moustachial stripe, which, however, is clearly indicated by the presence of broad black bases to the light greyish feathers of that region; secondly by the uniform rufous coloration of the underside, from the upper throat to the lower abdomen. On account of these characters and the very thin and slender long bill the species has been given monotypic generic rank (*Hypopicus* Bonaparte, 1854) by various authors (Stuart Baker, 1934: Stanford & Ticehurst 1939), although there is a general inclination to treat it as a member of *Dendrocopos* (also Peters in the 6th Vol. of his "Checklist"; *in litt.*, 1946).

The species has the whole interscapulary region, scapulars, back, and rump broadly transversely barred with black and white (quantitative degree of barring: 6; cf. p.84—85). In the adult male the whole upper head, including the sides of the neck and the postauricular feathers, is red, with the exception of a narrow white frontal band. In the female crown and occiput are black, each feather marked with a small apical white spot. White spots on the crown are in the Ladder-backed group found in the adult male and juvenile of *D. nuttallii*, and *D. scalaris*, moreover, white linear spots are a characteristic feature of the South American species; thus, showing this character to be innate to the group. Yet, in *scalaris*, and *nuttallii* the white spots appear to be more pronounced in juvenile than in adult specimens, whereas in the juvenile of *hyperythrus* of either sex the crown is black, the anterior portion being spotted with crimson instead of with white (Deignan, 1945). Moreover, the juvenile *hyperythrus* has the underparts not uniform brown, but dirty grey, irregularly transversely barred and streaked with blackish (not examined, but apparently like adult *ligniarius* and *mixtus*). In consequence, the juvenile *hyperythrus* much resembles the juvenile *atratus*, with which it apparently lives in the same regions and in equal altitudes (Mt. Victoria, Chin Hills: Stresemann & Heinrich, 1940). *Hyperythrus* has no eyes-stripe and possesses red under tailcoverts and lower abdomen, both characters being exclusively typical for the Asiatic members of the Ladder-backed group, opposite to the American ones.

In conclusion it appears that *hyperythrus* is a very old member of the Ladder-backed group, living in the higher regions of the S.E. and E. Asiatic distributional center of the group. It has one character in the adult stage that is more pronounced in the juvenile stage of others (white spots on head), whereas one of its juvenile characters is an adult character in the South American forms (regularly barred and streaked underside), indicating that *hyperythrus* not only has maintained original characters, but in addition having required its own taxonomic particularities. Its general rareness in S. and W. Chinese countries and its peculiar high mountain distribution furnish additional evidence in favour of the supposed relatively high age of the species. It is most common in Upper Burma and Assam (commonest Woodpecker in the Shan States: Cook, 1913), which may be supposed to be approximately the original center of origin of the group. Spreading from the high mountains of Farther India into the Himalayas, *hyperythrus* becomes gradually rarer in western direction (Stuart Baker, 1934). In some regions of S. E. Asia not less than 3 species of Ladder-backed Woodpeckers occur side by side, though in different biotopes (*hyperythrus* — *analis* — *atratus*; *hyperythrus* — *atratus* — *macei*: fig. 19) whereas in America only 2 relatively small areas are known, in which 2 members of the group occur simultaneously (*nuttallii* — *scalaris*; *ligniarius* — *mixtus*); thus, furnishing a new argument in favour of the hypothesis of the S.E. Asiatic origin of — at all events — this group of Woodpeckers.

Biotope: The species inhabits high mountain forests of apparently every kind, having been observed in dense coniferous forests, in deciduous woods of Willow, Birch, Oak, and Alder, and in park-like regions (N. Siam: Deignan, 1945), but also in *Rhododendron*woods (Stuart Baker, 1927), and thickets of *Hippophaë salicifolia* (Hsifan Mts.: Schäfer, 1938), breeding mostly in rotten stumps, or dead trees, often in dense patches of forest (Stuart Baker, 1934). With its thin bill it seems to be particulary feeding upon ants and beetles (Stanford & Mayr, 1941). Nevertheless, it has been observed quite fiercely drumming (Stresemann & Heinrich, 1940).

D. hyperythrus has been observed in the following altitudes:
Hsifan Mts. (Schäfer, 1938): 2500—3200 m.
Yunnan (Rothschild, 1921): 3350—3650 m.
N. Burma (Stanford & Mayr, 1941): 2200 m.
Chin Hills (Stresemann & Heinrich, 1940): 1400—2800 m.
Indo China (Delacour & Jabouille, 1931): 800—2000 m.
Bhutan (Ludlow & Kinnear, 1937): 1500—3050 m.
Sikkim (Stuart Baker, 1934): up to 3650 m.
Rawalpindi (Whistler, 1930): 1800—2700 m.

Subspecific characters: No subspecific discussion can be attempted, owing to lack of material. Races have been described on account of the intensity of the rufous red coloration of the underside, the extension of the crimson on the sides of the neck, and the general measurements.

The following races have been described:

D. h. hyperythrus (Vigors 1830: Himalaya).

It is an unsettled trouble in the literature, whether the type-locality of *hyperythrus* is Nepal (Hartert, 1912) or Kumaon (Ticehurst & Whistler, 1924 & 1926). Following Hartert, the N.W. birds were in need of a subspecific name (*marshalli* Hartert, 1912), whereas according to Ticehurst & Whistler the E. birds must get a name (*sikkimensis* Ticehurst & Whistler 1924). Different authors followed Hartert (Rothschild, 1926; Stuart Baker, 1926 & 1934; Hartert-Steinbacher, 1935; Stresemann & Heinrich, 1940; Stanford & Mayr, 1941; Deignan, 1945), whereas others sympathtized with Ticehurst & Whistler (Ludlow & Kinnear, 1944; Stanford & Ticehurst, 1939).

D. h. subrufinus (Cabanis & Heine 1863: N. China; Talien Bay and Tientsin).
D. h. marshalli (Hartert 1912: Murree, N.W. Himalaya).
D. h. sikkimensis (Ticehurst & Whistler 1924: Sikkim).
D. h. annamensis (Kloss 1925: Dahan, S. Annam).
D. h. miniakoruni (Meise 1934: Tatsienlu, W. Szechuan).
D. h. heinrichi (Stresemann 1940: Mt. Victoria, Chin Hills).

X DENDROCOPOS MINOR GROUP.

1. THE HISTORY OF THE DENDROCOPOS MINOR GROUP.

The *glacial history* of *D. minor* in *E. Asia* is indicated by the fact that the species is only found in the Ussuri and Amur regions, accidentally in Sakhalin, besides, very rarely breeding in Hokkaido (Jahn, 1942). It is absent in the other Japanese islands, as well as in China south of the Khinghan Mountains and the S. Manchurian mountain range. In Hokkaido *minor* is replaced by *D. kizuki*, which is a very common bird (Jahn, 1942), whereas in China *D. canicapillus* is taking its place, as the latter is the only smaller Woodpecker found in these regions. In the Manchurian region, however, 3 species of smaller Woodpeckers are found: *kizuki*, *canicapillus*, *minor* (fig. 25). These represent a faunal configuration which is nowhere to be found, and which can only be expected in an important glacial refugium. *Kizuki* belongs to that group of Pigmy Woodpeckers, to which also *moluccensis* and *maculatus* have been referred; these have been driven away from the continent into remote regions or island groups, *kizuki* being found in al Japanese islands from the S. Kuriles, even south to the Riu Kiu Islands. Its abundant occurrence in Japan leaves no place for either *minor* or *canicapillus*, from their central stock *kizuki* apparently has derived. *Canicapillus* and *minor*, however, show close taxonomic resemblances, which are especially apparent in the female plumage of e.g. Chinese specimens compared with Central or S. European ones. As *minor* has a very fragmentary E. Asiatic range, which is in conspicuous contrast to both the Eurasiatic species *major* and *leucotos*, which occur in Japan at least south to Hondo, and in the whole of China, one may conclude (1) that *minor* is a European offspring of a former, E. Asiatic population from which *canicapillus* is the remnant; (2) that *minor* secundarily has penetrated into Asia again, in its recent plumage reaching Manchuria not before the last glacial period. *D. minor*, like *Parus major* from its Manchurian representative (Rensch, 1933), proved to be physiologically distinct from *canicapillus*, with which at the moment it can live side by side, as far as is permitted by the ecological competition between these species.

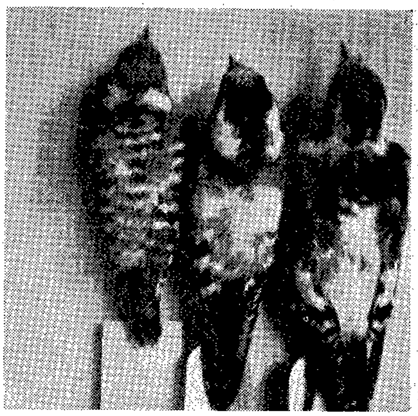

Fig. 25. *Manchurian Lesser Pied Woodpeckers* — From left to right: (females): *kizuki* (Suiffun River, S. Ussuria); *minor* (Amur region); *canicapillus* (Suiffun River, S. Ussuria). Note the resemblance between *minor* and *canicapillus* (J. Fokker, phot.).

Taxonomic differences between *canicapillus* and *minor* mainly refer to the colour of the head, which in the female *minor* is white instead of grey, posteriorly bordered by black, whereas the male *minor* has a red crown, a small white forehead and a black occiput, which is totally different from the black-bordered grey head with small often concealed red patches on each side of the head, found in *canicapillus*. The originally small amount of red in the secundarily sexual head coloration in *minor* is demonstrated in the fact that — in spite of many erroneous literature records, recently repeated in the work by Eijkman c.s. (1941), a mistake to which already Hartert called attention — the juvenile female has *no red* on the head, whereas in the male the red on the crown is only indicated by dull red tips to a small amount of reathers, being finally replaced by the total red crown in the adult male.

In conclusion it appears that *canicapillus* and *minor* have been *conspecific* forms at least up to the beginning of the pleistocene, having become physiologically and taxonomically distinct through geographic isolation.

The *postglacial history* of *D. minor* in *Asia* is not very complicated. The species is found in the Manchurian region and in Hokkaido, indicating that it had there a refugium, at all events during the last glacial epoch. In the geographic relation of its taxonomic characters *minor* agrees with *leucotos* in the fact that Manchurian specimens (*amurensis*) are close to Scandinavian ones (*minor*) from which they can hardly be separated. According to Stegmann (*fide* Hartert-Steinbacher, 1933) the difference between these races is only „dass *amurensis* im frischen Gefieder unten ohne den gelbbräunlichen Anflug ist, den *minor* dann zeigt" (p. 371). I could examine only 1 specimen from Sidemi, Amur Bay (Dec. 24; wing 93; culmen 17 mm) and found that it was almost identical in appearance and measurements with one from Naesodden, S. Norwegia (April 13; wing 93; culmen 17 mm). Consequently one may suppose that like many other animals and plants *minor* has extended its range postglacially in western direction, and, in close contact with the Siberian taiga vegetation it has spread through the whole of Siberia into European Russia and Fennoscandinavia. The biotope of *D. minor* in W. Siberia is according to Johansen (*in litt.*, 1946) about the same as that inhabited by *D. leucotos*; „die bevorzugten Biotope sind Birken-Espen Wäldchen, die Waldsteppe und Auen in Flusstälern. Doch hält er sich auch gern im Mischwald auf. Ausserhalb der Brutzeit im richtigen Nadelwald anzutreffen". In Manchuria, however, the species is said to prefer mixed park-like vegetation, being rarely found in pure *Larix*-forests (Stegmann, 1930). In its European range the species has retained the same kind of biotope: in E. Finland Pynnönen (1939) mentioned to have found it feeding most frequently in birches, alders, and willows, being especially fond of park-like landscapes.

The Siberian populations of *minor* (*kamtschatkensis*), like *D. leucotos*, have obtained the typical N. Asiatic plumage in which white prevails, showing a conspicuous reduction of melanine pigmentation and possessing long and soft, almost hair-like feathers. Typical Central Siberian specimens of *minor* have a pure white undersurface without any tinge of phaeomelanine and without black striations; the lateral tailfeathers show only a few remnants of broken dark cross bars; the back is white, the faint traces of dark cross bars being concealed by the long and hairy tips of the feathers; the scapulars and inner secondaries are more profusely marked with white and the white of the forehead in both sexes is broader and the red in the adult male more reduced. I found the purest type of *kamtschatkensis* in a specimen from Tarbagatai (Febr. 10), all other Siberian specimens having still traces of black streaks on the sides of the chest. Unlike *leucotos* the Central Siberian specimens are but faintly distinguishable from the N. European populations, since regulary black stripes on the chest, and occasionally pure white undersides are found in specimens originating from all parts of this range. Besides, the present author compared two specimens from the Tunkun Mountains, S.W. of Lake Baikal, with two specimens originating from Norwegian Lapland (Upper Pasvik River), and found that these were almost identical. With reference to the typical Siberian white specimens distinct transitional populations appear to occur in E. Manchuria along the middle current of the River Schilka, west to about Sretensk (Stegmann, 1930). In conclusion it appears justified to treat all populations west of the Janobloi and Stanovoi

Mountains, including European Russia and N.Fennoscandinavia (Lapland) under one name (*kamtschatkensis*), whereas the S. Scandinavian and Baltic populations should be kept separate (*minor*). *Minor* is an evident postglacial Asiatic invader into Europe, since all N. Eurasiatic populations have approximately the same dimensions; besides, *minor* is much less sharply barred on the back, and has a conspicuously purer ground tone of the underside than all central and W. European *D. minor* populations. Transitional forms between *minor* and *kamtschatkensis* have been described, dependant of the want of the authors to recognize faintly characterized races. These may be mentioned only in a successive order from pure *minor* to pure *kamtschatkensis*: *lönnbergi* (Domaniewski 1927: Karesuanda Lapland), *transitivus* (Loudon 1914: Lethonia; changed by Domaniewski (1927) in Pskov, S.E. of Esthonia), *menzbieri* (Domaniewski 1927: Saratov, Russia). They are treated here as *synonyms* of *kamtschatkensis*. Domaniewski (1927) was not the first to call attention to the fact that Lapland specimens of *minor* cannot be referred to typical *minor*; Collett (1891) already mentioned that specimens from Norwegian Lapland were „im Ganzen vollständig entsprechend dem sibirischen *P. pipra* Pall. (= *kamtschatkensis*). Er tritt aber nicht unvermischt in diesem Kleide auf, denn man trifft häufig Individuen mit deutlichen Übergängen zu der südlichen Form" (p. 18). As in *leucotos* it is suggested by the author that the taxonomic differences of *kamtschatkensis* are caused by environmental influences, since the original Manchurian populations, as well as the western outermost ones have kept the same appearance, whereas exactly *minor*- and *amurensis*-like specimens may still be found in all Siberian regions, a fact which is already mentioned by Sushkin (*fide* Hartert-Steinbacher, 1935). Kozlova (1932) thought *kamtschatkensis* "not to be well differentiated from *minor*" (p. 395), all intermediate forms having been found near Lake Baikal, Irkutsk, and in the Russian Altai. In conclusion it seems, that one Central and W. Siberian, and European Russian race may be recognized (*kamtschatkensis*), whereas the E. Asiatic, S. Scandinavian and Baltic populations may be referred to another race with a disjunct area (*minor*). The author suggests that *minor* has had the same history as *D. leucotos leucotos*, whereas the origin of *kamtschatkensis* is the same as that of *D. leucotos uralensis*.

The author has not seen specimens from the Anadyr and Kamtchatka regions, which have been described as a separate race (*immaculatus*) on account of the longer bill and the still more white general appearance of the specimens, which are said to possess uniform white or only very faintly spotted lateral tailfeathers (cf. Hartert, 1912). A female from the Amur regions from October 1st (coll. Meinertzhagen: wing 100; culmen 19 mm) examined by me, probably is a migratory specimen of this race. These N.E. Asiatic populations doubtlessly originate from the Manchurian region, whence the species has spread in N. and N.E. direction, *the environments* apparently inducing a considerable reduction of melanine pigmentation, since in both *D. major* and *D. minor* conspicuously white populations have been described from these regions, which, besides, is a well known climatic effect in northern bird-populations.

The author does not understand the significance of the fact that specimens from the E. slopes of the Hakuto Mountains in N.E. Corea (*nojidoensis*) are said greatly resembling Caucasian specimens, especially regarding the general colour of the undersurface (*Yamashina*, 1930). It would be of importance to know the transition between *nojidoensis* and Manchurian *minor*!

As in the case of *D. major, Poland* is the region where the eastern Asiatic and the western mediterranean forms (*hortorum*) meet. E. Prussia still appears to be inhabited by pure *minor*, but transitional birds between *minor* and *hortorum* have been described by Kleinschmidt (1927) from Silesia (*silesiacus*). These populations cannot be named by modern nomenclature since individual specimens apparently can be referred either to *minor* or to *hortorum*.

The *glacial* history of *D. minor* in *Europe* is by far not so conspicuously indicated by the recent distribution and the geographically located taxonomic characters, as in *D. major*. Nevertheless, the postglacial history of *minor* agrees with that of *major*, since Italian (*buturlini*) and French populations on the one hand, and Central and N. Balcan populations on the other hand resemble each other closely in the general measurements, the barring of the upperparts, and the streaking of the underparts, as well with reference to the general yellowish or buffy tone of the underparts, especially on the throat and upperbreast. In this respect, also Swiss and the rare Iberian (not examined; cf. Ticehurst & Whistler, 1933) populations are much like *buturlini*. Specimens from the Pyrenees have also been referred to this race (Whistler & Harrison, 1930). Dutch and German specimens, which cannot be distinguished (!, cf. also Hens, 1931) are slightly different in the dirty greyish or brownish tinge of the underparts, but Belgian birds apparently are slightly closer to the French than to the German birds. The name *bacmeisteri* (Kleinschmidt, 1916) given to French birds, however, can hardly be applied in nomenclature, since the difference between *buturlini* on the one hand, and *hortorum* on the other hand are visible in a series only; individual specimens cannot be distinguished. The name even has less value in nomenclature than the analogous *D. major arduennus*. Only British birds (*comminutus*) are markedly different, having a uniform dark dull brown underside with only few narrow shaftstreaks on the sides of the chest and on the flanks; besides, showing averaging smaller dimensions. In consequence it appears to me that the recent distribution indicates that W. and Central Europe has been peopled postglacially from the mediterranean refugia, spreading west of the Alps into W. Europe and thence turning eastward and northward into Central Europe, where it finally met with the Asiatic *minor*. Spreading along the W. coast of Europe *D. minor* has been able to reach England, apparently at the time that the English Channel was a narow stream only, but in Scotland the species is still only an extremely rare straggler (Witherby, 1924). In Ireland *D. minor* has not been recorded for the last 100 years (Humphreys, 1937: 6 or 7 records, but not later than 1848). Apparently this island could not be reached by *D. minor* and *major* in postglacial time. It is possible, although by no means certain, that the remarkable absence of *D. minor* as a breeding bird in Denmark (Jespersen, 1946; Löppenthin, 1946) and S. Sweden (Skane) is equally the result of the postglacial dispersal of the species into Europe: in this case neither *hortorum*, nor *minor* would not yet have reached Denmark, whereas with reference to the range of *D. major* the author has shown that influences of two generations (*pinetorum*, resp. *major*) are apparent in the Danish populations. It would be very remarkable, however, that even during the warmer postglacial periods *hortorum* would not have reached Denmark, whereas the European mixed forests have had a much wider postglacial northern distribution than at the moment. In conclusion I incline to agree with Jespersen (*in litt.*, 1946) when he writes: "I cannot tell you the reason why this species is not breeding in Danmark. As we have mixed population of trees in the woods of northern Zealand oecological circumstances may not be the reason; ...... the relatively few birds found as rare winter guests in Denmark seem to have been the scandinavian form. As far as I know the subspecies *hortorum* has never been found in this country". It also spread in E. direction into the Balcans and into the Alps; the birds described as *jordansi* (Götz, 1925: Salzburg, Austria) apparently being closer to *butur-*

lini than to *minor* with which they originally have been compared (underside described as "hellocker bis weiss" by Domaniewski, 1927, p. 71). A gradual spreading into the Alps appears to take place from the N. direction also (*hortorum*), but the series of 9 Swiss specimens examined is only slightly intermediate between *buturlini* and *hortorum*. In fact, the swiss birds resemble more the italian specimen (*buturlini*), than the series of french birds (*arduennus*). The same phenomenon is found in the range of *D. major pinetorum*, which is busy penetrating into the region of „*alpestris*". Rumenian specimens are close to Italian ones in the yellowish buff underside, but the narrow streaking of the underparts furnish a slight, though sufficient, character of subspecific distinction (*wagneri*). As in *major* intermediate zones are found in N. Hungaria and in Slovakia, but literature records from these regions are very scarce: Domaniewski (1927) has referred birds of these regions to "*jordansi*". Few records are known with reference to an intermediate zone in S.W. Russia, which according to the distributional phenomena described of *D. major* are to be expected. According to Grote (1942 B) "der Kleinspecht der Ukraine steht der mitteleuropäischen Rasse *hortorum* sehr nahe, jedenfalls gehört er nicht zur Nominatform" (p. 154); but Charlemagne (1934) states that in N.E. Ukraine "*transitivus*" is the breeding bird, whereas in the western parts *minor* (*sic*) should breed.

From the N. African race (*ledouci*), which has a few relatively more striking distinguishing features, it can only be stated that its range dates back to an older glacial isolation than that of the S. European races. Perhaps *ledouci* has had the same history as *D. major numidus*. This may be also the case with the Asia Minor form (*danfordi*), which has a closed postauricular black band connecting the black of the malar stripe with that of the hind neck. This character is also found in many S. and E. Balcan specimens, which therefore have been referred in the literature to either *buturlini* or *danfordi*. It is most probable that *danfordi* has penetrated secundarily into Europe, perhaps living side by side with *buturlini*-like birds. This may be the reason of the great disagreement in the literature concerning the subspecific status of the Balcan *minor*. The situation somewhat resembles that of *D. major syriacus*, and Domaniewski (1927) appears to be right when he says: „Es ist möglich, dass nach einer näheren Untersuchung, *D. m. danfordi* nicht als eine subspecies, sondern als eine prospecies aufgefasst werden müssen wird" (p. 87).

As the distinguishing characters of the Asia Minor, Caucasian, and Persian populations are but very faintly pronounced, the species apparently being very rare in most localities too, and in addition only few specimens having been examined, it is not justified te reconstruct from its present range an historical sketch of the species. It only can be remarked that the species has had glacial refugia in Caucasia and N. Persia, whereas the S.W. Persian birds apparently are also derived from retreated pleistocene European populations. N. Persian (*hyrcanus*) and Lenkoran (*quadrifasciatus*) birds are probably of a relatively old age, which is not only indicated by the present range, but also by the fact that only in these races no white spots are found on the lesser upper wing coverts. Nevertheless, a few remarks may be of importance concerning the Caucasian birds: these are very close to *buturlini*; 2 specimens examined are like *buturlini*, showing cross bars on the flanks and in the anal region like *danfordi*, but missing the postauricular black band found in the latter. Therefore, it seems justified to reach the same conclusion as in the case of *D. major*: Caucasian birds belong to the same glacial generation as the Italian and the W. European races, whereas Asia Minor and Persian birds (including those from the S. Caspian Mountains) are of an older age. The species is probably absent in Crimea, as it is only doubtfully recorded by Pusanov (1933); besides, Kozlova writes (*in litt.*, 1946) that "the breeding of *D. minor* in the Crimea has not been proved. Some existing records of its breeding there are unreliable".

XXVI **Dendrocopos canicapillus** (Blyth 1845: Arrakan).

Material examined: S. Ussuria (5: mouth of Suiffun River); Hupeh (1: Ichang); Kiangsu (1: Nanking); Fukien (6); Formosa (11); Laos (2: Phu Kobo, near Xieng Khouang; Muong Sovi); E. Bengal (1: Kalimpong); Burma (2: Rangoon, Mandalay); Siam (3); Tenasserim (2); Malacca (1); "Himalaya" (1); Sikkim (1); Darjeeling (2); Nepal (1).

Measurements:

1. *D. c. doerriesi* (Hargitt 1881: Askold Island, S. Ussuria): S. Ussuria: ♂ 103.5, 106, 107; ♀ 106, 108 mm.
2. *D. c. scintilliceps* (Swinhoe 1863: Pekin, Chihli): Hupeh: ♂ 99 mm; Kiangsu: ♀ 93 mm.
3. *D. c. nagamichii* (La Touche 1932: Fukien): Fukien: ♂ 100, 101, 102, 103; ♀ 104, 105 mm.
4. *D. c. kaleensis* (Swinhoe 1863: Formosa): Formosa: ♂ 96—104, average (6) 97.8; ♀ 97—103, average (5) 99.8 mm.
5. *D. c. tonkinensis* (Kuroda 1924: Yen Bai, Tonkin): Laos: ♂ 91; ♀ 97 mm.
6. *D. c. semicoronatus* (Malherbe 1848: Himalayas): Darjeeling, Sikkim: ♂ 85, 85.5, 88 mm.
7. *D. c. mitchellii* (Malherbe 1849: Nepal): Nepal: ♂ 88 mm.
8. *D. c. canicapillus* (Blyth: Arrakan): E. Bengal: ♀ 89; Burma: ♂ 87, ♀ 86 mm.
9. *D. c. pumilus* (Hargitt 1881: Maliwon, S. Tenasserim): S. Siam ♂ 78; ♀ 79; Tenasserim: ♂ 78; ♀ 82 mm.
10. *D. c. auritus* (Eyton 1845: Malacca): Malacca: ♂ 87 mm.

Range: E. Asia, from S. Ussuria and S. Manchuria (exact northern limits unknown: Worobiev, 1937), Corea (?), through China (?), (but not in the E. Tibetan range: absent in Hsifan Mts: Schäfer & De Schauensee, 1938) and Indo China, including Formosa and Hainan, the whole of Farther India, Siam, Tenasserim, and Malacca, south to Singapore Island (in the latter locality being scarce: Robinson, 1927), Yunnan, Burma (the race *obscurus* being a mountain bird (1200—2200 m); the race *canicapillus* being found in the lowlands: Stanford & Mayr, 1941), Khasia and Cachar Hills, Arrakan, E. Bengal, E. Himalayas, Bhutan (scarce: low altitudes: 600—900 m: Ludlow & Kinnear, 1937), into Nepal, but exact western limit in the Himalayas unknown (? subsp. *mitchellii*: Nepal = *Picus pygmaeus* Vigors 1831 (Oberholser, 1919); Pigmy Woodpeckers *west* of Nepal apparently must be referred to the *brown*-headed species *D. nanus*, of which a specimen could be examined by me from Mussoree, Garhwal), exact range in Bengal unknown; N. Sumatra, and — probably disconnected — parts of Borneo (Sarawak: Salvadori, 1868; Mengalung and Marabok River: Blasius, 1901; Melawi River: Kloss, 1930; Riam: Mayr, 1938).

Biotope: The species is found in different biotopes, either in the lowlands, in secundary jungle, in dry deciduous forests (N. Siam: Deignan, 1945), and in cultivated areas and plains (China!), or in the mountain forests (pine forests in Yunnan up to about 3000 m: Rothschild, 1921), in Oaks and Rhododendrons (E. Himalaya: Stuart Baker, 1934), or the outskirts of virgin forests, but never in heavy jungle. In Malacca the species has been observed side by side with *moluccensis* in mangrove and *Casuarina* forests (Robinson & Kloss, 1922). In those places where representatives of the brown-headed group occur side by side with it, *canicapillus* usually inhabits park-like vegetations in higher altitudes.

Specific characters, History: All members of the species are characterized by a grey head and a characteristic barring of the upperparts, as well as streaked underparts. The southern races are but faintly distinguishable from the brown-headed *moluccensis* and *nanus* groups, from which zoogeographically they appear to be distinct (see under *D. moluccensis* and *D. nanus*). There is conspicuous geographically located variability in the species, but between all types all necessary intermediate forms occur in geographically transitional zones (fig. 26). It is most probable that genetic relations exist between *canicapillus* and *minor* (see under that species). From a taxonomic point of view this relationship is only apparent in comparing the extreme northern races of *canicapillus* (S. Manchuria, N. China) with *minor*. Southern races are so conspicuously different that the suggestion of a close relationship with the brown-headed forms appears justified. Therefore it is thought by the author that *canicapillus* has maintained the characters of a central group from which both *minor* and the brown-headed forms have derived.

It is probable that the recent distribution of the races of this species, as reviewed by Greenway (1943), reflects the history of the species as far backward as into tertiarty times. The red hindneck of *semicoronatus* (E. Himalayas) against the narrow red patch on the sides of the head in all other races, indicates isolation of some unknown kind; the aberrant secundary sexual head coloration perhaps being obtained by mutation, as must be suggested in the distal races of *D. maculatus* in the Philippine Islands (a.o. the race *maculatus*). The author even thinks it possible that *semicoronatus* is not a subspecies of *canicapillus*, but of *nanus*, since a male from Darjeeling District (Bradamtam, ca. 600 m alt.: wing ♂ 85 mm: coll. Meinertzhagen) has a markedly greyish brown crown in addition to the typical red occiput and hindneck. The occurrence

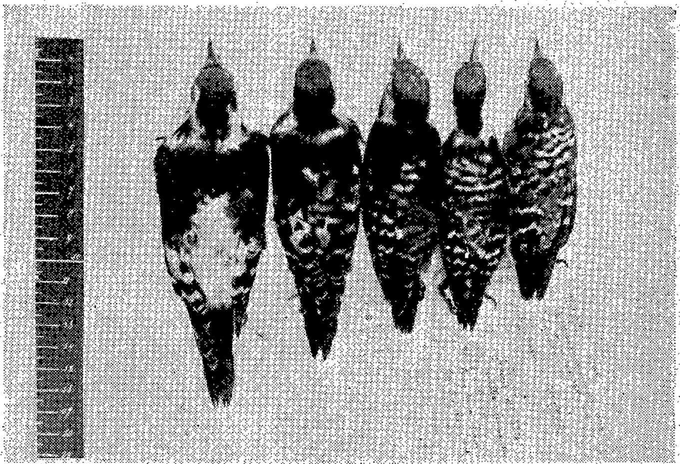

Fig. 26. *D. canicapillus* (Blyth) — Chain of races from north (left) to south (right), showing the gradual geographic transformation in size and transversely barring of the upperside. From left to right: Suiffun River, S. Ussuria (*doerriesi*); Hupeh, China (*scintilliceps*); Phù Kobo, Laos (*tonkinensis*); Bang Nara, Peninsular Siam (*canicapillus sive pumilus*); "Malacca" (*auritus*).

of distinct races of *canicapillus* in different parts of Malacca, Sumatra, and Borneo side by side with *moluccensis* proves the relatively old date of the separation between these apparently closely allied forms. The Sumatran and Bornean races of *canicapillus*, which — at all events in Sumatra — are found exclusively in higher elevations (Atjeh: Terpentine Pines in park-like highlands: 1100—2840 m: De Schauensee & Ripley, 1939; Chasen, 1941), might be considered to represent relict populations, which in the lowlands are surrounded by the brown-headed offspring of the same group, which has been pushed back into the outskirts of the S.E. Asiatic range, whereas it is possible that the simultaneous occurrence in Malacca is of a postglacial age: it seems that *canicapillus* is the original inhabitant of the Malayan Peninsula, whereas *moluccensis* has extended its range on the continent after the glacial geographic conjunction of Sumatra with Malacca.

Subspecific characters (fig. 26): Owing to lack of material subspecific examination could be done only with reference to the valuable work by Greenway (1943). It is probable that a thorough study of the Dwarf Woodpeckers inhabiting the Himalayas (Nepal!) and E. Bengal will be able to clear up the historic relations that exist between the race *canicapillus* on the one hand and *semicoronatus* on the other hand. With the available material and the knowledge of their respective ranges the only justified conclusions refer to the interrelationship with *minor*, and with the brown-headed Dwarf Woodpeckers (*nanus, moluccensis, maculatus,* also *kizuki*). Historic influences within the species could not be detected in the material before me.

Climatic influences, however, are clearly visible throughout the whole range. These refer to the important increase of dimensions (rule of Bergmann: cf. measurements given above!), and to the relative decrease of melanine pigmentation in northern races (rule of Gloger) which live in a temporate and cold climate, as compared with the southern ones inhabiting subtropic and tropic regions. The last named character is realized mainly in the degree of transversely barring of the upperparts, which is most strongly developped in southern races. The strongest type of barring including the upper tailcoverts and central rectrices is found in the typical race *canicapillus* (E. Bengal, Siam), indicating the primitive stage of the group, which, thus, is localized approximately in the hypothetical center of dispersal of all species groups of *Dendrocopos*.

For a discusion of the many proposed races (including the puzzling *Dryobates obscurior* Rothschild 1922: Lichiang Range, N.W. Yunnan) the author refers to Greenway (1943).

XXVII **Dendrocopos minor minor** (Linnaeus 1758: Sweden).

Probable synonyms:
Xylocopus minor amurensis Buturlin 1908: Bureia Mts., Lower Amur region.
Xylocopus minor minutillus Buturlin 1908: Sidemi, S. Ussuria.
Xylocopus minor yamashinai Momiyama 1928: Sakhalin.

Material examined: I. *Asia*: Sidemi (1). — (coll. Meinertzhagen).
II. *Europe*: 13: Sweden (Upland; Öland; Wermland; Dalsland), Norway (Naesodden near Oslo). — (Copenhagen Mus.; Stockholm Mus.).

Measurements:
Asia: wing ♂ 93; culmen 17 mm.
Europe: wing ♂ 92—96, average (6) 93.0; ♀ 92—95, average (7) 93.4 mm.
culmen ♂ 16—18, average (6) 17.1; ♀ 11—18, average (7) 16.8 mm.

Range: Discontinuous: Amur and Ussuri regions; Manchuria, occasionally in Sakhalin, rare in Hokkaido; a visually record by Snow in 1896 (*fide*

Yamashina, 1931 A) in the S. Kurile Islands needs confirmation. — S. and central Norway (rare along the westcoast: Kolthoff & Jägerskiöld, 1898), and Sweden; southern half of Finland, Baltic States to Litauen and E. Prussia.

Subspecific characters: Differs from *kamtschatkensis* in the brownish tone of the underparts which is especially apparent in freshly moulted plumage, in the conspicuous dark striping on the sides of the chest, and in having the feathers of the upperside shorter and in consequence more strongly transversely barred. From *hortorum* the race differs in being decidedly larger and in being either less heavily longitudinally striped on the underside, or having the underside of a more soft isabelline or reddish brown tinge, which is strongly contrasting with the earthy brown colour found in *hortorum*. The transitions with *kamtschatkensis* and *hortorum* occur very gradually: they are of a quantitative type only: that with *kamtschatkensis* is found in N. Fennoscandinavia (*lönnbergi* (Domaniewski)) and in north, and central W. Russia (*transitivus* (Loudon)); that with *hortorum* in Poland (*silesiacus* (Kleinschmidt)) and E. Prussia. Wing measurements of E. Prussian birds: 88—97, average (34) 92.2 mm (Tischler, 1941).

Dendrocopos minor nojidoensis (Yamashina 1930: eastern slopes of Mt. Hakuto, N.E. Corea).

Material examined. none.

Range: only known from the type locality.

Subspecific characters: According to Yamashina (1930) underparts very dark, greatly resembling *D. m. colchicus*. Wing ♂ 89—93; ♀ 90—92 mm.

Dendrocopos minor kamtschatkensis (Malherbe 1861: Okhotsk).

Probable synonyms:

Dryobates minor transitivus Loudon 1914: Lisden, Livonia.

Dryobates minor lönnbergi Domaniewski 1927: Karesuanda, Lapland.

Dryobates minor menzbieri Domaniewski 1927: Saratov, Russia.

Material examined: Siberia (10: Baikal Lake; Tunkun Mts.; Tarbagatai; Obdorsk on River Ob); Swedish Lapland (4: Kiruna; Torne River); Norwegian Lapland (2: Pasvik River). — (Brussels Mus.; Copenhagen Mus.; Leiden Mus.; Stockholm Mus.; coll. Hens; coll. Sillem-Van Marle).

Measurements:

Asia: wing ♂ 93—98, average (6) 96.1; ♀ 86—99, average (4) 94.0 mm.

Europe: wing ♂ 93, 94, 95; ♀ 95, 95, 96 mm.

Asia: culmen: ♂ ♀ 15—18, average (10) 17.0 mm.

Europe: culmen ♂ ♀ 17—19, average (6) 17.9 mm.

Range: Siberia, west of the range of *minor* and *immaculatus*, and south to the steppe range; westwards into Europe to Russia, central Poland, E. Prusia, and N. Fennoscandinavia (Lapland). The species is found up to the tree-line and also in the forest-steppe zone (Sushkin, 1914), but is apparently seldom found in the mountains. Migrant specimens of this race have been frequently noticed in Manchuria (cf. Domaniewski, 1927; Meise, 1934) and in Sakhalin (cf. Thayer & Bangs, 1916; Meise, 1934), as well as in most ranges directly south to the breeding range.

Subspecific characters: A conspicuously white and soft-hairy bird: see "History of *D. minor*".

Dendrocopos minor immaculatus (Stejneger 1884: Petropaulski, Kamchatka).

Material examined: ?1: migrant specimen from Amur region. — (coll. Meinertzhagen).

Measurements: ♀ wing 100; culmen 19 mm.
Range: Kamchatka and Anadyr regions.
Subspecific characters: Much like *kamschatkensis*, but said to be still whiter and with a slightly longer bill.

Dendrocopos minor butulini (Hartert 1913: Valdenza, Italy).
Probable synonym:
Dryobates minor jordansi Götz 1925: Salzburg, Austria.
Material examined: Italy (1); Switzerland (9). — (Basel Mus.; Leiden Mus.; Schweizerische Vogelwarte Sempach; coll. Huber; col. Sillem-Van Marle).
Measurements:
Italy: wing ♀ 87; culmen ♀ 16.5 mm.
Switzerland: wing ♂ 88, 89, 92; ♀ 88, 88, 93 mm. Culmen ♂ 16.5, 17; ♀ 15, 15, 15.5 mm.
According to Ticehurst & Whistler (1933) S. France, Italian, and Albanian specimens have wing lengths: ♂ 86—90; ♀ 84.5—87 mm.
Range: Iberian Peninsula (rare: Tait, 1924; Witherby, 1928); extreme S. France (Mayaud, c.s., 1936); Italy; very rare in Sicily and Sardinia (Arrigoni, 1904); Switzerland, Austria, Balcans; the exact northern limits unknown, as are also the boundaries with the race *danfordi*; the western parts of the Balcans appear to be inhabited by *buturlini*; a specimen from Athens and one from Mt. Olympus, Greece, examined by the author proved to be *danfordi*! Records from the Canarian Islands and from the Azores are undoubtedly erroneous (cf. Hartert & Ogilvie Grant, 1905; Bannerman, 1920).
Subspecific characters: Compared with *hortorum* the underparts are distinctly tinged with light yellowish brown, and — apparently in some specimens only — more broadly striped. Measurements averaging perhaps slightly shorter. The same characters I found in a series of 9 swiss birds, which was distinct from a series of 32 Dutch and 6 German birds, with which it has been directly compared. Alpine birds have been described as *jordansi* (Götz), the underside being according to Domaniewski (1927) "hellocker bis weiss, nicht so intensiv braun wie bei *hortorum*" (p. 71). Götz (1925) compared the birds from the Alps with those from Scandinavia, but regretted to find only relatively short wing lengths in the latter: wing ♂ 86—90, average (7) 87.7; ♀ 83—90, average (7) 86.9 mm! In contrast to *D. major* „*alpestris*" swiss *minor* apparently resemble more Italian than Scandinavian birds. In consequence *jordansi* has been treated here as a synonym of *buturlini*, and not of *hortorum*, as has been done by Hartert-Steinbacher (1935). They probably have derived from the Mediterranean glacial refugium. Balcan birds are said to remember *buturlini*, as do Iberian ones. Rumenian specimens can be distinguished by very slight characters only.

(**Dendrocopos minor bacmeisteri** (Kleinschmidt 1916: Tourauderie, N. France)).
This name which is based on 3 specimens only applies to intermediate populations between *buturlini* and *hortorum*. It should certainly not be used as a valid subspecific name, being even a more „feeble" race than *D. major arduennus!*
Material examined: France (10: Maine-et-Loire); Belgium (24). — (Brussels Museum, Leiden Mus.; coll. Mayaud).
Measurements:
France: wing ♂ 86—88, average (6) 88.0; ♀ 86—88, average (4) 87.0 mm.

Belgium: wing ♂ 82—91, average (18) 87.3; ♀ 85—92, average (8) 88.4 mm.
France: culmen ♂ 16.5—18, average (6) 16.9; ♀ 15—16, average (4) 15.6 mm.
Belgium: culmen ♂ 16—19, average (14) 16.8; ♀ 15.5—17, average (8) 16.3 mm.
Range: France, Belgium, S. France specimens 'ave been referred to *buturlini*.
Subspecific characters: The original diagnosis of the range is: "Zwei ♂ ♂, ein ♀ sind viel kräftiger gezeichnet als deutsche, englische, italienische und nordafrikanische Stücke, so dass also die dunkelste europäische Form vorliegt. Bei einem Stück, verdichten sich die Flecken an den Seiten zu beginnenden Querbinden" (Kleinschmidt, 1916, p. 14). I find the general striping of the undersides a little more pronounced in French specimens than in Dutch ones, but this character is by no means sufficient to warrant subspecific distinction. Belgian birds on the contrary are somewhat less heavily striped, in this respect beginning to approach British ones. French specimens, however, have a distinct light reddish brown to isabelline tinge on the underparts, especially on the upperbreast, becoming light yellowish brown in spring. As a whole they are intermediate in this respect between the more light yellowish brown *buturlini* and the more dirty greyish brown *hortorum*. This character is also to be detected in a series of Belgian specimens when compared with a series of Dutch birds. Individual specimens, however, can hardly be distinguished. By Van Hâvre (1928) and Verheyen (1941) the Belgian populations have been referred to *hortorum*. In S. France the intermediate populations gradually merge into true *buturlini*. Even specimens from Maine-et-Loire have been treated by Verheyen (1941) as *buturlini*, whereas I find specimens from the same region apparently intermediate between *buturlini* and *hortorum*. According to Mayaud (1945) two specimens from Lyonnais agree in coloration with *buturlini*, but have somewhat too large measurements for this race.

Dendrocopos minor hortorum (Brehm 1831: Renthendorf, Germany).
Material examined: Germany (10); Netherlands (59). — (Amsterdam Mus.; Brussels Mus., Leiden Mus.; coll. Hens; coll. Ten Kate; coll. Van der Meer; coll. Neijssel; coll. Sillem-Van Marle).
Measurements:
Germany: wing ♂ 86—90, average (7) 88.3; ♀ 91.5, 92, 93 mm.
Germany: culmen ♂ 15—17, average (7) 16.3; ♀ 15, 16.5, 16.5 mm.
Netherlands: wing ♂ 84—91, average (37) 88.1; ♀ 86—92, average (15) 89.4 mm.
Netherlands: culmen ♂ 15.5—18, average (37) 16.6; ♀ 15—17, average (14) 16.1 mm.
According to Niethammer (1938) wing of 19 German breeding birds 86—92 m.
Range: Netherlands, Germany, Bohemia, and W. Poland; absent in Denmark.
Subspecific characters: Ground colour of underside much more dirty greyish brown and more strongly striped than in *minor*; upperside darker and more conspicuously transversely barred; measurements smaller. Dutch specimens cannot be distinguished from German ones in spite of the contrary statement by Snouckaert van Schauburg (1908) who suggested that Dutch specimens were like the British race (cf. Hartert, 1913, p. 921). Freshly moulted specimens have a clear brownish underside, but spring birds are strongly faded and have a whitish or light greyish ground tone.

Dendrocopos minor comminutus (Hartert 1907: Tring, England).
Material examined: 4: Somersetshire; Derby. — (Leiden Mus.; coll. Hens).
Measurements:

Wing ♂ 86, 87, 88; ♀ 83 mm. Culmen ♂ 15, 16, 5, 17; ♀ 15.5 mm.
Wing according to Hartert (1907): ♂ 85.5—88.5; ♀ 86—90 mm.
Range: England and Wales, though rare in the northern and the extreme western parts. Breeding records are known as far north as Cumberland. A few records from Scotland and Ireland (Witherby, c.s., 1924). Authentical Irish specimens are not in existence (Humphreys, 1937).
Subspecific characters: Underside very dark buffy brown, clearly different from all other W. European races. Striping on the underside much reduced in size and in number and mostly developed on the sides of the breast and on the flanks.

Dendrocopos minor wagneri (Domaniewski 1927: Balta neagra, Rumenia).
Material examined: Rumenia (4: Prundu, Prov. of Muntenia). — (coll. Sillem-Van Marle).
Measurements:
Wing ♂ 89, 90; ♀ 90, 91 mm. Culmen ♂ 15, 17.5; ♀ 15, 15 mm.
According to Domaniewski (1927) wing of 9 Rumenian specimens 87—92 mm.
Range: Rumenia, whether other Balcan populations are distinct from *buturlini* is unknown to the author.
Subspecific characters: Much like *buturlini*, but ground colour perhaps somewhat more isabelline, and the striations on the flanks sharper defined, narrower, and less in number. The specimens examined are close to *buturlini*, and conspicuously distinct from *hortorum*!

Dendrocopos minor subspec.
Material examined (Brussels Mus.):
1. Molnasrasëd, Hungary, ♂ 12.VIII.1931, wing 89, culmen 17 mm.
2. Doröske, Hungary, ♀ 1.II.1932, wing 88, culmen 16 mm.

Two *Hungarian* specimens examined differ slightly from *hortorum* in being somewhat browner on the underside. It is possible that in Hungary and Slovakia transitional populations occur between *hortorum* and *buturlini* and probably between the typical *minor* (*kamtschatkensis*)-populations. Domaniewski (1927) has referred birds from Slovakia and the Tatra Mts. to "*jordansi*", which I think to be synonymous with *buturlini*.

Dendrocopos minor colchicus (Buturlin 1908: N. Caucasus).
Synonyms:
Dryobates minor harterti Domaniewski 1927: Tiflis, Transcaucasia.
Dryobates minor ernsti Domaniewski 1927: new name for *harterti* (1927), which is preoccupied.
Material examined: 2: Mouth of Ashej River, coast of Black Sea, W. Caucasus; Tiflis, Transcaucasus. — (coll. Meinertzhagen).
Measurements:
Wing ♂ 89.5: ♀ 88 mm. Culmen ♂ 16; ♀ 15.5 mm.
Range: Caucasia and Transcaucasia; absent in Crimea (Pusanov, 1933).
Subspecific characters: Intermediate between *buturlini* and *danfordi*. The two specimens examined have the flanks and the anal region distinctly cross barred like *danfordi*, but they agree with *buturlini* in the absence of a complete post-auricular black band. The general colour of the underparts is just intermediate between 2 specimens from Cremona (N. Italy: *buturlini*) and Athens (Greece: *danfori*) before me.

Dendrocopos minor ledouci (Malherbe 1855: Algeria).
Material examined: 2: Algeria. — (coll. Meinertzhagen).
Measurements: Wing ♀ 88, culmen ♂ 19, ♀ 19 mm.
Wing according to Domaniewski (1927): 88—93 mm.

Range: Tunis, Algeria; apparently not yet found in Morocco (cf. Hartert & Jourdain, 1923).
Biotope: Oak forests, especially those of *Quercus suber*. The species is not easily to detect and still more hard to obtain. In Algeria Charrière (1913) mentions it to be 'moins exclusivement arboricole que les autres Picidés, on voit souvent l'Epeichette à terre cherchant les insectes ou leurs larves dans la terre et la mousse ou saccageant les fourmilières" (p. 178).
Subspecific characters: Much like *buturlini*, but differing in having broader cross bars on the upperside; besides, the black coloration is more intensively black than in *buturlini*.

Dendrocopos minor danfordi (Hargitt 1883: Taurus, Asia Minor).
Material examined: 2: Mt. Parnasse; Mt. Olympus, Greece. — (Leiden Mus.; coll. Sillem-Van Marle).
Measurements: Wing ♂ 83, 86; culmen ♂ 15, 16 mm. Wing of 14 specimens according to Hartert (1913): 84.5—88 mm.
Range: Asia Minor, E. Balcans. The exact range in S.E. Europe is not known. Apart from specimens from Constantinople, Bulgaria, Macedonia, and Greece, Stresemann (1920) has referred to this race even those from Rumenia (Dobrudscha), whereas those from Hercegowina are said to show tendencies to *danfordi*. However, Rumenian specimens examined by me certainly do not belong to this group of races, and Gengler (1920) even states: „Der Zwergspecht vom Balcan gehört zweifellos zur Form *buturlini*" (p. 142). Special remarks have been given in the '*History of D. minor*" (see above).
Subspecific characters: Like *buturlini*, but differing in having a closed postauricular band connecting the black of the malar stripe with the black of the hindneck. Underparts somewhat darker reddish brown, and heavily longitudinally striped; flanks and crissum with distinct transversely cross bars.

Owing to lack of material the following described races will be mentioned only; they are discussed in Hartert (1913 & 1921) and in Hartert-Steinbacher (1935):
1. *D. m. hyrcanus* (Sarudny & Bilkewitsch 1933: Astrabad, N. Persia).
2. *D. m. quadrifasciatus* (Radde 1884: Talysh, Lenkoran).
3. *D. m. morgani* (Sarudny & Loudon 1904: Schalil River, S.W. Persia): very rare, not found by Witherby (1903) and Paludan (1938).

XI DWARF WOODPECKERS.

A. *Asiatic Dwarf Woodpeckers.*

1. INTRODUCTION.

It is a noteworthy fact that on the eastern and southern borders of the range of the genus *Dendrocopos* in Asia species occur of small dimensions and with brownish or even greenish coloured dark parts, where in typical species black is predominant: Japanese Islands and Manchuria (*kizuki*), S. Malacca, Sunda Islands (*moluccensis*), Peninsular India, S. Burma (*nanus*), Philippine Islands (*maculatus*), Sulu Islands (*ramsayi*), Celebes (*temmincki*). Though inhabiting quite remote regions *kizuki*, *moluccensis*, *nanus*, and *maculatus* have many characters in common, of which the small size, the strong transversely barring of the upper parts and the small red patch on the sides of the hind crown in the male are at once apparent. The resemblance has led to the uniting of at least *kizuki*, *moluccensis*, and *maculatus* to one species by various authors (*Hachisuka*, 1934; Peters,1939). After having established the peculiar distribution and the taxonomic similarity it does not seem to be premature to suppose that all mentioned forms have arisen from a main stock and have been pushed back from the continent either by competition with other species or by various unknown causes, and have been isolated on the islands which surround the continent: Japan, Philippines, Sulu Islands, Celebes, Sunda Islands, Gondwana Island. Judged from the remarkable resemblance of some Philippine forms (*validirostris, maculatus*) with those from the Sunda Islands, it is possible that the isolation in these different island groups is of approximately the same — quite recent — age, dating back at all events not earlier than to pleistocene times. As *moluccensis* is found at the moment to occur in S. Malacca, Sumatra, Borneo, Java, and Lesser Sunda Islands, one may suppose that it has spread over the whole accessible Sunda area during the pleistocene period of the geographic coherence of the Sunda-land, which after the postglacial rising of the sea-level is now crumbled into separate islands. *Kizuki* shows more resemblances with the S. Asiatic and Sundanese forms than with either *minor* and *canicapillus* with which it occurs side by side in the Manchurian region, thus, showing that its date of isolation is more remote than late pleistocene: it must be isolated either before or at the beginning of the pleistocene period. *Nanus* almost wholly agrees with the southern races of *canicapillus*, and with *moluccensis*, so it is safe to suppose that the beginning of its isolation is not of a very remote time. Perhaps the isolation started during one of the glacial (here pluvial) epochs during which the N. Indian plains formed a continuation of the old Middle Sea (*Tethys*), going as far east as to the Gulf of Assam. As is also the case in *mahrattensis*, *nanus* has spread in postglacial times in N. and N.E. direction, but probably owing to competition with the still much alike forms of *canicapillus* it has not gone as far east as *mahrattensis*, which even occurs in Indo China.

As to nomenclature I think it — as in many cases — a question of personal appreciation whether *kizuki, maculatus, moluccensis*, and *nanus* should be united into one species (*moluccensis*), as Peters (*in litt.*, 1946) wants to do in the 6th volume of his Checklist, or should be kept separate. As the question refers to island forms which apparently have arisen independently from the continental stock, I am inclined to take the last mentioned solution. Even Delacour (1946) in his revolutionary proceeding of lumping species and genera keeps the Philippine forms as a distinct species (*maculatus*), whereas all other Malaysian brown-headed Pigmy Woodpeckers are united within the species *moluccensis*. All forms mentioned may be united in a *superspecies*.

The distribution of Pigmy species of E. Asiatic *Dendrocopos* on the outskirts of the range of the genus, more or less has a parallel in the distribution of the Negroid human populations (*Negritos*): Tonkin, Indo China, Malacca, Pegu, Megui Archipelago, Andamans, Naga Hills, Philippines, Palawan Island, (?) Sulu Islands, Ceylon. Nippold (1936) describes the history of these races as follows: "Unter dem Drucke zahlreicher Völkerverschiebungen wurden die Negritos von stärkeren Völkern und Rassen auseinandergesprengt. Der Zusammenhang ging verloren und die versprengten Reste wurden mehr und mehr in die abgelegensten Rand- und Rückzugsgebiete des Asiatischen Lebensraumes, wo allein sie heute noch nachweisbar sind, hineingedrängt" (p. 139). Thus, in the distribution of the Philippine Negritos the results of successive human invasions are clearly visible; the same phenomenon can be traced back in the history of the Woodpeckers.

XXVIII **Dendrocopos kizuki** (Temminck 1836. Japan).

Material examined: 15; only few with exact locality: mouth of Suiffun River (Sidemi; Vladivostok), S. Ussuria (6); Mt. Fuji, Hondo (1); all others "Japan" (8). — (Copenhagen Mus.; Leiden Mus.; coll. Meinertzhagen; coll. Sillem-Van Marle).

Range: Japanese Islands, from Sakhalin (breeding: Lönnberg, 1908) and the southern two Kurile Islands (Kunashiri, Yeterofu: Bergmann, 1931) to the southern islands of the Riu Kiu chain (Iriomotejima, Yayeyama Islands: cf. Kuroda, 1925), including: Hokkaido, Hondo, Shikoku, Kiushu; Seven Islands of Izu (Mijakeshima: Kuroda, 1921; Hachijojima, O-Shima: Kuroda, 1927); Tsushima, Quelpart Island; Yakushima, Amami Oshima, Tokunoshima, Okinawajima, Jagachishima, Iriomoteshima. Also S. Ussuria, Corea, and the Eastern Tombs near Pekin, Chihli (Kuroda, 1926; *fide* Hartert-Steinbacher, 1935).

Specific characters; History; Biotope: The species is closely allied to *maculatus* and *moluccensis*, but differs taxonomically in having the upper tailcoverts and central rectrices uniform black. With the exception of Sakhalin and Hokkaido *kizuki* is the only Smaller Woodpecker found within the Japanese boundaries. It is apparently an offspring of the E. Asiatic Lesser Pied Woodpeckers of which at present *canicapillus* and *minor* stand closest to the original stock. From the Japanese Islands it has returned to the Manchurian region, like *minor*, who has come back into Manchuria from the western part of Eurasia. Insular and climatic conditions have induced a relatively small size and a dark appearance in most members of the group. In agreement with the zoogeographic rules of Bergmann and Gloger, there is a general tendency in the species to become larger, greyer, and whiter in northern direction, and smaller, browner, and darker in southern direction. S. Riu Kiu specimens, and also those from Tsushima (*kotataki*), are said to have blackish, not brownish dark parts! On the gradual development of these characters a great number of mostly very doubtfully distinguishable island races have been described, mainly by Japanese authors. Even in the Riu Kiu Islands the northern representatives are larger than the southern ones. The following wing measurements are borrowed from Kuroda (1925):
Yakushima: ♂ 80, 80.5, 83; ♀ 79, 81.5, 82.5, 82.5 mm.
Amami Oshima: ♂ 81, 82, 83; ♀ 84.5 mm.
Okinawajima: ♂ 76, 76.5, 77, 78; ♀ 79, 79 mm.
Iriomotejima: ♀ 78.5, 79 mm.

Within the species *kizuki* a division can be made into two groups (1) one comprizing light grey-headed birds with light brown markings along the sides of the head and occiput, in addition with a continuous white eye stripe, running to the white patch on the sides of the neck; (2) uniting those birds with a brown crown bordered with dark brown, and with the eye stripe short and separated by a dark band from the white patches on the sides of the neck. To the first group the continental subspecies belong (perhaps except Corean forms!) as also those from Hokkaido and the Kuriles. These are large birds with a light grey general appearance and with much white in the plumage. I found the following wing measurements in S. Ussurian birds: ♂ 87, 89, 89; ♀ 90, 91, 92 mm. It is probable that the group has an historical, and not an exclusive climatic origin: it may be interpreted to have lived in the last glacial Manchurian-Hokkaido refugium together with *Garrulus glandarius bambergi* group, whence it has spread into the S. Kuriles, which are said to have even more lighter greyish and whiter inhabitants (Bergmann, 1931). It is thought to have split from the second group, which even may have had a preglacial range in Japan (see below!). As in the case of *D.major*, and *D. leucotos*, as also in *Garrulus glandarius*, series of *kizuki*, originating from S. Manchuria and Hokkaido, appear to be hardly distinct. Two Japanese birds, without exact locality ("Japan") examined by me, apparently originate from Hokkaido; I cannot separate these from the S. Manchurian birds (wing ♂ 87, ♀ 90 mm). Therefore, as also judging from the literature records, the name *permutatus* (Meise 1934: Sidemi) seems to be a synonym of *seebohmi*, just like *G. glandarius pallidifrons* (Kuroda 1927: Hokkaido) has considered by me to be a synonym of *bambergi* (Lönnberg 1909: Transbaicalia) (Voous, 1945). Specimens from the second group are darker, and more strongly barred and banded on the underparts. One specimen from Mt. Fuji, C. Hondo, examined, even resembles Burmese specimens of *D. canicapillus* in general appearance!

Kizuki is a fairly well pronounced ubiquist inhabiting all kinds of biotope either in the mountains and in the lowlands, and taking possession even of the smallest islands in the Japanese range. Therefore it is not justified to conclude from its occurrence even in the S. Riu Kiu Islands that it is a tertiary inhabitant from Japan, as is the case in *D. leucotos*. The rare occurrence (Iriomotejima, southernmost Riu Kiu: "very rare", only 2 specimens known: Kuroda, 1925) of the clearly distinct Riu Kiu races, as well as the interrelation with *D. canicapillus*, and *D. minor*, and the taxonomic resemblance with *D. maculatus*, and *D. moluccensis* make this conclusion, however, apparent.

Jahn (1942) gives a very striking description of the biotope of *D. kizuki* in Japan: "Zwischen Meeresniveau und der Waldgrenze in den Hochgebirgen findet er sich in gleicher Anzahl in reinen immergrünen (Südshikoku) oder sommergrünen (Nordhondo, Hokkaido) Laubwäldern, den lichten *Pinus densiflora*-Wäldern Westjapans, dunklen Kryptomerien- Tempelwäldern sowie der subalpinen *Abies-Tsuga-Betula*-Zone der höheren Gebirgslagen" (p. 218).

The following races have been described:

D.k. ijimae (Taka-Tsukasa 1922: Sakhalin).
D.k. kurodae (Bergmann 1931: Yeterofu, S. Kurile Islands).
D.k. kurilensis (Bergmann 1931: Kunashiri, S. Kurile Islands).
D.k. seebohmi (Hargitt 1884: *"in insulis Niphon et Yezo dictis"*; restricted to Hokkaido; cf. Hartert-Steinbacher, 1935; Meise (1934) restricts the type locality to Yokohama!).
D.k. toohukuensis (Kumagai 1928: Miyagi, N.E. Hondo).
D.k. nippon (Kuroda 1922: Prov. of Suruga, Central Hondo).
D.k. shikokuensis (Kuroda 1922: Prov. of Iyo, Shikoku).
D.k. kizuki (Temminck 1836: Japan: restricted to Kiushu).
D.k. matsudairai (Kuroda 1921: Mijakeshima, Seven Islands of Izu).
D.k. kotataki (Kuroda 1922: Tsushima).
D.k. saisiuensis (Momiyama 1926: Quelpart Island).
D.k. harterti (Kuroda 1923: Yakushima).
D.k. petersi (Kuroda 1929: new name for *harterti*, which is preoccupied by *D. major harterti* Arrigoni 1902).
D.k. amamii (Kuroda 1922: Amami Oshima).
D.k. nigrescens (Seebohm 1887: Okinawajima).
D.k. orii (Kuroda 1923: Iriomotejima).
D.k. permutatus (Meise 1934: Sidemi, S. Ussuria).
D.k. siragiensis (Momiyama 1927: Koryo, Central Corea).
D.k. acutirostris (Yamashima 1931: Kongosan, Kogendo, E. Corea).
D.k. wilderi (Kuroda 1926: Pekin, Chihli).

XXIX **Dendrocopos moluccensis** (Gmelin 1788: Malacca; cf. Oberholser, 1919; *contra Riley, 1927*).

Material examined: Malacca (3); Sumatra (57); Banka (1); Billiton (6); Borneo (11); Java (38); Lombok (2); Soembawa (2); Flores (6); Alor (1). — (Amsterdam Mus.; Basel Mus.; Brussels Mus.; Buitenzorg Mus.; Leiden Mus.; coll. Van Dedem; coll. Van Heurn).

Measurements:
Malacca: wing ♂ 79; ♀ 72, 73 mm.

Sumatra: wing ♂ 73—79, average (30) 76.0; ♀ 70—80, average (27) 76.6 mm.
Banka: wing ♂ 72 mm.
Billiton: wing ♂ 76; ♀ 75, 77, 77, 77, 79 mm.
Borneo: wing ♂ 71—77, average (7) 72.2; ♀ 70—74, average (4) 72.0 mm.
Java: wing ♂ 73—77, average (16) 74.0; ♀ 72—81, average (21) 76.2 mm.
From the above measurements it appears that Bornean birds average slightly smaller than those from Sumatra and Java, but I agree with Chasen & Kloss (1933) that this difference does not justify the distinction of the race *tantalus* Riley (1927: Tanggaroeng, Mahakkam River, E. Borneo; wing of type adult ♂ 69.5 mm).
An instructive case of increase of size is found in those populations of *moluccensis* inhabiting the Lesser Sunda Islands. Rensch (1931 A, 1931 B) repeatedly has called attention to the fact that Lesser Sundanese bird populations incline to become larger in eastern direction, which according to Rensch is correlated with the increasing relative coolness and dryness of the climate in the same direction, thus, furnishing a splendid example in support of the zoogeographic rule of Bergmann. The following wing measurements are combined from measurements given by Rensch (1931 B, 1931 C, 1929) and from personal examination.
Java: 72—78 (once 81), average (28) 76.1 m.
Lombok: 84—85, average (3) 84.3 mm.
Sumbawa: 84—86, average (6) 85.2 mm.
Flores: 84—89, average (10) 86.0 mm.
Alor: 89—91, average (2) 90 mm.
From these it appears justified to recognize 3 races: one inhabiting the Greater Sunda Islands (*moluccensis*), one inhabiting the Leser Sunda Islands from Lombok to Sumbawa and Flores Islands (*grandis* (Hargitt 1882: Lombok)) and one inhabiting Alor and Lomblen Islands (*excelsior* (Hartert 1898: Alor)).
Range: Malay Peninsula S. of Penang, including Sauh in the Rhio Archipelago (Siebers, 1926; Robinson, 1927), Sumatra, Banka, Billiton (Chasen, 1937 A), Borneo, Labuan Island (Blasius, 1901), and Balambangan Island, 21 km (13 miles) to the north of N. Borneo (Chasen & Kloss, 1930), Java, Krakatau, Verlaten, and Sebesi Islands in the Sunda Strait (shortly after closing the manuscript 7 specimens could be examined from the islands of the Krakatau group from the collection of the Buitenzorg Museum), Onrust Island, and Poeloe Sakit (Bartels, 1908) in the Bay of Batavia, Madura, Bali (?: its occurrence needs confirmation!), Lombok, Soembawa, Flores, Alor Islands. It is not known from the W. Sumatran Islands, as also from the Karimata Islands, where no Woodpeckers have been collected (Chasen & Kloss, 1933).

Although it is of course not proved that the species is a breeding bird from every above mentioned locality, it nevertheless is apparent that the range is in a period of a rapid increase, the species even taking possession of the little islands of the Krakatau group in the Sunda Strait, about 32 km off the W. coast of Java, which were totally depopulated by the eruption in the year 1883. On Sebesi Island, more to the S. point off Sumatra the species was not found by Jacobson in 1908, but it was present there in 1921. After the eruption no other Woodpecker has been found in the Krakatau group (Bartels & Siebers, 1922). So the sea does not seem to have been an important barrier in the course of the dispersal of this little Woodpecker.
Specific characters: The specific status of the *brownheaded* Pigmy Woodpeckers is much clearer in Malacca, than in India. Especially in the S. part of the Peninsula the *grey-headed D. canicapillus auritus* (Eyton) is an unusual bird,

being apparently greatly outnumbered by *D. moluccensis*, with which it has been observed even in the same trees (Robinson, 1927). Nevertheless, in these regions *moluccensis* is still more a bird of the lowlands and the mangrove forests than *canicapillus*, which prefers the forests in the hills and in the mountains. The Sumatran race of *canicapillus* (*volzi*) is known only from the highlands of Atjeh, where it has been collected by Hoogerwerf at 1000 m altitude (Atang Poetar: Chasen, 1941), whereas the Vanderbilt Expedition collected specimens at about 1050, 2400, and 2800 m: Blangnanga; Mt. Leuser (De Schauensee & Ripley, 1939). From the same region only one specimen of *moluccensis* is known, collected by Hoogerwerf (l.c.). However, the specimen was not shot in the Terpentine forests where *canicapillus* usually was found, but in the gardens employed by the natives. From these remarks the ecological divergency between the brown-headed *moluccensis* and the grey-headed *canicapillus* in Sumatra is apparent. In Borneo *moluccensis* has been recorded from all parts, whereas *canicapillus aurantiiventris* (Salvadori) is known only from the W. half of the island (Sarawak; Marabok River; Melawi River; Riam). No information regarding the biotope of *canicapillus* in that region is known to the author.

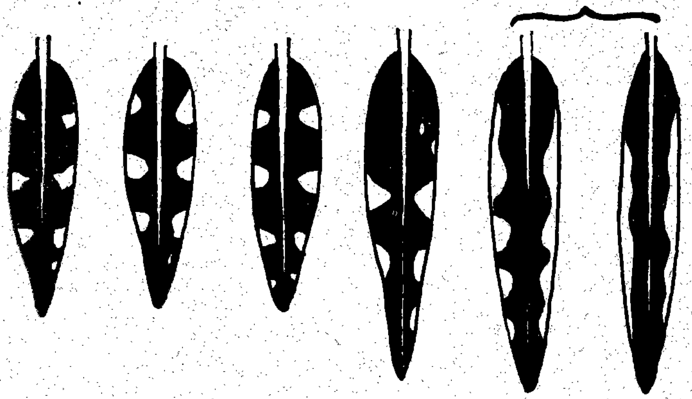

Fig. 27. *D. moluccensis* (Gm.) — Central rectrices to show different pattern of Lesser Sundanese birds: from left to right: Palembang, Sumatra; Pontianak, Borneo; Buitenzorg, Java; Maumeri, Flores; Reo, Flores (left and right feathers, to show different pattern in one bird!).

It is not without hesitation that I have not included *nanus* into *D. moluccensis*, since the taxonomic differences between these brownheaded Woodpeckers appear to be very slight (see under „*nanus*"), and since Peters wrote me (*in litt.*, 1946) that he was planning to treat *moluccensis* and *nanus* as conspecific. However, as I do not understand the specific proportion of *nanus* and *canicapillus* in Bengal, whereas the specific and ecological differences between *moluccensis* and *canicapillus* in Malacca and Sumatra are very clear, I did not like it to unite these brown-headed forms within one species. Nevertheless, I do not deny their probable close relationship, which, however, is not apparent to me in the ranges of the respective species compared with the range of *canicapillus*. Therefore I have kept them apart, but I will be among the first to follow anyone in considering *moluccensis* and *nanus* to be subspecies of one species, who can prove that *moluccensis* and *nanus* arose simultaneously from the grey-headed *canicapillus*. As this appears to be equally not the case with reference to *maculatus* and *moluccensis*, I have also kept *maculatus* apart.

Subspecific characters: The species is very constant in taxonomic characters. Local distinguishing characters only refer to the differences in measurements mentioned above, and the increase of white on the central rectrices in the Lesser Sunda Island specimens. Here the individual white spots on both webs are confluent, forming a continuous undulating white margin to both webs of the feather (fig. 27).The origin of these white margins from the typical spots is clearly demonstrated in a female specimen from Reo, Flores Island (Leiden Mus.) in which not only the left and right middle tailfeathers show a different pattern, but even both webs of one (left) feather are different.

History: The preference of this species to mangrove forests makes it easily to spread over a great number of small islands in the archipelago which have been enumerated above. In Durian Island, Rhio-Lingga archipelago, which is situated about 60 km from Singapore, and 35 km from the E. coast of Sumatra a specimen has been collected by Siebers (1926), which "even was busy making a hole in a pile put in the sea near the kampong Jora" (p. 307). Nevertheless, its occurrence in the Lesser Sunda Islands, east of the line of Wallace is remarkable, since, with the exception of Bali, these islands do not appear to have been connected with Java in recent geologic times. Even during the relative low sealevel in the pleistocene the Lombok Strait appears to have been too deep to realize a land connection between the islands Bali and Lombok. As in the 20th century the species has never been collected in Bali, and taxonomic differences are found in the Lesser Sundaic populations only, it is likely that they have penetrated into the Lesser Sundaic chain before the last glacial period, flying from one island to the other.

Biotope: *D. moluccensis* is a lowland species, occurring mostly in coastal mangroves, *Casuarina*- and secondary forests, and in cultivated areas; in old virgin forests it has been found along the margins only. The species is common in the very tall trees (a.o. *Pithecolobium*) in native villages, where it is not easily observed. On Mt. Papandajan (W. Java) the species apparently is absent, whereas the other species of *Dendrocopos* (*analis*) is quite common there (Stresemann, 1930); on Mt. Pangerango, however, it is found up to 850 m altitude (Bartels, 1906), and on Mt. Tjibodas it has been collected even up to 1200 m (Robinson, 1927). In Flores the species appears to be a ubiquist, occurring from 0—2299 m. Its behaviour is that of a true little Woodpecker, hammering actively and rather loudly during the whole day (Coomans de Ruiter, 1932), its cry being the typical high-pitched and rapidly uttered kee-kee-kee-kee-kee (Bernstein, 1861).

1. PHILIPPINE FORMS.

Probably the Philippine Islands have not been originally a part of the continent; on the contrary, they appear to be " a series of eruptive dikes and bodies of various dimensions, which have risen from the depths along the line of contact between the floor of the China Sea and the bottom of the Pacific Ocean " (Willis, 1937). They were formed through large tectonic movements by indigeneous masses at the border of the two continents. Therefore the Philippine fauna has been derived wholly from these continents, thus, showing in its recent composition the representatives of both the Asiatic and the Australian faunae. So the endemic Philippine races of *Dendrocopos* must be considered to be the remnants of more than one faunal invasion coming from the Asiatic mainland. As the Philippines are situated at the borders of a densely populated continent it has not only been subject to successive invasions, but the archipelago furnished also refugional habitats either to men and to animals against migratory movements of stronger populations. The extensive distribution of *Negrito elements* in the human populations inhabiting the Philippines forms a parallel with the general distribution of the Dwarf Woodpeckers in these islands, both finding here a refugional habitat far away from their center of distribution. Pure Negritos are only very locally distributed in the Archipelago, being found only in remote regions of the islands Luzon. Polillo, Tablas, Sibuyan, Panay, Negros, and Mindanao. They may belong to the oldest human populations in the Philippines (Nippold, 1936). Remnants of the oldest *Dendrocopos* invasions in the Philippines are found in the species *ramsayi* (Sulu Islands) and *temmincki* (Celebes). Compared with the generally strongly barred Philippine races these species are so differently coloured, that it is not difficult to come to the conclusion — which may be correct too — that they have been isolated on separate islands long before the pleistocene invasion and successive isolation of the Philippine *maculatus*. In the Philippines these species have become extinct either before the last invasion, or they have been substituted through competition by the newly arrived forms, leaving only a remnant population in the Sulu Islands as an evidence showing the way along which this first invasion has reached Celebes. By the peculiar Celebesian isolation *temmincki* has been altered in such a way, that at the moment it even possesses a partly olive-greenish coloration, thus making its generic separation from *Dendrocopos* to some extent desirable. The pleistocene invasion of forms which more or less resemble *moluccensis* has not penetrated farther than to Basilan. It is a noteworthy fact, however, that the subspecies formation in the Archipelago clearly demonstrates the fact that the firstly arrived populations which have penetrated farthest, have become changed much more strongly than the most recent arrivals of the invasion. Thus, the race inhabiting the islands Mindoro and Basilan (*fulvifasciatus*) which in the Archipelago are most distally situated with respect to the Asiatic mainland, differ much more conspicuously from *moluccensis* than the race *maculatus*, which inhabits Luzon, Marinduque, and Mindoro. The gradual changes in the subspecific characters of the Philippine races of *D. maculatus* can be summarized as follows (Table 1).

TABLE 1

	general colour of upper parts	*barring on mantle and back*	*barring on rump*	*red stripes on sides of occiput in males*
1. Luzon, Lubang, Mindoro, Marinduque, Catanduanes: *validirostris*	blackish brown	very strongly	faintly	very narrow
2. Panay, Guimaras, Negros, Cebu: *maculatus*	olive brown	very strongly	faintly	broader
3. Samar, Leyte, Bohol: *leytensis*	fulvous brown	less strongly	almost absent	as above
4. Mindanao, Basilan: *fulvifasciatus*	fulvous brown	less strongly	almost absent	very broad, almost uniting on the medium hind neck

The form *menagei*, however, inhabiting Sibuyan Island (fig. 28), differs much more strongly from the above mentioned races of *maculatus* than should be expected from the situation of its range, which is surrounded by at least 3 races of *maculatus*, and directly south of that of *validirostris*. Not only are the red stripes on the sides of the occiput in the male uniting on the nape, thus, forming a confluent red patch, but the birds are much less barred than even *fulvifasciatus*, and have a more dark olive brown tinge. The dark eye stripe, which is characteristic for the whole superspecies and which is hardly subject to subspecific differentiations is very broad, almost totally obscuring the side of the head, leaving only a white lore-patch, and a small white patch above and behind the eye. In fact, *menagei* shows some morphological approaches to *ramsayi*. *Menagei* is considered by the author to be a less modified member with a more proximal habitat than *ramsayi* and *temmincki*, having been derived from the same old inhabitants of the Philippines. The consideration that *menagei* should represent an older faunistic element than the other Philippine forms of Pigmy Woodpecker has led the author to recognize it as a *distinct species* and not as a subspecies of *maculatus* as up to now has been done in the literature. The geographic situation of Sibuyan Island rising above in the middle of one of the 3 important sea-basins within the range of the Philippine Archipelago, and separated by depths ranging between 1000 and 1500 m from the neighbouring islands where races of *maculatus* occur, is in close confirmation with this hypothesis. Tablas Island, which is also situated in the Sibuyan Basin, in wich no form of *Dendrocopos* occurs, is according to Smith (1925) covered almost exclusively with miocene sediments, whereas Sibuyan Island is constituted of plutonic, metamorphic, and volcanic rocks. The Sibuyan Basin "has been the scene of vigorous volcanic activity during the pleistocene and recent ages and its configuration has been greatly modified thereby" (Smith, 1925, p. 46). Thus, it seems, most probable that Sibuyan Island, owing to its isolated geographic situation and to the fact that it is now surrounded by a deep sea, after having been populated by the firstly arrived forms of *Dendrocopos*, could not be reached by the second invasion, thus, furnishing a refugium for a member of an older fauna (fig. 28). I may add that in Sibuyan and Tablas Islands pure *Negrito* populations occur, whereas in the surrounding islands (Luzon, Mindoro, Panay) these are more or less strongly intermingled with the elements of other human races (Nippold 1936).

Fig. 28. *Pigmy Woodpeckers* Invasion into the Philippine Islands (indicated by the arrows). The lines indicate the areas of distinct island races. A. Remnants of the first invasion: 1 *ramsayi*, 2 *menagei*. B. Second invasion (*D. maculatus*): 3 *fulvifasciatus*, 4 *maculatus*, 5 *leytensis*, 6 *validirostris*. There is a general decrease of barring and increase of red on the head of the male in the direction of the arrows.

It thus seems that the following species and subspecies inhabiting the Philippine Islands can be recognized (cf. Hachisuka, 1934)!

XXX **Dendrocopos menagei** (Bourns & Worcester 1894: Sibuyan).

Material examined: (coll. Sillem-Van Marle): Sibuyan (Worcester & Bourns coll.) 7.X.1892, ♂, wing 79.5; culmen: broken.

XXI **Dendrocopos maculatus** (Scopoli).

Dendrocopos maculatus validirostris (Blyth 1849: Luzon).

Material examined: (Leiden Mus.; coll. Sillem-Van Marle):

Baguio, Luzon (Mearns coll.) 15.VII.1907, ♂, wing 84; culmen 19 mm.

Bay, Luzon (Everett coll.): 15.I.1895, ♀, wing 82; culmen 17 mm.

Mindoro (Everett coll.): 2.XII.1894, ♂, wing 79; culmen 17 mm.

Dendrocopos maculatus maculatus (Scopoli 1786: Panay).

Material examined: none.

Dendrocopos maculatus leytensis (Steere 1890: Leyte).

Material examined: none.

Dendrocopos maculatus fulvifasciatus (Hargitt 1881: Basilan).

Material examined: (Leiden Mus.; coll. Sillem-Van Marle):

Basilan (Worcestor & Bourns coll.): 22.VIII.1891, ♂, wing 84; culmen 19.5 mm.

Davao, Mindanao (Platen coll.): 17.IV.1889, ♂, wing 84; culmen 17.5 mm.

Davao, Mindanao (Platen coll.): 15.V.1898, ♀, wing 85.5; culmen 19.5 mm.

Dendrocopos maculatus apo (Hachisuka 1934: Mt. Apo, S.E. Mindanao).

Material examined: none.

XXXII **Dendrocopos ramsayi** (Hargitt 1881: N.E. Borneo, but apparently Sulu Islands (corrected in Cat. Birds Brit. Mus. 18, 1890, p. 335)).

Material examined: (Leiden Mus.):

Lapac Island (Everett coll.): 3.II.1892, ♂, wing 87; culmen 19.5 mm.

Siassi Island (Everett coll.): 5.II.1895, ♀, wing 90; culmen 19.5 mm

Range: Bongo, Jolo (Sulu), Tawi Tawi (including Tataan and Popohag Islands, Friedmann, *in litt.*, 1946), Siassi and Lapac Islands in the Sulu Archipelago.

Subspecific examination: Mearns (1909) has described a ♂ and a ♀ from Siassi Island as a separate race (*siasiensis*) on account of having (1) less white on the uppersurface of the wingfeathers, (2) a smaller bill, and (3) a more restricted golden yellow coloration on the chest. With the exception of the Leiden specimen apparently only the type specimens of this race are known to exist in collections (not present in the U. S. National Museum, Washington, Friedmann, *in litt.*, 1946; *contra* Hachisuka, 1934). After comparison of the Leiden specimens with the coloured plates of the ♂ and ♀ of *ramsayi* in Proc. Zool. Soc. London 1885, pl. 17, and with Hachisuka (1934), pl. 36, I have not been able to find that the bird from Siassi has less white on the wing than the figured *ramsayi*; the ♂ from Lapac Island, which is very near Siassi Island, has slightly less white on the inner tertials than the Siassi ♀. As regards the length of the bill I find that in the Siassi bird this is a trifle longer than in the specimen from Lapac Island, but Hachisuka (1934), who accepts the race *siasiensis* gives the following measurements, which are in conspicuous contradiction to his description of *siasiensis*, which he litterally quotes from Mearns (1909) without recording the origin:

ramsayi: culmen (from base): ♂ 20; ♀ 18 mm.

siasiensis: culmen: ♂ 19.5; ♀ 20.2 mm.

Finally I cannot find that the bright yellow coloration on the chest in the birds examined is narrower than in the birds figured in pl. 17 mentioned above. Thus,

Yungipicus siasiensis Mearns seems to be only very doubtfully distinguishable from typical *ramsayi*, from which it is considered here to be a synonym.
History: This species belongs to the oldest invasion element of Dwarf Woodpeckers within the Philippine range, from which also *temmincki* from Celebes has derived (fig. 28). Like this species the white barring of the uppersurface and the white spotting of the wingcoverts has been reduced to such extent, that only the dark brown upper tailcoverts are faintly spotted with white, whereas the white blotches on the wing quills are only very small both in size and in number. It thus appears that the barring is much more reduced, than in the still more aberrant *temmincki*, whereas the other philippine representatives are strongly barred, resembling the *moluccensis* group. A dark brown eye stripe is present as in all original members of *Dendrocopos*. *D. ramsayi* has a plain olive or sandy brown appearance, with a small white median dorsal stripe, and apparently stands quite isolated when compared with the typical Philippine birds. It belongs to the oldest members of the genus, inhabiting a very remote and isolated part of a during the whole tertiary and quarternary period strongly moving and highly volcanic part of the Indian Archipelago, situated on the limits of the range of the genus.

XXXIII **Dendrocopos temmincki** (Malherbe 1849: N. Celebes).

Material examined: Minahasa (16); Gorontalo (2); Macassar (7). — (Basel Mus.; Leiden Mus.; coll. Van Marle-Coomans de Ruiter).
Measurements: No other differences between N. and S. populations appear to exist than the fact that in the S. peninsula very large females occur, whereas the measurements of the S. males fully agree with those of the N.
Wing: N. ♂ 72—79, average (9) 76.7; ♀ 75—80, average (8) 77.0 mm.
S. ♂ 74—78, average (4) 76.2; ♀ 76—84, average (3) 79.0 mm.
According to Stresemann (1940):
Wing: N. ♂ 75—79, average (7) 77.0; ♀ —, average (3) 78.0 mm.
S. ♂ 75—81, average (8) 78.8; ♀ 79—85, average (10) 82.0 mm.
Culmen: N. ♂ ♀ 14—18, average (17) 16.4 mm.
S. ♂ ♀ 14—19, average (7) 16.7 mm.
Range: Celebes.
Subspecific examination: Differences in the general tinge of the plumage are apparent in the series; they are due to seasonal fading and staining from the bark of the trees, and are of no importance for subspecific distinction: in freshly moulted plumage (Aug. 10; Sept. 28; coll. Van Marle-Coomans de Ruiter) the birds have a fresh olive tinge on upper and underparts; in worn plumage, however, a rufous brown tone becomes conspicuous especially on the breast and on the tailfeathers, but also on the rump and on the wing quills, which may be caused by close contact with the bark of the trees, or the walls of the frequently used narrow sleeping holes (May; June; even August 17). According to observations made by Coomans de Ruiter the iris in adult birds is red, but in a juvenile male it was light brown (August 8).
Specific characters and history: Several characters demonstrate the close historic relationship, between *temmincki* and *ramsayi*: light (in some cases almost white) rump, which is not banded; very broad black eye stripe; wholly red nape in male; predominancy of brownish (olive) and not of blackish coloration. Nevertheless, *temmincki* belongs to the most aberrant species of the genus: although the general colour pattern, the transversely banding of the upperside, and the white blotches of the wings are present, all black parts are substituted by greenish colorations, even the back being banded with white and olive. In

few species of *Dendrocopos* the underparts are so profusely procured with melanine (broad brownish and greenish striations) than in this species. If Bates (1936) is correct in considering colours to be "a better ground for separation than colour patterns" in Woodpeckers, then *temmincki* should surely be put in a separate genus, for the genus *Dendrocopos* is characterized by a black or blackish coloration with various white markings, the Ethiopian genera *Dendropicos* and *Mesopicos* having been mainly separated from *Dendrocopos* on account of a greenish or golden green general coloration. In considering, however, the history of the present species, which is the outermost member of the much reduced chain of populations — to which also *ramsayi* and *menagei* belong — originating from the first invasion into the Philippine regions (fig. 28), it appears justified to maintain its presence within the genus *Dendrocopos*.

Biotope:

In its characters *temmincki* proves to be a true *Dendrocopos*: according to Coomans de Ruiter (1946, *in litt.*) its drumming is rather strongly performed, and apart from a usual call-note „tirr-tirr" Heinrich has mentioned the characteristic call to be that of the typical Lesser Woodpeckers (a.o. *minor*): "sehr schnell hintereinander ausgestossenes gigigigigigigi" (Stresemann, 1940, p. 393). Nest-drilling has been observed only in dead trees or in dead branches of sound trees, the species being especially fond of the Rain tree (*Pithecolobium*), but it may be observed also in other high trees, such as *Canarium commune*, Mangifera *indica*, *Swietenia mahagoni*, *Tammarindus indica*, *Terminalia catappa*, *Eugenia* spec., a.o. (Coomans de Ruiter, *in litt.*, 1946). In N. Celebes *temmincki* appears to be much more common in the mountain forests than in the lowlands; specimens could be examined from the Volcanoe Sopoetan (900 m alt.) and from the Mahawoe Mountains (100—1200 m alt.). In the Quarles Mountains, Central Celebes (Bolong, 1350 m alt.) Coomans de Ruiter observed it busy excavating a nesting hole in a branch of a dead tree. In S. Celebes (Macassar), however, it is a common bird of the city and of the cultivated areas where big trees grow along the road sides.

3. INDIAN FORMS.

XXXIV. **Dendrocopos nanus** (Vigors 1831: W. Himalayas, Simla-Almora).

Material examined: Mussoree, Garhwal (1: Mussoree); Ceylon (3): — (Basel Mus.; Leiden Mus.; coll. Meinertzhagen).

Range: South and West of the range of *D. canicapillus*, with which species it perhaps occurs side by side in Bengal (?): westwards from N. and central Bengal, through the foot hills of the Himalayas (Sikkim, Nepal, Kumaon), westward to Kangra District and Rawalpindi (Ticehurst, 1931), south to Ceylon.

Specific characters: There has been much disagreement in the literature with reference to the correct name and the specific status of the brown-headed Pigmy woodpeckers of India. By most authors they have been specifically united with the grey-headed forms of *canicapillus*, either under the specific names *pygmaeus*, *nanus*, *hardwickii*, or *semicoronatus*. Nevertheless, after the arguments given by Greenway (1943) it seems clear that the brown-headed forms of India (*nanus*) are specifically distinct from the grey-headed group (*canicapillus*), and that *Picus nanus* of Vigors (1831) refers to the brown-headed forms: "*Pic. supernè fusco-brunneus, ... capitis fronte verticeque brunneis occipite nigro*". (Vigors, 1831, p. 172). To the taxonomic differences with *canicapillus* can be added those referring to the biotope: „*nanus*" being a bird of the plains and the open countries, not ascending into the mountains; *canicapillus*, however, being the Pigmy Woodpecker of the Himalayas, going westward at least to Nepal. Neither the geographic status, nor the ecological status in Bengal seems to be satisfactorily settled, but here the typical race *canicapillus* appears to be the common Woodpecker. The present author has no clear view on what happens in those regions of W. Bengal where the grey-, and the brown-headed forms meet.

The taxonomic differences between *nanus* and *canicapillus* are rather pronounced. These refer not only to the colour of the crown, but also (1) to the general colour of the upperparts, being black or blackish brown in *canicapillus*, and more or less clear brown in *nanus*, and (2) to the degree of striping of the lowersurface, which is clearly developed in *canicapillus*, and very faintly developed, or even obsolete in *nanus*. The last named character also distinguishes *nanus* from *moluccensis*; besides, *nanus* has not so conspicuous dark brown borders to the brown crown, as typical *moluccensis*.

As regards the relationship with *D. moluccensis* see under that species.

Subspecific characters: Judging from literature records the following races appear to be recognizable (no personal subspecific examination) (cf. Stuart Baker, 1927):

1. *D. n. nanus* (Vigors 1831: W. Himalayas, Simla-Almora).
Synonym: Picus pygmaeus Vigors 1831: N.W. Himalayas (preoccupied by *Picus pygmaeus* Lichtenstein 1823).
Yungipicus hardwickii brunneiceps Stuart Baker 1926: Jelwara, Oodeypore.
Range: N. India: "north of a line drawn roughly from Kandesh in the west, through Bellary in the centre, to the Nallamalai Hills in Madras" (Stuart Baker, 1934, p. 295—6). "Forests of the base and the lower valleys of the W. Himalayas from about Katmandu in Nepal to Mussoree" (Whistler, 1913).

2. *D. n. hardwickii* (Jerdon 1844: Goomsoor in Ganjam: Whistler & Kinnear, 1934, not Wynaad, as indicated by Stuart Baker, 1927).
Range: S. India, south to the range of *nanus*. Not in Travancore (incl. Wynaad: Whistler & Kinnear, 1934).

3. *D. n. cinereigula* (Malherbe 1849: Madras, Travancore). Cf. Whistler & Kinnear, 1934.
Synonym: *Iyngipicus peninsularis* Hargitt 1882: S. Peninsular India.
Range: Travancore, S.E. coast of Peninsular India.

4. *D. n. gymnophthalmos* (Blyth 1849: Ceylon).
Range: Ceylon only; trade skins from Travancore may originate from Ceylon (Whistler & Kinnear, 1934)!

B. *African Dwarf Woodpeckers.*

XXXV **Dendrocopos obsoletus** (Wagler 1829: Senegambia).

Material examined: 12: Nigeria (Zaria: 1); Sudan (Sennar; Yei Labo: 2); Uelle District, Belgian Congo (9). — (Congo Mus., Tervueren, Belgium; Transvaal Mus., Pretoria, South Africa).

Measurements:
Uelle District: wing ♂ 79—82, average (6): 80.3; ♀ 80, 80, 83 mm.
Sudan: wing ♂ 78, 84 mm.
Nigeria: wing ♀ 85 mm.

Range and biotope: Savanna belt of Africa south of the Sahara, from Gambia through the northern parts of Portuguese Guinea, Ivory Coast, Sierra Leone (one record from the northern part: Bannerman, 1931), Gold Coast, Nigeria, north to Tillia in French Nigeria (Bannerman, 1933), Cameroon, Uelle District of Belgian Congo, Sudan, to Uganda, Abyssinia and Eritrea to the Red Sea, south to Kenya (Nairobi); besides, with a remarkable discontinuity, also occurring in the Rift Valley in Tanganyika (Mbulu district).

In most localities the species seems to be confined to a dry and relatively poorly vegetated savanna vegetation with scattered trees, even occurring in the better wooded parts of the semi-arid regions, light woodland and bush, usually in low elevations. In central Africa *D. obsoletus* appears to be not uncommon in suitable localities (Darfur and Kordofan: Lynes, 1925), but in the savanna formations of W. Africa it is said to be scarce (Bannerman, 1933); in its E. African range it even might be called rare: only few skins apparently being preserved in museum collections: of the race *ingens* (Kenya) only 1 specimen is present in the British Museum (Macdonald, *in litt.*, 1946), and 3 in the Coryndon Museum, Nairobi (Leakey, *in litt.*, 1946); whereas of the race *crateri* only one pair (among which the type) appears to be known (British Museum; l.c.). In the field the species is said to be overlooked quite easily, but Dr. Schouteden from the Congo Museum, Tervueren, told me (verbal information, 1946) that he had found them not uncommon in the true savanna formation in the Uelle District, N. Belgian Congo, where he kept a special lookout for the smaller birds occurring in the widely separated trees. In the Uelle District *obsoletus* is a characteristic bird of the dry bushy savannas, living side by side with a.o. *Lamprocolius c. chloropterus, L. chalybeus emini, Campephaga phoenicea, Campethera punctuligera balia, Lybius leucocephalus* (Chapin, 1932). Here it is "usually seen climbing silently about small dead trees in the savannas, especially on native farms, and reminds one of a tiny *Dryobates*" (Chapin, 1939, p. 587). The type of distribution is that of those savanna and steppe birds that enclose the Central African basin of tropical virgin forests (cf. Stresemann & Grote, 1929, fig. 6, p. 367), but south of the Congo Basin the species has not been observed. It is most remarkable, however, that a separate race has been found occurring in the Tanganyika Territory (Rift Valley: Mt. Ngorongoro: Sclater & Moreau, 1935), where the species lives in a biotope that is totally different from that inhabited in the other pars of is range: the "mid stratum" of the mountain forest, where it is the only Woodpecker found: "cloud forest rather than rain forest, of a somewhat dry type, which is comparatively poor in plant species, little encumbered with lianes, and not containing a heavy undergrowth except in the ravines. Moss is abundant on the trees almost everywhere, but beard lichen (*Usnea*) chiefly above 7000 ft." (Moreau & Sclater, 1938, p. 9).

Specific characters: Taxonomically *D. obsoletus* is very close to the S. Indian races of *D. nanus*, although differences exist in the fact that in the adult (and juvenile!) male a red occiput and hindneck is present, and that the mantle is uniform brown without barring. But in the small measurements, the transversely barring of rump, upper tailcoverts, and central rectrices, and the brown instead of black coloration, the similarity with the S. Asiatic Pigmy Woodpeckers is apparent. *D. obsoletus* is the only member of the genus *Dendrocopos* found within ethiopian borders. It has been abusively referred to the genus *Dendropicos* (a.o. Grote, 1928; Bannerman, 1933), which genus is quite distinct in having at all events reddish or yellowish shafts of either rectrices or remiges, or in addition a distinct greenish tinge of the plumage. In recent years it has quite correctly considered to belong to the genus *Yungipicus*, which is suggested here to be a synonym of *Dendrocopos*. Sclater (1924), however, probably was mistake, when he also referred *Dendropicos stierlingi* (Reichenow 1901) from Songea, north of Lake Nyasa to *Yungipicus*. Although only very few specimens are in existence originating from the type locality and from Portuguese E. Africa (Milange, Furancungo, Malema: Vincent, 1935) the description by Reichenow forces me to believe that *stierlingi* is a member of the genus *Dendropicos*, and not a member of *Dendrocopos*: many characters at least apply more to *Dendropicos* than to *Dendrocopos*: (1) larger measurements than most other races of the Pigmy group (wing 99—103 mm); (2) greenish tinged back, abdomen and outer edges of the remiges (Vincent, 1935); (3) yellowish coloured shaft of tailfeathers; (4) "Unterkörper und Unterschwansdecken auf weissem Grunde mit dunkelbrauner kreuzförmiger Zeichnung und zackigen kurzen Querbinden" (Reichenow, 1901, p. 106).

History: In agreement with the above mentioned fact the author suggests that *D. obsoletus* is an Asiatic invader into Africa, which has spread during the pliocene conjunction of the Asiatic and Ethiopian savanna and steppe formations, from S. Asia to within the limits of the ethiopian region. Thus, *obsoletus* originally is a member of the S. Asiatic *nanus* group, from which it has split in tertiary times. *Obsoletus* is the westernmost member of the Pigmy group, its total range connecting the Pacific with the Atlantic ocean. Formerly the range might have been continuous. At present there is an important S.W. Asiatic gap (Arabia, Persia), which makes the distribution of these Dwarf Woodpeckers typically discontinuous. The forest dwelling *D.o. crateri* (Tanganyika: see above) therefore is considered to be an aberrant representative of the species with a secondary forest life.

Subspecific characters: Through lack of material it can only be proposed to give a list of the described races with some literature notes on possible synonymy. Racial characters refer to measurements and general tinge of the brown coloration of the upperparts, which, however, is strongly subject to seasonal fading.

D. o. obsoletus (Wagler 1829: Senegambia).
D. o. ingens (Hartert 1900: Nairobi, Kenya).
D. o. heuglini (Neumann 1904: Ghati Saati, Mareb River, Eritrea).
D. o. nigricans (Neumann 1904: Uma River in Konto, Omo System, S. Abyssynia); synonym of *obsoletus*: Grant & Mackworth-Pread, 1935.
D. o. kirensis (Reichenow 1918: Redjaf, on River Kir); synonym of *obsoletus*: Sclater, 1924.
D. o. camerunensis (Reichenow 1918: Uam and Bakari, Cameroon).
D. o. batesi (Sclater 1921: new name for *Dendropicos obsoletus camerunensis* Reichenow 1918, which is preoccupied by *Dendropicos camerunensis* Sharpe 1907); synonym of *obsoletus*: Bannerman & Bates, 1924; Grote, 1925.
D. o. crateri (Sclater & Moreau 1935: Ngorongoro Volcanoe, Mbulu District, Tanganyika Territory).

XII DENDROCOPOS MAHRATTENSIS (Latham 1801: Belgaum, Mahratta).

Material examined: Ceylon (1); Haidarabad (1); Deccan (2); Rajputana (2); Nepal (2); "Himalayas" (1). — (Leiden Mus.; coll. Meinertzhagen).

Measurements: Ceylon, Haidarabad, Deccan: wing ♂ 96, 97; ♀ 91, 97 mm (♂ ♀ 94—101; Stuart Baker, 1927).
Rajputana, Nepal, Himalaya: wing ♂ 96, 101, 104, 108; ♀ 105 mm (♂ ♀ 99—105; Stuart Baker, 1927).

Range: Ceylon, India through the Indo-Gangetic plains to Sind, and the foothills of the Himalayas, north to Peshawar (Whitehead, 1909), rare in the plains and the river valleys of Burma (Stanford & Ticehurst, 1939), east into the Shan States and Indo China (Laos: Delacour & Jabouille, 1940).

Biotope: *D. mahrattensis* is a lowland form inhabiting mostly semi-arid regions with a scarce vegetation of thin forest, low tree jungle, cultivated countries, road sides, gardens, and orchards, being rare in better wooded areas and in the mountains. Nevertheless, the northern race has been observed in heights up to about 1500 m (Stuart Baker, 1927). It has been found breeding in the hottest and driest parts of Peninsular and Northern India, but also, but scarcely, in the warm rainy countries of Assam and Bengal. Nests have been found in almost any kind of tree, but especially in Acacias and Babools (Stuart Baker, 1934), and in Ceylon in *Euphorbia* trees (Wait, 1925). In spite of its relatively poorly vegetated biotope the species has remained a true Woodpecker, since according to Stuart Baker (1927) is has never been seen on the ground. In the N.W. part of its range *mahrattensis* touches the area of *D. assimilis*, which appears to inhabit the same semi-arid biotope. Thus, in Sind and the W. Punjab both species occur side by side, only there being locally common, where the other is absent (cf. Whistler, 1916; Ticehurst, 1923).

Subspecific examination: The distinction of a smaller and darker southern race and a larger and lighter coloured northern one appears justified when specimens from the opposite regions are compared. The slight distinctions are especially apparent when comparable individual feathers of a southern and a northern specimen are compared (fig. 29). Nevertheless, the racial characters, both of pigmentation and of size are only of a quantitative type; therefore, no exact boundary between the ranges of the two races can be defined, although specimens from the Deccan Plateau, and from the E. Ghats (Whistler & Kinnear, 1934) appear to be unseparable from southern ones (cf. Stuart Baker, 1926).

There is a certain amount of unconformity in the nomenclature of the northern race, since various authors disagree, wehther specimens from Borabhum (= Birbhum = type-locality of *Picus aurocristatus* Tickell 1833) are referable to the northern or to the southern (typical) race. It is most likely that they are intermediate (Whistler & Kinnear, 1934), in which case the race cannot be exactly determined. To northern populations usually the subspecific name *blanfordi* (Blyth 1863: Tounghoo, Burma) is applied (*contra* Ticehurst, 1928 and 1930).

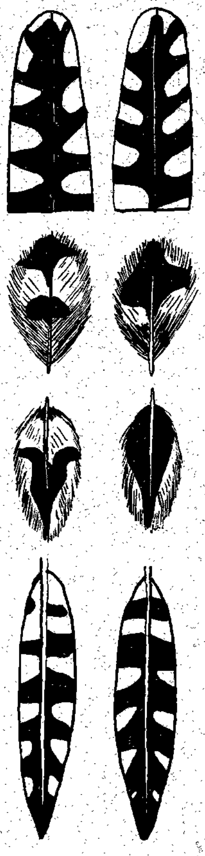

Fig. 29. *D. mahrattensis* (Hempr. & Ehrenb.) — From above to below: first (innermost) secondaries, feathers of upper back, upper tailcoverts, and central rectrices, to show the relative dark appearance of the southern race. Right series: *m. mahrattensis*: Mullug, Deccan; compared with the northern race (*blanfordi*): left series: Bharatpur, Rajputana.

History and Discussion: D. mahrattensis is most abundant in suitable localities in S. India, being rare in most N. parts of its range, and exceedingly rare in the N.E.; it is, however, also "nowhere very common" in Ceylon (Wait, 1925). From this, and from its absence in S. Chinese countries one may conclude that the center of the recent dispersal of *D. mahrattensis* must be sought in Peninsular India and in Ceylon. Originating from the old stock of Pied Woodpeckers in E. Asia the species has been isolated since tertiary times in the Gondwana continent, which, during the pleistocene has been separated from the Asiatic continent by the eastern arm of the *Tethys* Sea, connecting the Persian Gulf with the Gulf of Bengal through the N. Indian plains. In Peninsular India the species has been transformed in such a way, that at the moment it seems to be a question of mere appreciation, wheter the species should be treated as a member of the genus *Dendrocopos*, or should be ranked as a separate genus (*Leiopicus* Bonaparte 1854). Although I find the general appearance of the upperside rather irregularly spotted with white, more than regularly barred, still this pattern is reached by an extraordinary strong development of the white spots on all dorsal feathers. On the tertials the white spots on both webs are narrow and long, and stand oblique to the shaft, whereas in typical *Dendrocopos* the spots are more or less rounded or approximately as long as wide. The presence in the male of a yellow instead of a red colour on forehead and crown to which is added a red occiput and hindneck does not seem to have a generic value, since red lipochromes of the *Picidae* appear to be constituted by at least two components, a basal yellow, and an additional (oxydated) red one, both components which could be separated by a chromatographic absorbtion method (Völker, 1939).

In conclusion *mahrattensis* is considered here to be a member of *Dendrocopos*, which is the most suitable systematic place of the species (cf. Ticehurst, 1930). It probably represents one of the rare (secundary!) autochthone bird species of the Gondwana continent, whence it has spread into northern and northeastern direction.

XIII CONCLUSIONS.

1. From the genus *Dendrocopos* 35 species have been recognized (including a great number of subspecies). The genus *Xenopicus* (with 1 species) has been provisionally maintained.
2. The genus *Dendrocopos* has a world-wide range. From its absence in the S. Ethiopian and Madagascarian regions, the tropics of South America, and the Papuasian and Australasian regions,however, its relatively recent dispersal into the world is apparent.
3. Within the genus *Dendrocopos* a division into 6 great groups has been made. These include a number of species which not only are taxonomically closely related, but which also show apparent geographic relations, the latter being detectable in the recent distribution of the members of the group. The groups have the systematic value of superspecies or subgenera.
4. No geographic relations are apparent between different groups, although taxonomic relations are mostly noteworthy. Nevertheless, theoretical speculations on the historic base of their geographic and taxonomic relations fall beyond the scope of this study, since these are not apparent in the recent distribution of the separate forms.
5. With the exception of the American White-backed species (*stricklandi, villosus, pubescens*) the recent distribution of all other groups indicate a direct origin from S.E. Asia (S. China, Burma, E. Tibet). The author has made many

suggestions in favour of the significance of S.E. Asia as a center of origin of the genus *Dendrocopos*.

6. The recent distribution of the holarctic species has been severely influenced by the glacial periods, causing a glacial survival of the species in disconnected forest refugia. The significance of three North American and a number of Asiatic and European refugia have been discussed. Glacial isolation in separate refugia has contributed much to the formation of subspecies and species.
7. The results of important migrations of whole populations in interglacial and postglacial periods, spreading out of the glacial refugia, are considered to be detectable in the recent distribution of at least *D. major*, *D. leucotos*, *D. minor*, and *D. villosus-pubescens*.
8. Discontinuous ranges have been discussed in the subspecies *D. l. leucotos*, and *D. m. minor*. An historic geographic base of this unusual phenomenon has been given.
9. Ecologically distinct forms, occurring in the same region have been treated as separate systematic species, though they might have belonged to one historic specific unity: *D. leucopterus*, *D. syriacus*, *D. atratus*.
10. The dynamic character of the subspecies has been discussed in the instructive case of the W. European races of *D. major* ("*arduennus*") and *D. minor* ("*bacmeisteri*"), and in *D. leucopterus*.
11. The dynamic character of the species has been discussed in the cases of *D. major numidus*, *D. syriacus*, *D. leucopterus*, *D. ligniarius*, *D. mixtus*, *D. minor*, *D. canicapillus*, *D. moluccensis*, *D. maculatus*, *D. nanus*.
12. The dynamic character of the genus has been discussed in the cases of *D. mahrattensis*, and *X. albolarvatus*.

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