Size variation in samples of fossil and recent murid teeth

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The variability coefficient proposed by Freudenthal & Cuenca Bescós (1984) for samples of fossil cricetid teeth, is calculated for about 200 samples of fossil and recent murid teeth. The results are discussed, and compared with those obtained for the Cricetidae.

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Introduction

Freudenthal & Cuenca Bescós (1984) published an analysis of variability of c. 140 samples of fossil cricetid teeth from the European Tertiary. From these samples those with less than 5 specimens were eliminated, which resulted in a total of 85 (for M^3 to 126 (for M_1) useful populations. They came to the conclusion that the frequently used variability coefficient of Pearson, 100 s/x, is not a good tool in palaeontology. They proposed another coefficient, 100 R/M, where R is the range (difference between maximum and minimum), and M is the median (the mid-point between minimum and maximum).

Their analysis led to the recognition of almost 30 populations with excessive variability values. In c. 50 % of these 30 cases they suggested the possibility that such a sample contained 2 different species. In 5 of these populations, that were studied afterwards, this suggestion was confirmed. These samples are identified by the same symbol as used in the publication of Freudenthal & Cuenca Bescós (1984):

B) *Eucricetodon atavus* from Hoogbutsel. According to Freudenthal (1988) three species of *Eucricetodon* are present in Hoogbutsel.

V) *Megacricetodon crusafonti* from Valalto 2C. According to Daams & Freudenthal (1988) this locality contains two species of *Megacricetodon*: *M. rafaeli* and *M.* sp. ex gr. *collongensis-crusafonti.*

W) *Megacricetodon crusafonti* from Las Planas 5 H. According to Daams & Freudenthal (1988) this locality contains two species of *Megacricetodon*: *M. minor* and *M.* sp. ex gr. *crusafonti-ibericus.*

Z) *Megacricetodon* sp. ex gr. *crusafonti-ibericus* from Alcocer 2. According to Daams & Freudenthal (1988) this locality contains two species of *Megacricetodon*: *M. minor* and *M.* sp. ex gr. *crusafonti-ibericus.*

2) *Megacricetodon crusafonti* from Valalto 2B. According to Daams & Freudenthal (1988) this locality contains two species of *Megacricetodon*: *M. rafaeli* and *M.* sp. ex gr. *collongensis-crusafonti.*

Apparently this coefficient of variability may serve to decide whether a sample is homogeneous or not.

Freudenthal and Cuenca Bescós made an attempt to apply the same method to Gliridae and Sciuridae, but found the number of populations available insufficient to get reliable results. We estimate this method can only be applied when some 100 or more samples are available.

For the Muridae this condition is fulfilled, so the present authors decided to make an analysis of variability in samples of fossil and recent murid teeth.

All programs used for the computation of V', $V'/\sqrt{\log N}$ and σ, and for drawing the diagrams were written by the first author. We have two versions: one written in IBM Assembler and Fortran, that was run on the main frame computer of the Leiden University; and a second version written in GW-basic, that can be run on any IBM compatible PC.

Measurements are given in tenths of millimetres, even when the original author used an other scale. Apart from that change, measurements were taken as published. Of course various measuring techniques do not present the same degree of reliability. For example, measuring by means of an ocular micrometer, or a system based on displacement in the ocular, present poor accuracy, especially in hypsodont teeth. A system based on a vertical optical axis and horizontal displacement of the microscope stage is to be preferred. This paper does not enter into the problem of the excess of variability that may be caused by an insufficiently accurate measuring method.

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(Sabadell); C. Castillo (Granada) provided us with data from her yet unpublished doctor's thesis.

Material

For our analysis we used a total of over 200 samples, mainly published data, and a smaller number of yet unpublished samples, as specified in the following list. Since this is not a taxonomic list, the original designations like cf., aff., etc. have been omitted.

182A	*Progonomys debruijni*	Jacobs, 1978
Aguanaces	*Occitanomys sondaari*	Adrover, 1986
Aguanaces	*Valerymys vireti*	Adrover, 1986
Aïn Guettara	*Apodemus jeanteti*	Brandy, 1979
Alcoy	*Stephanomys* sp.	Cordy, 1976
Aldehuela	*Apodemus dominans*	Adrover, 1986
Aldehuela	*Paraethomys meini*	Adrover, 1986
Aldehuela	*Stephanomys margaritae*	Adrover, 1986
Alfambra	*Occitanomys sondaari*	van de Weerd, 1976
Aljezar B	*Occitanomys adroveri*	Adrover, 1986
Aljezar B	*Parapodemus barbarae*	Adrover, 1986
Aljezar B	*Valerymys turoliensis*	Adrover, 1986
Argoub Kemellal	*Paraethomys anomalus*	Coiffait et al., 1985
Argoub Kemellal	*Stephanomys numidicus*	Coiffait et al., 1985
Aridos 1	*Apodemus sylvaticus*	López Martínez, 1980
Arquillo	*Stephanomys fontana*	Cordy, 1976
Arquillo 3	*Apodemus dominans*	Adrover, 1986
Arquillo 3	*Apodemus gorafensis*	Adrover, 1986
Arquillo 3	*Castillomys gracilis*	Adrover, 1986
Arquillo 3	*Occitanomys brailloni*	Adrover, 1986
Arquillo 3	*Paraethomys meini*	Adrover, 1986
Arquillo 3	*Stephanomys margaritae*	Adrover, 1986
Atapuerca TD 4	*Apodemus flavicollis*	Gil, 1990
Atapuerca TD 6	*Apodemus flavicollis*	Gil, 1990
Bagur 2	*Castillomys crusafonti*	López et al., 1976
Balaruc 2	*Apodemus dominans*	Pasquier, 1974
Balaruc 2	*Apodemus jeanteti*	Pasquier, 1974
Bali 2	*Kritimys catreus*	Mayhew, 1977
Barranco Cañuelas	*Stephanomys thaleri*	Sesé, 1989
Barranco Quebradas	*Stephanomys thaleri*	Sesé, 1989
Belmez	*Apodemus dominans*	Castillo Ruiz, 1990
Belmez	*Apodemus jeanteti*	Castillo Ruiz, 1990
Belmez	*Castillomys gracilis*	Castillo Ruiz, 1990
Belmez	*Stephanomys thaleri*	Castillo Ruiz, 1990
Belmez	*Stephanomys calveti*	Castillo Ruiz, 1990
Belvedère 4	*Apodemus maastrichtiensis*	van Kolfschoten, 1985
Belvedère 4	*Apodemus sylvaticus*	van Kolfschoten, 1985
Berlin	*Apodemus flavicollis*	Pasquier, 1974
Biancone	*Microtia maiuscula*	Clanet, 1985
Biancone	*Microtia parva*	Clanet, 1985

Botardo C	*Apodemus gorafensis*	Martín Suárez, 1988
Burgos	*Apodemus sylvaticus*	Pasquier, 1974
Camargue	*Apodemus sylvaticus*	Pasquier, 1974
Cañada del Castaño	*Apodemus agustii*	Martín Suárez, 1988
Cantatore 3A	*Microtia* sp. 5	Clanet, 1985
Canteras de Jun	*Valerymys juniensis*	Padial Ojeda & Ruiz Bustos, 1989
Capo Figari	*Rhagamys minor*	Brandy, 1979
Caravaca	*Castillomys gracilis*	Adrover, 1986
Casa del Acero	*Occitanomys adroveri*	Agustí et al., 1981
Casa del Acero	*Parapodemus barbarae*	Agustí et al., 1981
Casa del Acero	*Valerymys turoliensis*	Agustí et al., 1981
Casablanca 1	*Stephanomys balcellsi*	Gil & Sesé, 1984
Casablanca B	*Stephanomys balcellsi*	Gil & Sesé, 1985
Chiro 19	*Microtia* sp. 4	Clanet, 1985
Claux	*Apodemus sylvaticus*	Pasquier, 1974
Combe Grenal	*Apodemus flavicollis*	Pasquier, 1974
Conca	*Rhagamys orthodon*	Brandy, 1979
Concud 2	*Occitanomys adroveri*	van de Weerd, 1976
Concud 2	*Parapodemus barbarae*	van de Weerd, 1976
Concud 3	*Occitanomys adroveri*	van de Weerd, 1976
Concud 3	*Parapodemus barbarae*	van de Weerd, 1976
Concud 3	*Valerymys turoliensis*	van de Weerd, 1976
Concud CC	*Occitanomys adroveri*	van de Weerd, 1976
Concud CCL	*Occitanomys adroveri*	van de Weerd, 1976
Concud CCL	*Parapodemus barbarae*	van de Weerd, 1976
Concud CCB	*Occitanomys adroveri*	van de Weerd, 1976
Concud CCB	*Parapodemus barbarae*	van de Weerd, 1976
Corte	*Rhagamys orthodon*	Brandy, 1979
Crevillente 1	*Parapodemus lugdunensis*	de Bruijn et al., 1975
Crevillente 1	*Valerymys vireti*	de Bruijn et al., 1975
Crevillente 2	*Occitanomys sondaari*	de Bruijn et al., 1975
Crevillente 2	*Parapodemus lugdunensis*	de Bruijn et al., 1975
Crevillente 2	*Valerymys vireti*	de Bruijn et al., 1975
Crevillente 2	*Occitanomys sondaari*	unpublished
Crevillente 2	*Parapodemus lugdunensis*	unpublished
Crevillente 2	*Valerymys vireti*	unpublished
Crevillente 3	*Occitanomys sondaari*	de Bruijn et al., 1975
Crevillente 3	*Parapodemus lugdunensis*	de Bruijn et al., 1975
Crevillente 3	*Valerymys vireti*	de Bruijn et al., 1975
Crevillente 4	*Occitanomys sondaari*	de Bruijn et al., 1975
Crevillente 4	*Parapodemus gaudryi*	de Bruijn et al., 1975
Crevillente 4B	*Occitanomys sondaari*	unpublished
Crevillente 4B	*Parapodemus lugdunensis*	unpublished
Crevillente 4B	*Valerymys vireti*	unpublished
Crevillente 5	*Occitanomys adroveri*	de Bruijn et al., 1975
Crevillente 5	*Parapodemus* sp.	de Bruijn et al., 1975
Crevillente 5A	*Occitanomys adroveri*	unpublished
Crevillente 5A	*Parapodemus lugdunensis*	unpublished
Crevillente 6	*Occitanomys adroveri*	de Bruijn et al., 1975
Crevillente 6	*Paraethomys anomalus*	de Bruijn et al., 1975
Crevillente 7	*Occitanomys adroveri*	unpublished
Crevillente 7	*Parapodemus barbarae*	unpublished

Crevillente 8	*Occitanomys adroveri*	unpublished
Crevillente 8	*Parapodemus barbarae*	unpublished
Crevillente 14	*Occitanomys adroveri*	unpublished
Crevillente 14	*Stephanomys ramblensis*	unpublished
Crevillente 15	*Occitanomys adroveri*	unpublished
Crevillente 15	*Parapodemus barbarae*	unpublished
Crevillente 15	*Valerymys turoliensis*	unpublished
Cueva del Agua	*Apodemus sylvaticus*	López Martínez & Ruiz Bustos, 1977
Cueva las Graderas	*Apodemus flavicollis*	Gil, 1986
Cueva Victoria	*Apodemus mystacinus*	Agustí, 1982
DP13	*Karnimata huxleyi*	Jacobs, 1978
DP13	*Mus auctor*	Jacobs, 1978
DP13	*Parapelomys robertsi*	Jacobs, 1978
Eichkogel	*Parapodemus lugdunensis*	Daxner-Höck, 1977
Escorihuela	*Stephanomys minor*	van de Weerd, 1976
Escorihuela A	*Apodemus dominans*	van de Weerd, 1976
La Fontana	*Apodemus gudrunae*	van de Weerd, 1976
France	*Apodemus flavicollis*	Pasquier, 1974
France	*Apodemus sylvaticus*	Pasquier, 1974
Gerani 2	*Mus minotaurus*	Mayhew, 1977
Gondrenans	*Apodemus flavicollis*	Pasquier, 1974
Guadarrama	*Apodemus sylvaticus*	Pasquier, 1974
Gumbes B	*Mus minotaurus*	Mayhew, 1977
Kharoumes A	*Kritimys catreus*	Mayhew, 1977
Kharoumes 4	*Kritimys catreus*	Mayhew, 1977
Kharoumes 4*	*Kritimys catreus*	Mayhew, 1977
Kirchdorf	*Apodemus flavicollis*	Pasquier, 1974
Kirchdorf	*Apodemus sylvaticus*	Pasquier, 1974
Layna	*Apodemus dominans*	Pasquier, 1974
Layna	*Castillomys crusafonti*	Michaux, 1969
Layna	*Occitanomys brailloni*	Michaux, 1969
Lazaret	*Apodemus sylvaticus*	Pasquier, 1974
Librilla	*Apodemus gudrunae*	Brandy, 1979
Librilla	*Paraethomys meini*	Brandy, 1979
Librilla 1	*Stephanomys* sp.	Cordy, 1976
Liko	*Mus minotaurus*	Mayhew, 1977
Loma Quemada	*Micromys minutus*	Martín Suárez, 1988
Málaga	*Apodemus flavicollis*	Pasquier, 1974
Los Mansuetos	*Occitanomys adroveri*	van de Weerd, 1976
Los Mansuetos	*Parapodemus barbarae*	van de Weerd, 1976
Los Mansuetos	*Valerymys turoliensis*	van de Weerd, 1976
Los Mansuetos 2	*Occitanomys adroveri*	van de Weerd, 1976
Maritsa 1	*Castillomys crusafonti*	de Bruijn et al., 1970
Maritsa 1	*Paraethomys anomalus*	de Bruijn et al., 1970
Maritsa 1	*Pelomys europeus*	de Bruijn et al., 1970
Maritsa 1	*Rhagapodemus vandeweerdi*	de Bruijn et al., 1970
Mas Genelas	*Apodemus jeanteti*	Pasquier, 1974
Mas Rambault	*Castillomys crusafonti*	Michaux, 1969
Masada del Valle 2	*Occitanomys adroveri*	van de Weerd, 1976
Masada del Valle 2	*Parapodemus barbarae*	van de Weerd, 1976
Masada del Valle 2	*Valerymys turoliensis*	van de Weerd, 1976
Masada del Valle 3	*Occitanomys adroveri*	van de Weerd, 1976

Masada del Valle 3	*Valerymys turoliensis*	van de Weerd, 1976
Masada del Valle 4	*Occitanomys adroveri*	van de Weerd, 1976
Masada del Valle 4	*Parapodemus barbarae*	van de Weerd, 1976
Masada del Valle 5	*Occitanomys adroveri*	van de Weerd, 1976
Masada del Valle 5	*Parapodemus barbarae*	van de Weerd, 1976
Masada del Valle 5	*Valerymys turoliensis*	van de Weerd, 1976
Masada del Valle 7	*Occitanomys adroveri*	van de Weerd, 1976
Masada del Valle 7	*Stephanomys ramblensis*	van de Weerd, 1976
Masía del Barbo	*Progonomys cathalai*	van de Weerd, 1976
Masía del Barbo	*Progonomys hispanicus*	van de Weerd, 1976
Masía del Barbo A	*Progonomys hispanicus*	van de Weerd, 1976
Milatos 1	*Kritimys catreus*	Mayhew, 1977
Milatos 2	*Mus minotaurus*	Mayhew, 1977
Milatos 3	*Kritimys catreus*	Mayhew, 1977
Milatos 4	*Mus minotaurus*	Mayhew, 1977
Mont Hélène	*Apodemus dominans*	Aguilar et al., 1986
Mont Hélène	*Apodemus jeanteti*	Aguilar et al., 1986
Mont Hélène	*Castillomys gracilis*	Aguilar et al., 1986
Mont Hélène	*Occitanomys montheleni*	Aguilar et al., 1986
Mont Hélène	*Paraethomys meini*	Aguilar et al., 1986
Mont Hélène	*Rhagapodemus hautimagnensis*	Aguilar et al., 1986
Mont Hélène	*Stephanomys donnezani*	Aguilar et al., 1986
Montredon	*Progonomys cathalai*	Aguilar, 1981
Moreda	*Stephanomys amplius*	Ruiz Bustos, 1986
Moreda 1A	*Apodemus dominans*	Castillo Ruiz, 1990
Moreda 1A	*Castillomys gracilis*	Castillo Ruiz, 1990
Moreda 1A	*Stephanomys donnezani*	Castillo Ruiz, 1990
Moreda 1A	*Stephanomys minor*	Castillo Ruiz, 1990
Moreda 1B	*Apodemus dominans*	Castillo Ruiz, 1990
Moreda 1B	*Apodemus jeanteti*	Castillo Ruiz, 1990
Moreda 1B	*Castillomys crusafonti*	Castillo Ruiz, 1990
Moreda 1B	*Stephanomys minor*	Castillo Ruiz, 1990
Moreda 1B	*Stephanomys thaleri*	Castillo Ruiz, 1990
Moreda 3A1	*Castillomys gracilis*	Castillo Ruiz, 1990
Moreda 3A1	*Stephanomys vandeweerdi*	Castillo Ruiz, 1990
Moreda 3A2	*Castillomys crusafonti*	Castillo Ruiz, 1990
Moreda 3A2	*Stephanomys vandeweerdi*	Castillo Ruiz, 1990
Moreda 3A3	*Castillomys crusafonti*	Castillo Ruiz, 1990
Moreda 3A3	*Stephanomys vandeweerdi*	Castillo Ruiz, 1990
Moreda 3A4	*Castillomys crusafonti*	Castillo Ruiz, 1990
Moreda 3A4	*Stephanomys vandeweerdi*	Castillo Ruiz, 1990
Moreda 3A5	*Castillomys crusafonti*	Castillo Ruiz, 1990
Moreda 3A5	*Stephanomys vandeweerdi*	Castillo Ruiz, 1990
Moreda 3A6	*Stephanomys vandeweerdi*	Castillo Ruiz, 1990
Moreda 3AB	*Apodemus dominans*	Castillo Ruiz, 1990
Moreda 3AB	*Castillomys crusafonti*	Castillo Ruiz, 1990
Moreda 3AB	*Stephanomys minor*	Castillo Ruiz, 1990
Moreda 3AB	*Stephanomys thaleri*	Castillo Ruiz, 1990
Moreda L4	*Castillomys crusafonti*	Castillo Ruiz, 1990
Nîmes	*Apodemus jeanteti*	Pasquier, 1974
Nîmes	*Occitanomys brailloni*	Michaux, 1969
Orce 7	*Apodemus mystacinus*	Agustí et al., 1987

Orgnac	*Apodemus sylvaticus*	Pasquier, 1974
Orrios	*Paraethomys meini*	van de Weerd, 1976
Orrios 3	*Apodemus dominans*	Adrover, 1986
Orrios 3	*Castillomys crusafonti*	Adrover, 1986
Orrios 3	*Stephanomys vandeweerdi*	Adrover, 1986
Oued Athmenia 1	*Paraethomys anomalus*	Coiffait et al., 1981
Oued Athmenia 1	*Paraethomys athmeniae*	Coiffait et al., 1981
Oued Zra	*Progonomys cathalai*	Jaeger, 1977
Peralejos 4	*Progonomys hispanicus*	van de Weerd, 1976
Peralejos A	*Progonomys cathalai*	van de Weerd, 1976
Peralejos C	*Progonomys cathalai*	van de Weerd, 1976
Peralejos C	*Progonomys hispanicus*	van de Weerd, 1976
Peralejos D	*Progonomys hispanicus*	van de Weerd, 1976
Perpignan	*Stephanomys donnezani*	Adrover, 1986
Pertuis	*Occitanomys sondaari*	Aguilar, 1981
Pikermi	*Parapodemus gaudryi*	de Bruijn, 1976
Pirro Nord 1	*Apodemus flavicollis*	de Giuli & Torre, 1984
Prince à Grimaldi	*Apodemus sylvaticus*	Pasquier, 1974
Pul-e Charkhi	*Mus elegans*	Sen, 1983
Pul-e Charkhi	*Parapelomys charkhensis*	Sen, 1983
Pul-e Charkhi	*Saidomys afghanensis*	Sen, 1983
Rebielice	*Apodemus dominans*	Pasquier, 1974
Rethymnon	*Mus minotaurus*	Mayhew, 1977
Rinascita 1	*Microtia* sp. 1	Clanet, 1985
Rinascita 1	*Microtia* sp. 2	Clanet, 1985
Rinascita 1	*Microtia* sp. 3	Clanet, 1985
Salobreña	*Apodemus gudrunae*	Brandy, 1979
Santenay	*Apodemus flavicollis*	Pasquier, 1974
Sarcaro	*Stephanomys minor*	Castillo Ruiz, 1990
Sarrión	*Apodemus dominans*	Adrover, 1986
Sarrión	*Castillomys crusafonti*	Adrover, 1986
Sarrión	*Stephanomys minor*	Adrover, 1986
Schernfeld	*Apodemus dominans*	Pasquier, 1974
Sète	*Apodemus jeanteti*	Pasquier, 1974
Sète	*Castillomys crusafonti*	Michaux, 1969
Sète	*Stephanomys vandeweerdi*	Adrover, 1986
Seynes	*Apodemus dominans*	Pasquier, 1974
Seynes	*Apodemus jeanteti*	Pasquier, 1974
Seynes	*Castillomys crusafonti*	Michaux, 1969
Sierra Elvira	*Castillomys* sp. 1	Agustí et al., 1988
Skaleta	*Mus minotaurus*	Mayhew, 1977
Stavros SID	*Kritimys catreus*	Mayhew, 1977
Stavros SID	*Mus bateae*	Mayhew, 1977
Stavros SA	*Kritimys catreus*	Mayhew, 1977
Stavros SGI	*Kritimys catreus*	Mayhew, 1977
Stavros SGO	*Kritimys catreus*	Mayhew, 1977
Tortajada	*Occitanomys adroveri*	van de Weerd, 1976
Tortajada A	*Occitanomys sondaari*	van de Weerd, 1976
Tortajada A	*Parapodemus lugdunensis*	van de Weerd, 1976
Tortajada A	*Valerymys vireti*	van de Weerd, 1976
Tortajada B	*Valerymys turoliensis*	van de Weerd, 1976
Tortajada C	*Occitanomys adroveri*	van de Weerd, 1976

Tortajada C	*Parapodemus barbarae*	van de Weerd, 1976
Tourkobounia 1	*Apodemus dominans*	de Bruijn & v. d. Meulen, 1975
Tourkobounia 1	*Orientalomys similis*	de Bruijn & v. d. Meulen, 1975
Tourkobounia 1	*Rhagapodemus frequens*	de Bruijn & v. d. Meulen, 1975
Trefossi 1	*Microtia* sp. 6	Clanet, 1985
Treviers	*Apodemus sylvaticus*	Pasquier, 1974
Valdecebro 3	*Apodemus gudrunae*	van de Weerd, 1976
Valdecebro 3	*Occitanomys adroveri*	van de Weerd, 1976
Valdecebro 3	*Stephanomys ramblensis*	van de Weerd, 1976
Valdecebro 4	*Occitanomys sondaari*	van de Weerd, 1976
Valdeganga 3	*Castillomys* sp.	Mein et al., 1978
Varkiza 1	*Apodemus mystacinus*	van de Weerd, 1973
Venta del Moro	*Stephanomys ramblensis*	Brandy, 1979
Venta del Moro	*Stephanomys* sp.	Cordy, 1976
Villafranca d'Asti	*Apodemus dominans*	Pasquier, 1974
Villalba Alta	*Apodemus dominans*	Adrover, 1986
Villalba Alta	*Apodemus gorafensis*	Adrover, 1986
Villalba Alta	*Paraethomys meini*	Adrover, 1986
Villalba Alta	*Stephanomys margaritae*	Adrover, 1986
Villalba Baja 1	*Stephanomys ramblensis*	van de Weerd, 1976
Villalba Baja 2	*Occitanomys adroveri*	van de Weerd, 1976
Villalba Baja 2	*Parapodemus barbarae*	van de Weerd, 1976
Vivero de Pinos	*Occitanomys sondaari*	Adrover, 1986
Vivero de Pinos	*Parapodemus lugdunensis*	Adrover, 1986
Vivero de Pinos	*Valerymys vireti*	Adrover, 1986
Wageningen	*Apodemus maastrichtiensis*	van Kolfschoten, 1988
Wageningen	*Apodemus sylvaticus*	van Kolfschoten, 1988
Wèze	*Apodemus dominans*	Pasquier, 1974
Xeros	*Kritimys catreus*	Mayhew, 1977
Yedras	*Apodemus flavicollis*	López Martínez & Ruiz Bustos, 1977
YGSP 182A	*Karnimata darwini*	Jacobs, 1978

Remarks on samples with a high variability coefficient

Samples with a high variability have been marked in the graphs (Figs. 1-12) by a letter, a number, or a special symbol. When a sample shows extreme variability in one of the twelve graphs, it is marked with the same symbol in the other graphs too.

A) *Apodemus dominans* from Aldehuela, published by Adrover (1986). This sample contains few specimens. Only the length of the M_2 shows a high variability (Fig. 5). This may be due to the shape of the terminal heel, which, according to the description by Adrover, is either well-developed and rounded, or transversal and compressed.

B) *Apodemus dominans* from Rebieliece, studied by Pasquier (1974). We have not been able to study this material. The fossil locality of Rebielice is a karst fissure, and in this type of localities heterogeneous faunas may be expected, due to the mechanism of accumulation.

C) *Apodemus dominans* from Seynes, studied by Pasquier (1974). This population shows a high value for V' for the length of M_3 (Fig. 9). This material, and new material from the same site, is at present being studied by B. Bachelet, University of Montpellier; the measurements of 12 M_3, that she kindly put at our disposal, show a range for the length of 9.4-10.7 and for the width of 9.0-10.4 mm. These values represent a normal variability coefficient.

D) *Apodemus dominans* from Wèze, studied by Pasquier (1974). This locality is a karst fissure. See the remarks under B.

E) *Apodemus flavicollis* from Atapuerca TD-4, and
F) *Apodemus flavicollis* from Atapuerca TD-6, both published by Gil (1990). The author speaks of a morphological and biometrical homogeneity of this material, that is dated between 700.000 and 118.000 years BP. However, these samples are small and show extremely high values for V'. A revision of the material appears to be desirable.

G) *Apodemus flavicollis* from Málaga, studied by Pasquier (1974). This material comes from a karst fissure. See the remarks under B.

H) *Apodemus flavicollis* from Cueva de las Graderas, published by Gil (1986). The analysis of this sample gave high values for V' in some cases (Figs. 1 and 4), normal values in other cases, and a very low one in the case of the length of M_2 (Fig. 5). The author says that this population presents the morphological features of *A. flavicollis* and the biometrical features of *A. sylvaticus*. Possibly it contains specimens of both these species.

I) *Apodemus flavicollis* from Las Yedras, published by López Martínez & Ruiz Bustos (1977). Variability is very high in M^3. If this is not due to a measurement error we are inclined to think that this material cannot belong to one single species.

J) *Apodemus gudrunae* from Salobreña, studied by Brandy (1979). This population shows a high variability for the length of M^2 (Fig. 7). Dr J.P. Aguilar (Montpellier) was so kind to remeasure the material. The minimum for the length turned out to be 13.0, which brings variability back to normal.

K) *Apodemus mystacinus* from Cueva Victoria, published by Agustí (1982), probably contains two different species, distinguishable only by their M3 (Agustí, pers. comm.).

L) *Apodemus mystacinus* from Varkiza 1, published by van de Weerd (1973). The published value of 10.6 for the width of M_1 was taken on a digested specimen, that cannot be measured reliably; the correct value for the minimum is 11.9 (according to van de Weerd's catalogue). Variability is normal.

M) *Apodemus sylvaticus* from Orgnac, and
N) *Apodemus sylvaticus* from Prince à Grimaldi, both studied by Pasquier (1974). These populations were first mentioned by Chaline, 1972. Chaline states that in both localities *Apodemus* material was collected from various levels that differ in age. From Pasquier's work it is not clear whether she took her sample from one level only, or whether she studied the entire *Apodemus* material from these localities.

O) *Apodemus sylvaticus* from Wageningen, published by van Kolfschoten (1988). The M_1 with a width of 8.8 is a digested specimen, and does not permit a reliable measurement. We do not know the correct minimum, but variability appears to be normal.

P) *Castillomys crusafonti* from Layna, published by Michaux (1969). We had the opportunity to revise this material at the University of Montpellier. Within the genus *Castillomys* two morphotypes can be distinguished that have been described as two subspecies: *C. crusafonti gracilis* and *C. crusafonti crusafonti*. In the large collection of *C. crusafonti* from Layna both these morphotypes are present. Part of the material shows the morphotype *'gracilis'*: M_1 with symmetrical anteroconid and very low longitudinal crest, M^1 and M^2 without t2bis and with weakly developed crests; the other part of the collection presents the morphology of *'crusafonti'*: M^1 with asymmetrical anteroconid and well-developed longitudinal crest, M^1 and M^2 with a small t2bis and high crests. Moreover, the morphotypes *'gracilis'* have smaller dimensions than the *'crusafonti'*, a difference that is strongest in the length of M_1, where it is caused by the symmetry or asymmetry of the anteroconid mentioned above.

Q) *Mus minotaurus* from Gerani 2, published by Mayhew (1977). Gerani 2 is a cave deposit with various fossiliferous levels (Mayhew, 1977, p. 188). Mayhew's ample discussion of biometrical data of *Mus minotaurus* from various localities shows a complicated pattern. He suggests that his sample from Liko (LIP) is more homogeneous than the other samples. In table 1 he calculates V as $100s/\bar{x}$, and finds the highest value of his entire material (11.0) for the length of M_3 from Gerani 2, precisely the measurement that gave a high value in our analysis. Evidently something is wrong, but we are not in a position to give an explanation.

R) *Occitanomys adroveri* from Concud Cerro de la Garita (CCB), published by van de Weerd (1976). The minimum value for the length of M^2 is 11.9 in van de Weerd (1976). We found 12.9 for the same specimen, which makes variability normal.

S) *Occitanomys brailloni* from Nîmes, published by Michaux (1969). Variability for the width of M_1 is high. Keeping in mind that this material was published as early as 1969, a revision and redescription seems appropriate, the more so since the second and third molars of this species were not described, neither from the type-locality Layna, nor from Nîmes.

T) *Occitanomys sondaari* from Tortajada A, published by van de Weerd (1976). The M^2 with a width of 10.5 is a digested specimen and cannot be measured reliably. We found a minimum for the width of 10.6 in well-preserved specimens. Even then variability is rather high.

U) *Paraethomys anomalus* from Maritsa 1, published by de Bruijn et al. (1970). The M_3 with a width of 9.7 is not a *P. anomalus*, but an *Apodemus dominans*. De Bruijn has noted this already in his catalogue of measurements, but the correction was not made in the publication. The correct minimum is 10.9, which makes variability normal. The same goes for the M^3. The width of 12.6 refers to a specimen, that has already been recognized as an *A. dominans* by de Bruijn. The correct range for the width of M^3 of *P. anomalus* is 10.1-11.5, with a normal variability.

V) *Paraethomys athmeniae* from Oued Athmenia, published by Coiffait & Coiffat (1981). The width of M_1 shows a high variability. This may be due to the fact that 3/4 of the material has a broad labial cingulum, which is absent in the rest of the material, if we interpret the original description correctly.

W) *Parapodemus barbarae* from Casa del Acero, published by Agustí et al. (1981). The M^2 presents a high variability value. We remeasured the part of this population that is stored in the Museo de Paleontología in Sabadell; our measurements differ from the values published by Agustí et al. (1981); we found a higher minimum and a lower maximum. We were not able to revise the other part of the material that is stored in the Villalta collection.

X) *Parapodemus barbarae* from Crevillente 8 (unpublished). In all dental elements two different morphotypes are present; these are best recognized in M^1 and M^2. Probably we are dealing with two different species, but the small number of specimens does not allow a sound taxonomic separation.

Y) *Parapodemus lugdunensis* from Tortajada A, published by van de Weerd (1976). Van de Weerd states a maximum value of 13.5 for the width of M^1. According to the catalogue of van de Weerd's measurements, which was kindly put at our disposal by Dr H. de Bruijn (Utrecht), the maximum is 12.5, which makes variability normal.

Z) *Parapodemus lugdunensis* from Vivero de Pinos, published by Adrover (1986). This is a sample with few specimens. Nevertheless Adrover (1986) already noted the existence of two morphotypes. Furthermore, in the length/width diagrams of his fig. 46 two groups of data may be recognized. Probably the sample contains two species, but the scarcity of the material does not permit a separation.

1) *Progonomys hispanicus* from Peralejos C, published by van de Weerd (1976). The maximum value of 13.9 for the length of M_2 was taken on a misidentified specimen. The specimen is damaged postero-labially, in such a way that the accessory cusps of the labial cingulum are missing. Van de Weerd probably did not notice the

damage, and classified the specimen as *P. hispanicus*, a species with poorly developed accessory cusps. In reality it belongs to *P. cathalai*. The true limits for the lengths of M_2 in Peralejos C are for *P. hispanicus* 10.2-12.5, and for *P. cathalai* 13.9-14.9.

2) *Rhagamys orthodon* from Conca, published by Brandy (1978, 1979). Brandy (1978) states that his data are incomplete and present only an indication, and that the mean degree of wear of the teeth in this locality is very high. In a genus like *Rhagamys* a combination of fresh and very worn specimens may account for a high variability value. Furthermore he says that the material comes from fragments of bone-bearing breccia that were kept at the 'Ecole normale supérieure, Rue d'Ulm, Paris'. Since faunistic homogeneity in karst fissure is always a problem, such a collection taken from blocks that are no longer in situ, should be treated with greatest care.

3) *Rhagapodemus frequens* from Tourkobounia 1, published by de Bruijn & van der Meulen (1975). The minimum value of 11.4 for the width of M_1 is incorrect; we remeasured the specimen and found 13.0. Since this is not the smallest specimen the correct range is 12.7-14.9, with a normal variability.

4) *Stephanomys amplius* from Moreda, published by Ruiz Bustos (1986). He treats this material as one single species from a homogeneous locality. We agree with all other authors who have studied the fauna of Moreda (de Bruijn, 1973, 1974; Castillo, 1990; Cordy, 1976; van de Weerd et al., 1977), that there are more than one species of *Stephanomys* in this locality, and that there are various phases of karst infilling, that present lithological and faunistical differences (Agustí et al., 1986; Castillo, 1990). It is not surprising that Ruiz Bustos' interpretation of the situation leads to the highest variability values found in our entire study.

5) *Stephanomys balcellsi* from Casablanca B, published by Gil & Sesé (1985). The length of M^2 shows a high variability. The locality is a karst fissure. See the remarks under B. In view of the description, the figures, and the measurements, it is not impossible that the material contains a few specimens of a smaller form.

6) *Stephanomys donnezani* from Moreda 1A, and
7) *Stephanomys minor* from Moreda 1B, both studied by Castillo (1990). Moreda 1A and Moreda 1B represent two different phases of deposition in a single karst cavity (Moreda). Separate sampling reduced the value of V' considerably in comparison with the original global sampling (see remarks under 4), though several values still are high.

In the population of *Stephanomys donnezani* from Moreda 1A a large number of teeth is very much worn, and a combination of fresh and very worn specimens (in hypsodont teeth) may result in a high variability value, specially in M^1 (Fig. 3).

The population of *Stephanomys minor* from Moreda 1B shows a high value of V' for the length of M_2. According to Castillo (pers. comm.) this may be due to the shape of the terminal heel: in some specimens it is narrow, and restricted to the space between the hypoconid and entoconid; in other specimens it is a cingulum that partly surrounds the entoconid, and is connected to the lingual wall of this cusp.

8) *Stephanomys ramblensis* from Masada del Valle 7, published by van de Weerd (1976). The true value for the minimum width of M^1 is 15.1, according to van de Weerd's catalogue. The published value of 13.1 was erroneously taken from a different column in van de Weerd's catalogue. Variability is normal.

9) *Stephanomys thaleri* from Belmez, studied by Castillo (1990). We found a high variability value for the width of M^1 (Fig. 4). In this locality two species of *Stephanomys* are found; the M^1 are difficult to separate, because they are morphologically similar, and the size ranges overlap (Castillo, pers. comm.).

×) *Valerymys juniensis* from Canteras de Jun, published by Padial Ojeda & Ruiz Bustos (1989). We have not been allowed to study this material, so, unfortunately, our discussion cannot be conclusive. The material was first studied by Padial Ojeda (1986), who described it as *V. turoliensis juni* subsp. nov. In view of the differences in measurements and number of specimens between the paper by Padial Ojeda and the one by Padial Ojeda & Ruiz Bustos a revision of the material is desirable.

$) *Valerymys vireti* from Tortajada A, published by van de Weerd (1976). Van de Weerd states a minimum value of 13.0 for the width of M^2. In van de Weerd's catalogue we have seen that this value refers to an M^3, which follows the M^2's immediately. The real minimum for M^2 is 15.9, which results in a normal variability.

&) *Kritimys catreus* from Stavros, published by Mayhew (1977). Width of M^2 and M^3, and to a lesser extent length of M^1, are quite variable. Mayhew (1977) recognizes considerable differences between various populations of *Kritimys*, but rejects the suggestion by Kuss & Misonne (1968) that various species may be present. In our opinion his biometrical proof for the existence of only one species is insufficient.

□) The samples marked by this symbol are samples of Recent *Apodemus sylvaticus* and *A. flavicolis*, from Burgos, Claux, Guadarrama, Kirchdorf, and Treviers, studied by Pasquier (1974). In these samples the M2 and M3, both from the lower and the upper jaw show high variability values. This may be due to the technical difficulty of measuring dental elements in jaws. This difficulty is less in the upper and lower M1, which may explain, that in these cases variability is normal.

Δ) The samples of *Karnimata huxleyi* and *Mus auctor* from the locality DP13, and *Progonomys debruijni* from locality 182A, published by Jacobs (1978) are marked by this symbol. In several cases they show high variability values for which we do not have an explanation because we are not familiar with the material.

Discussion

In Table 1 the results of the calculations for the Muridae are given, and compared with the results obtained by Freudenthal & Cuenca Bescós (1984) for the Cricetidae.

In general the variability values in Cricetidae show the following pattern: Variability is lowest in the lengths of M_1, M^1, and M_2, and highest in the lengths of M_3 and M^3. In the M1 and M2 the lengths are less variable than the widths; in the M3 the lengths are more variable than the widths. The standard deviations in the M1 and M2 vary between 3.22 and 3.90, in M_3 they are 4.12 and 4.76, in M^3 they are 5.36 and 5.12.

The pattern in Muridae is quite similar, but there are some differences: The standard deviations are lowest in the M1 and M2, higher in M_3, and highest in M^3, but all values are higher than the corresponding ones in Cricetidae. The widths of M^1 and M^2 present lower variability values than the lengths. This may be due to the shape of these elements, that may cause considerable differences between measurements of fresh and worn specimens in hypsodont species. For that reason we decided to make a separate analysis for the genus *Stephanomys*, where hypsodonty is an important feature, and the rest of the genera, where hypsodonty is less marked. This analysis is represented in Table 2.

The variability values for the lengths of M^1 and M^2 in the group of 'Muridae without *Stephanomys*' are lower than they are for all murid genera, but still the widths of these molars are less variable than the lengths; in fact the width of M^1 now is only 13.02, the lowest of the 12 values.

On the other hand, within *Stephanomys*, the values for the lengths of M^1 and M^2 are extremely high. The unreliability of measurements of the lengths of M^1 and M^2 in hypsodont murid molars is confirmed by this result. When we leave out the

Table 1. List of means and standard deviations of $V'/\sqrt{\log N}$ in Muridae and Cricetidae.

	Muridae			Cricetidae		
lement	N	$V'/\sqrt{\log N}$	σ	N	$V'/\sqrt{\log N}$	σ
Length M_1	222	13.30	4.41	126	13.48	3.22
Width M_1	225	15.71	5.18	126	15.30	3.90
Length M^1	213	14.44	4.45	118	13.38	3.38
Width M^1	217	13.25	4.02	118	15.18	3.62
Length M_2	191	14.02	4.29	124	13.03	3.60
Width M_2	194	14.38	4.22	124	14.55	3.77
Length M^2	187	16.20	4.66	113	14.82	3.69
Width M^2	188	14.22	5.15	113	15.15	3.66
Length M_3	120	17.78	5.92	96	16.24	4.12
Width M_3	121	16.19	5.26	99	15.77	4.76
Length M^3	105	19.68	6.58	85	19.61	5.36
Width M^3	104	18.69	6.76	85	16.51	5.12

Table 2. List of means and standard deviations of $V'/\sqrt{\log N}$ for Muridae without *Stephonomys*, and *Stephanomys* separately.

	Muridae except *Stephanomys*			*Stephanomys*		
Element	N	$V'/\sqrt{\log N}$	σ	N	$V'/\sqrt{\log N}$	σ
Length M_1	190	13.24	4.37	32	13.63	4.71
Width M_1	192	15.89	5.24	33	14.65	4.78
Length M^1	180	13.94	4.01	33	17.14	5.71
Width M^1	183	13.02	3.95	34	14.45	4.26
Length M_2	160	14.08	4.43	31	13.70	3.47
Width M_2	163	14.30	4.33	31	14.80	3.66
Length M^2	153	15.87	4.50	34	17.64	5.13
Width M^2	144	14.15	5.26	34	14.50	4.66
Length M_3	99	17.96	6.00	21	16.93	5.58
Width M_3	99	16.57	5.46	22	14.48	3.93
Length M^3	85	19.82	7.19	20	19.07	2.78
Width M^3	84	19.26	7.13	20	16.28	4.22

population of *Stephanomys* described by Ruiz Bustos (1986) from Moreda, all values for *Stephanomys* are considerably lower (e.g. length M^1 16.48 instead of 17.14), which simply means that this cannot be a homogeneous population. It would be interesting to make a further detailed analysis of the variability differences per genus, but the number of populations (e.g. 20 to 30 in *Stephanomys*) is not sufficient to give reliable results.

We made one other analysis of our material: comparing the variability in *Apodemus* with that in four genera of comparable size: *Progonomys, Parapodemus, Occitanomys*, and *Castillomys*. These four genera were taken together, because none of them separately yielded a sufficient number of samples. The results are given in Table 3.

Apparently variability is higher in *Apodemus* than in the other genera. There may be various explanations for this feature: many of our *Apodemus* samples are from karst fissures, where heterogeneous faunas are more frequent than in stratified deposits; *Apodemus* species tend to have more hypsodont molars than the species in the other genera, which makes measuring more difficult; all our samples of Recent material belong to species of the genus *Apodemus*, and consist mainly of complete jaws, in which the teeth are difficult to measure; in the other genera we generally have isolated teeth that can be measured more easily. The high variability in *Apodemus* may be due to a combination of these circumstances, but other factors may be involved too.

We have analyzed a total of 67 samples of *Apodemus* (part of them with insufficient data). This material contains 12 populations of *A. flavicollis* or *A.* cf. *flavi-*

Table 3. List of the means and standard deviations of $V'\sqrt{\log N}$ for *Apodemus* compared with the values for *Progonomys, Parapodemus, Occitanomys,* and *Castillomys.*

Element	*Progonomys, Parapodemus Occitanomys, Castillomys*			*Apodemus*		
	N	$V'/\sqrt{\log N}$	σ	N	$V'/\sqrt{\log N}$	σ
Length M_1	75	13.00	4.29	56	15.13	5.63
Width M_1	76	15.29	4.59	56	17.63	6.64
Length M^1	76	13.91	3.58	55	14.93	4.51
Width M^1	78	13.66	4.05	55	13.05	4.00
Length M_2	65	13.55	4.11	48	14.88	5.29
Width M_2	68	14.21	4.50	48	15.26	4.34
Length M^2	63	16.06	4.58	45	16.41	4.64
Width M^2	63	14.54	4.45	45	14.27	5.99
Length M_3	28	17.35	5.08	37	19.16	6.72
Width M_3	28	15.28	5.26	37	18.64	5.41
Length M^3	23	21.45	6.89	27	22.77	8.01
Width M^3	23	19.17	6.94	26	23.59	7.66

collis, and 14 samples of *A. sylvaticus* or *A.* cf. *sylvaticus*; among these are 6 and 7 samples respectively with high variability: 50% of the total number. In many of these cases the authors express their doubts about the specific determination. Possibly many of these samples contain a mixture of the two species. This is no wonder, since even biologists working with complete animals instead of merely teeth and bones, have serious trouble in distinguishing these two species in those areas where they concur.

From our samples of five or more teeth (c. 200 samples per element for M1 and M2; 100 to 120 samples per element for M3) we selected c. 40 populations with high variability coefficient V'. Revision of the material in various institutions showed that in 11 cases the high variability was due to an error in the published measurement. In many other cases study of the original publication made us suggest that the population possibly was not homogeneous and contained more than one species. Only in a small number of cases we did not find a reasonable explanation. On the whole we may say, that V' is a good tool to judge the homogeneity of a population.

In our total material of over 250 samples for the first molars, over 200 for the second molars, and about 150 for the third molars, c. 20% of the samples contain less than 5 specimens. These samples were not used in the calculation of V' and σ and they do not appear in the plots and histograms. However, after calculation of the mean variability and σ of the samples of 5 or more specimens, the small samples were compared with these values. As a rough conclusion we may say, that about half the small samples fall within the range of -1.5 σ to +1.5 σ. The other half have variability values lower than -1.5 σ. Only rarely the variability value of a small sample exceeds +1.5 σ. Though not a decisive criterium, this may help in deciding whether a small sample (less than 5 specimens) is homogeneous or not.

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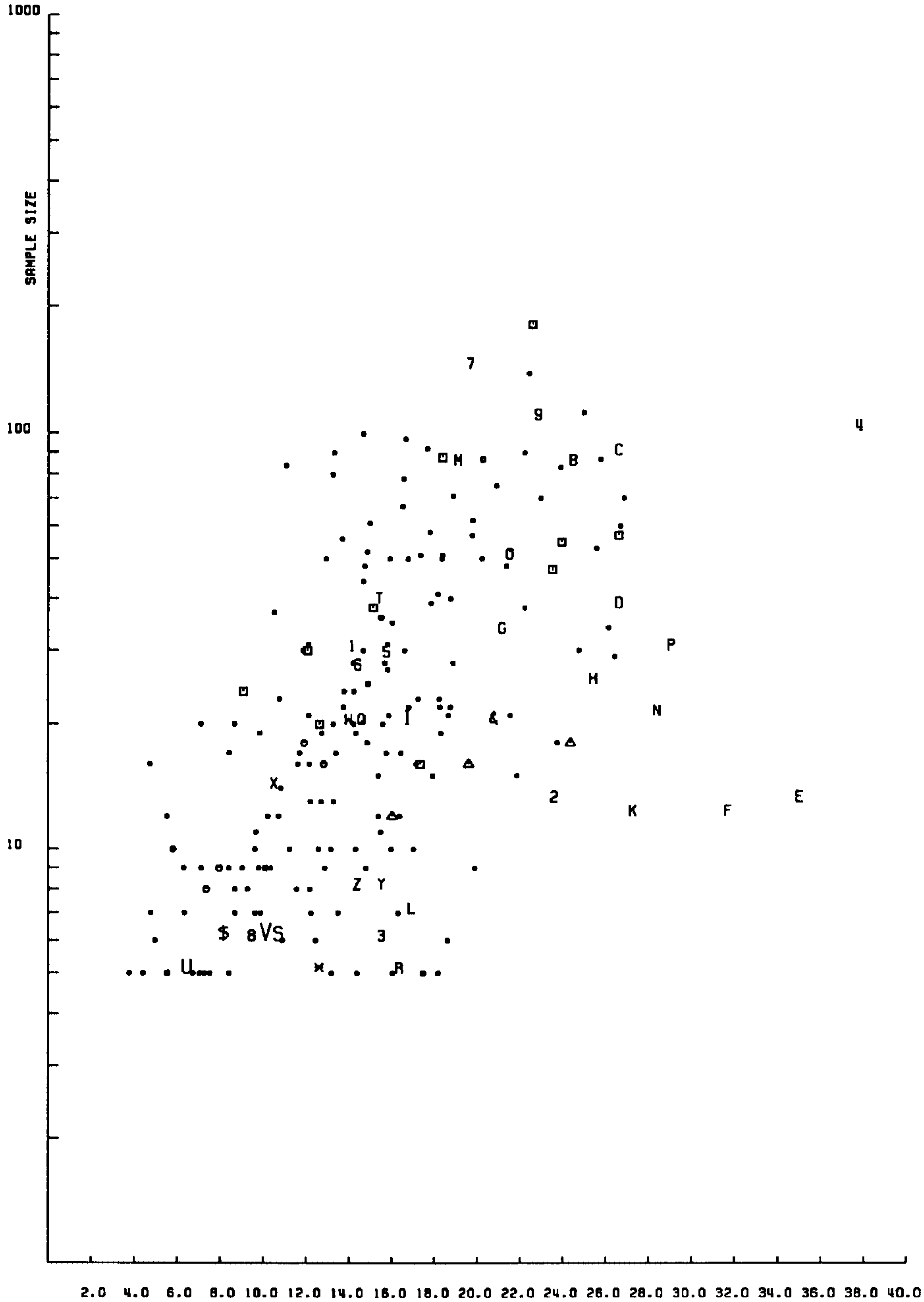

Fig. 1. Relation of V' and sample size for length of M_1. Vertical scale is logarithmic.

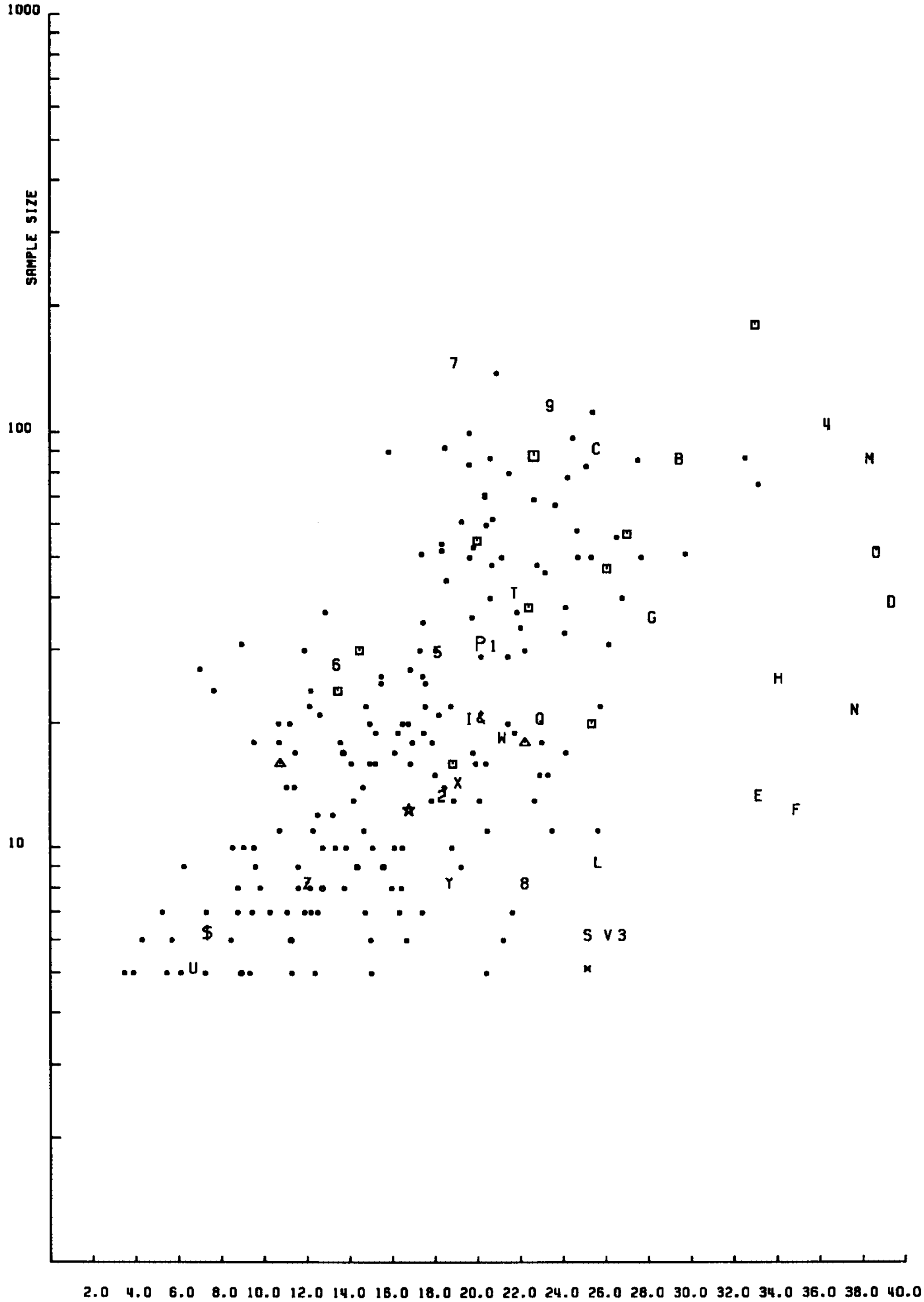

Fig. 2. Relation of V' and sample size for width of M_1. Vertical scale is logarithmic. The ★ indicates the position of the symbols K and Δ (*Apodemus mystacinus* from Cueva Victoria and *Progonomys debruijni* from loc. 182A).

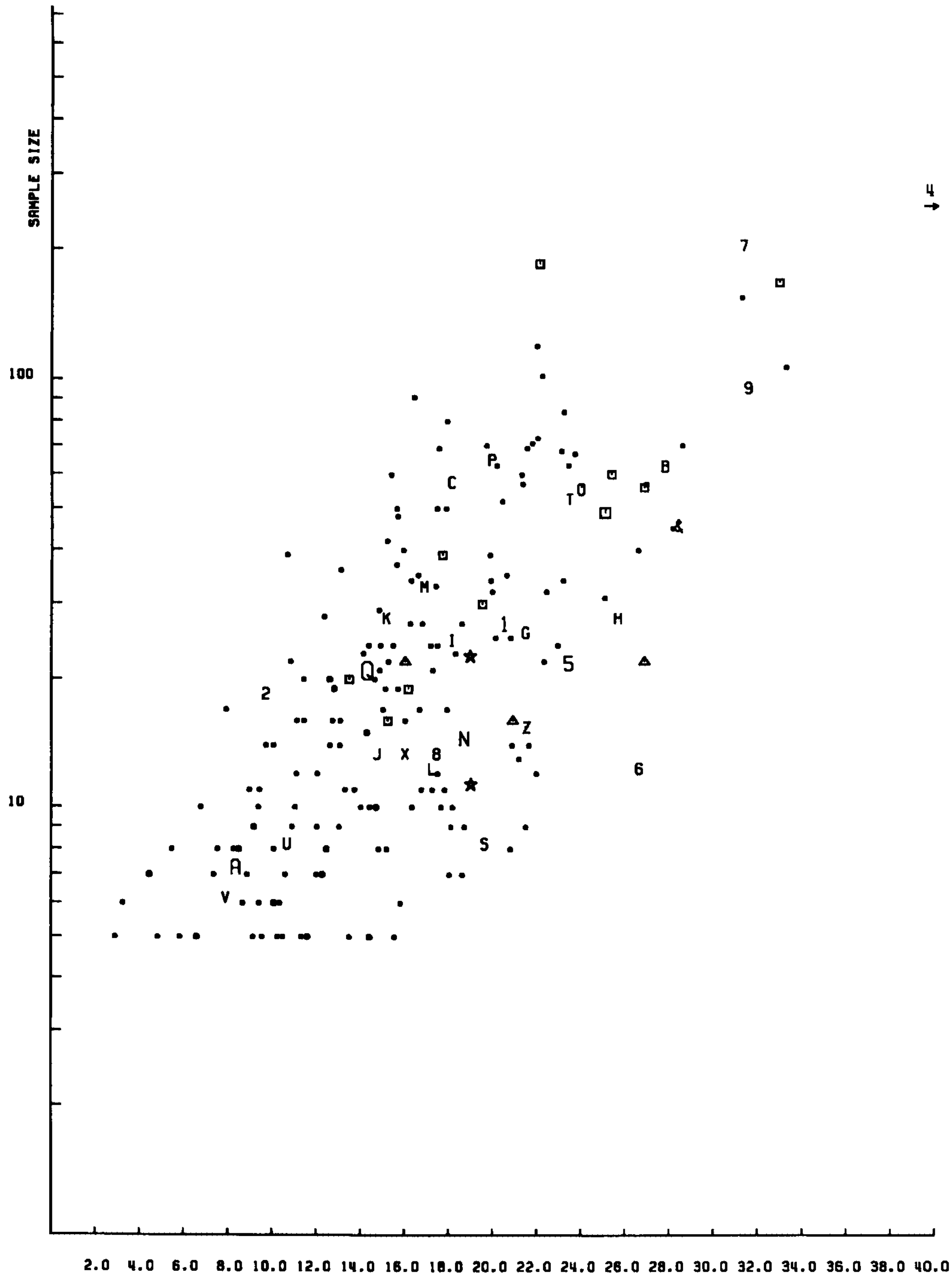

Fig. 3. Relation of V' and sample size for length of M¹. Vertical scale is logarithmic. The upper ☆ indicates the position of the symbols D and W (*Apodemus dominans* from Wèze and *Parapodemus barbarae* from Casa del Acero); the lower ☆ indicates the position of the symbols F and 3 (*Apodemus flavicollis* from Atapuerca TD-6 and *Rhagapodemus frequens* from Tourkobounia 1).

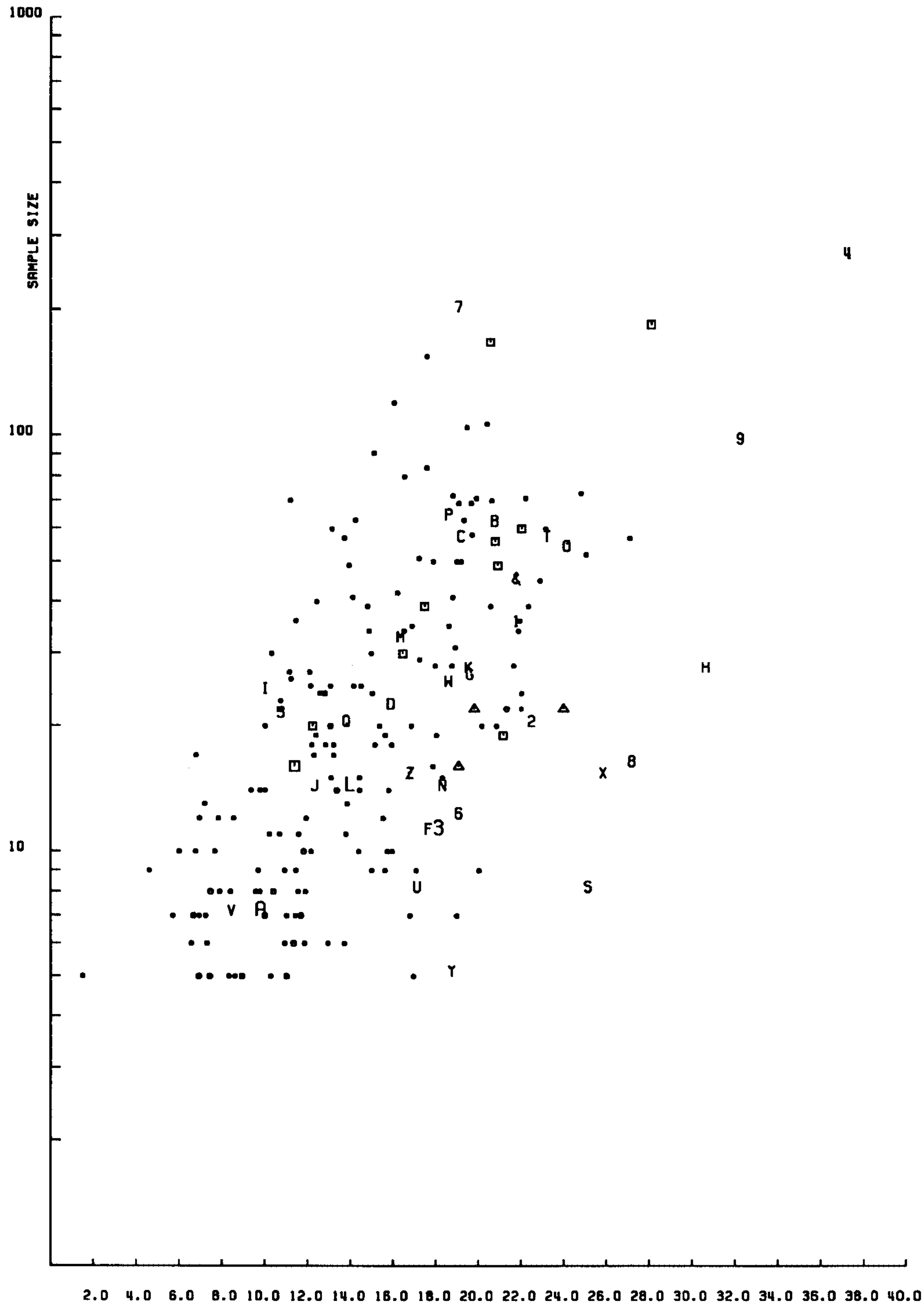

Fig. 4. Relation of V' and sample size for width of M^1. Vertical scale is logarithmic.

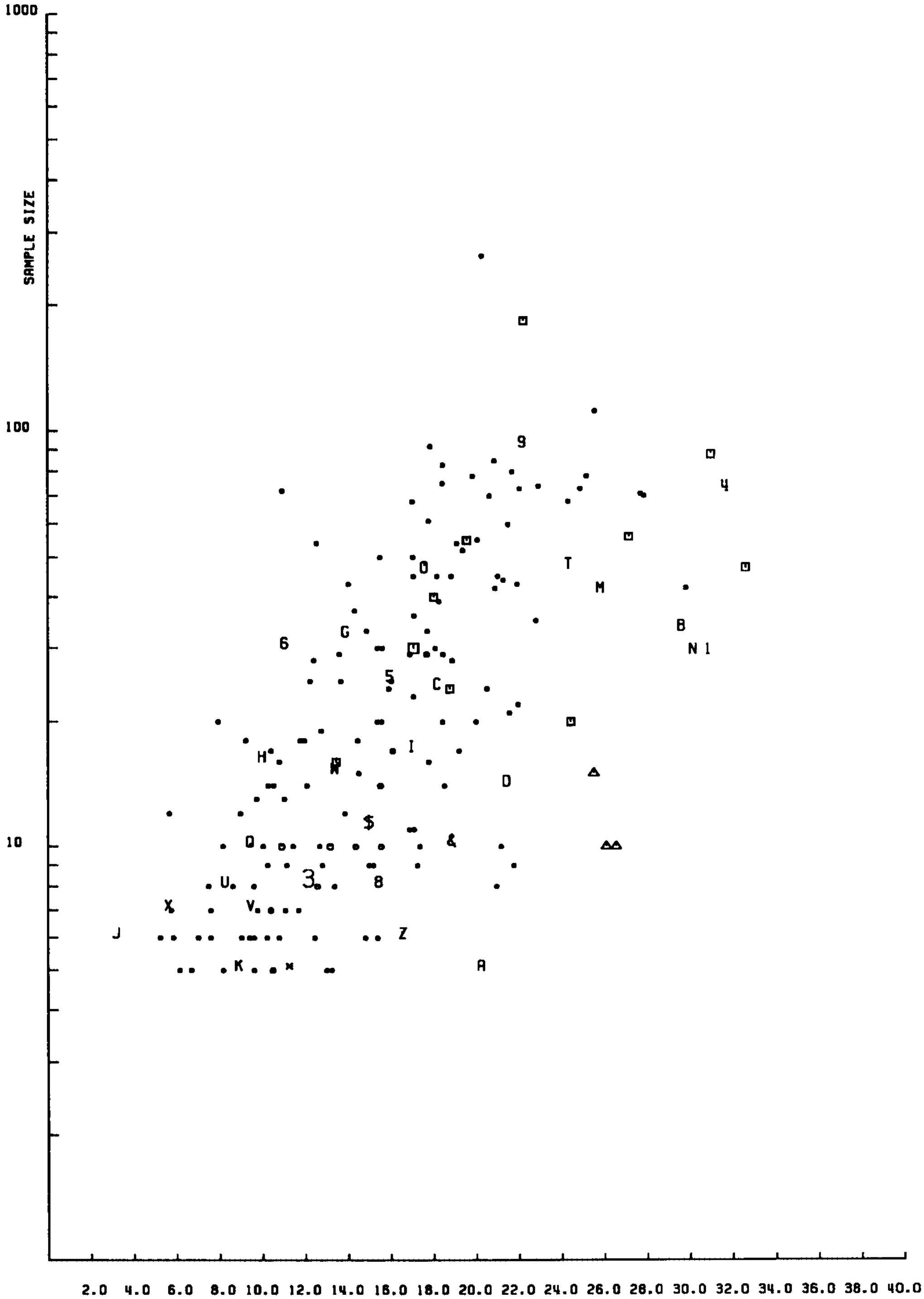

Fig. 5. Relation of V' and sample size for length of M_2. Vertical scale is logarithmic.

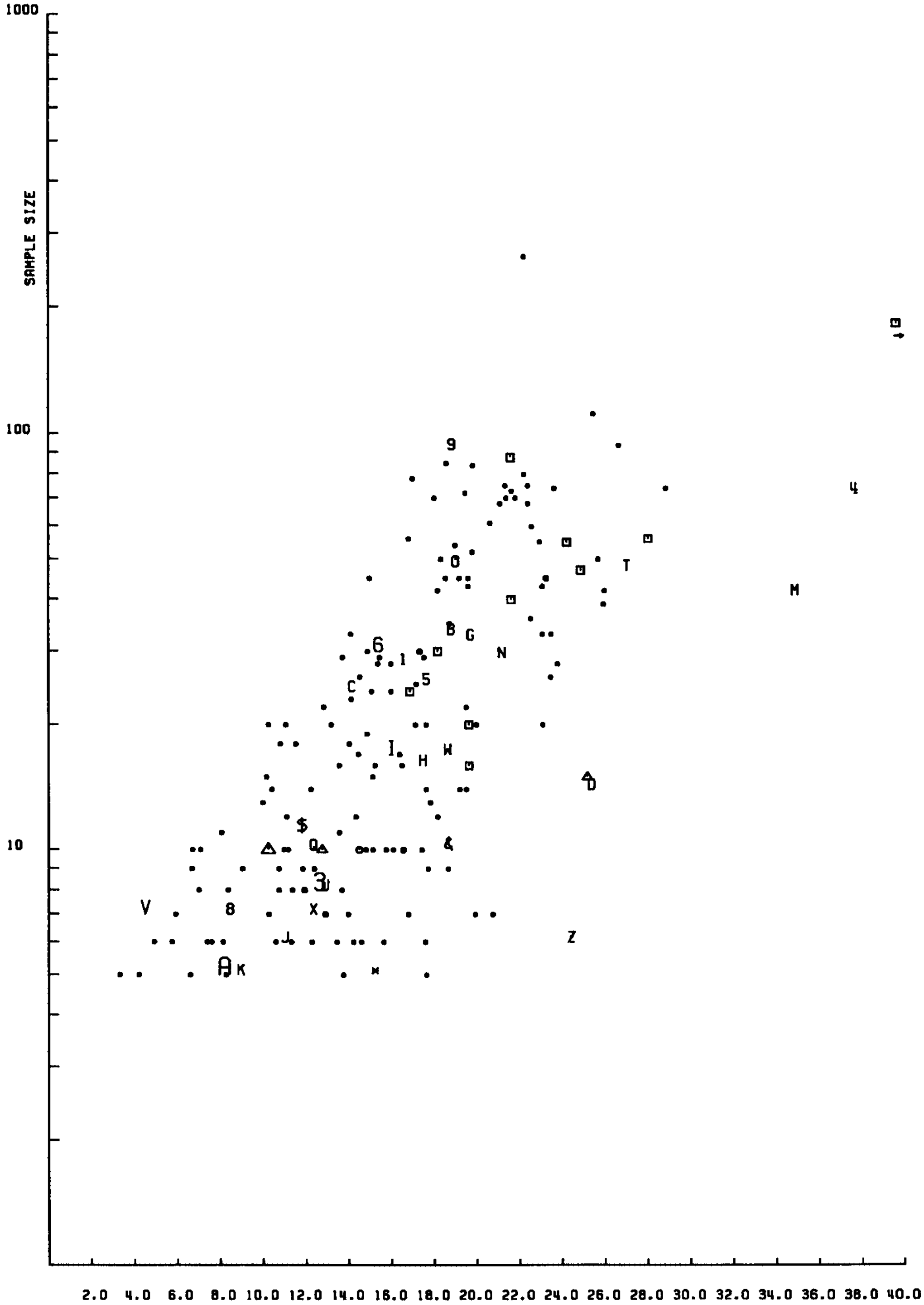

Fig. 6. Relation of V' and sample size for width of M_2. Vertical scale is logarithmic.

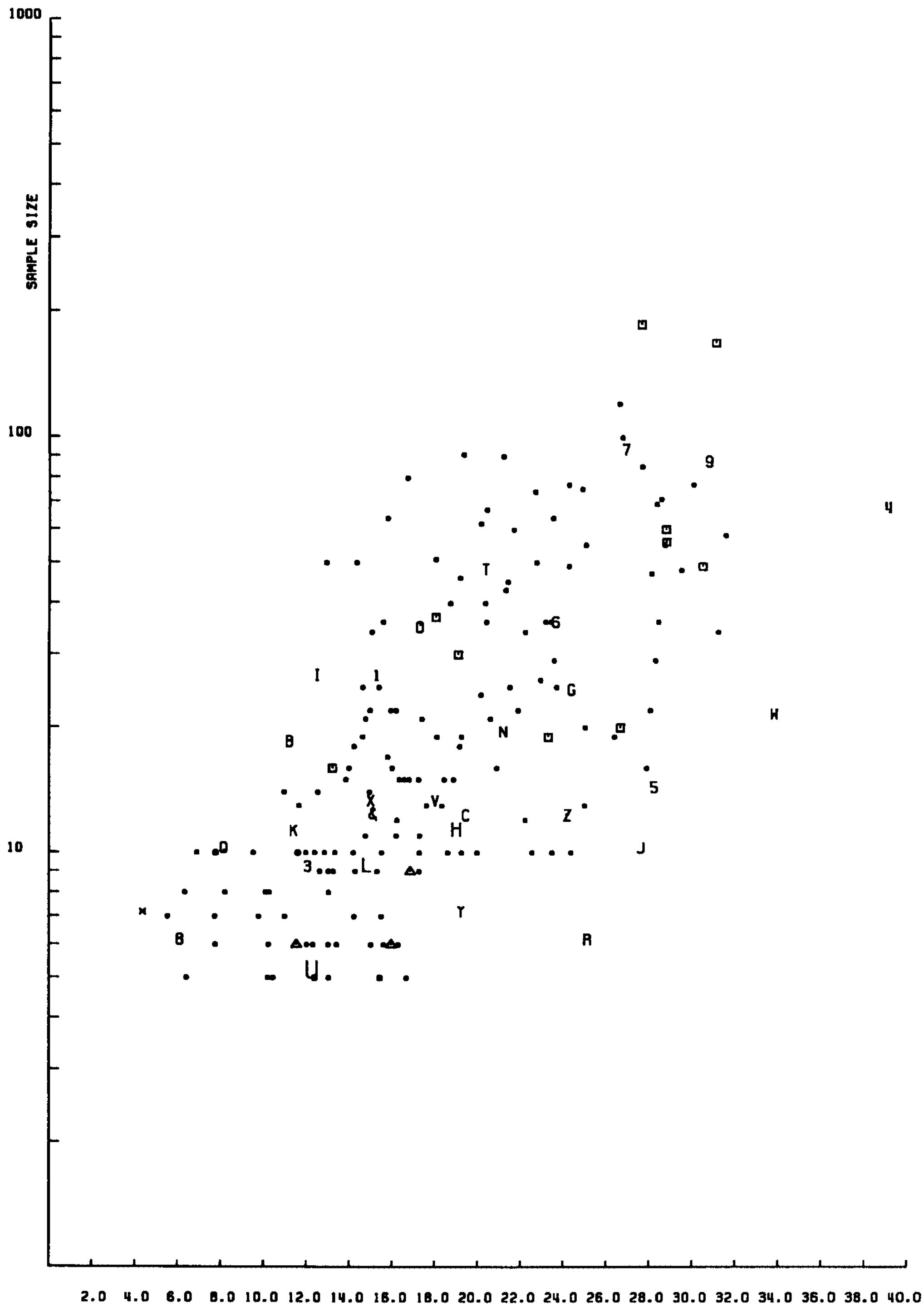

Fig. 7. Relation of V' and sample size for length of M^2. Vertical scale is logarithmic.

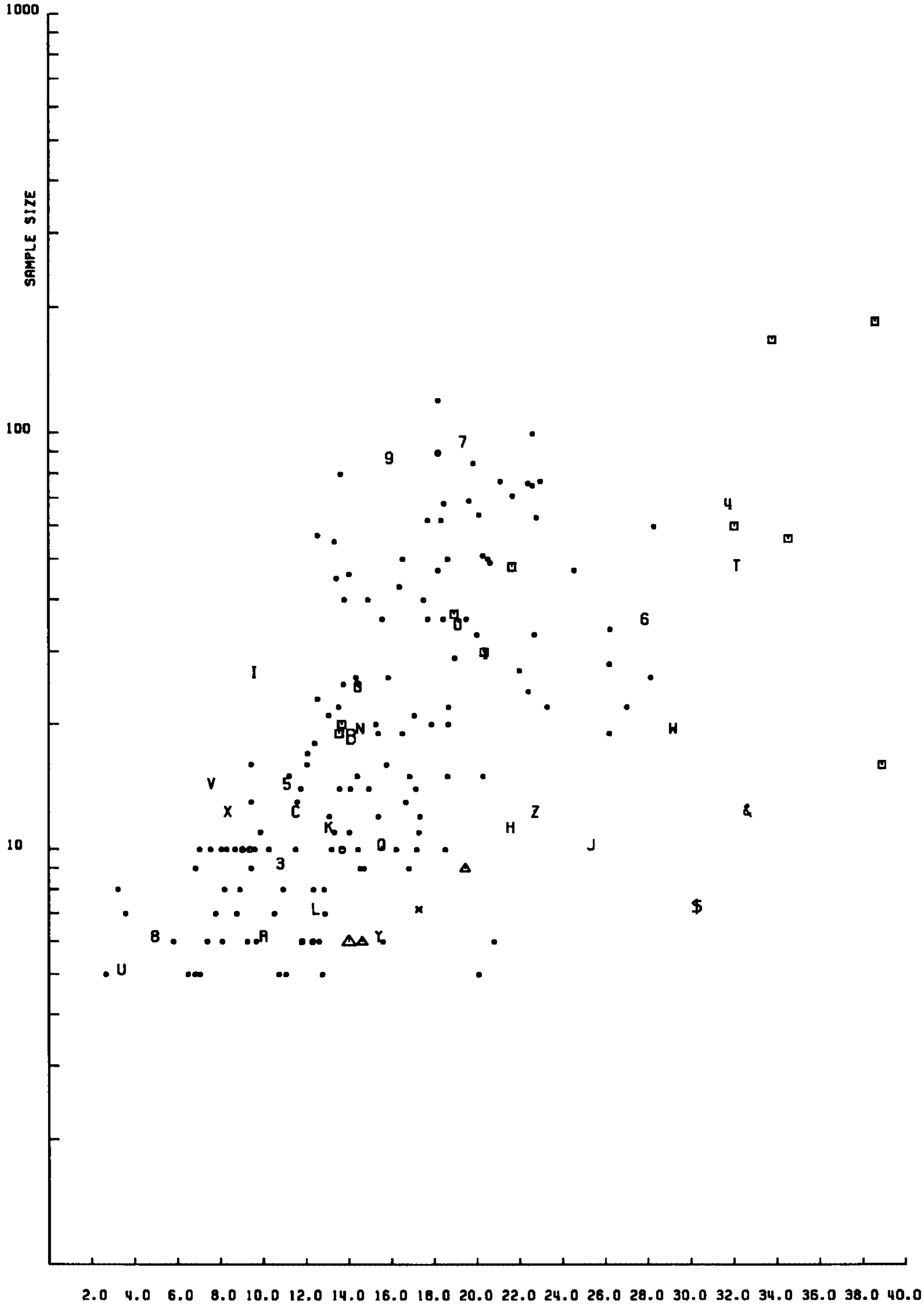

Fig. 8. Relation of V' and sample size for width of M^2. Vertical scale is logarithmic.

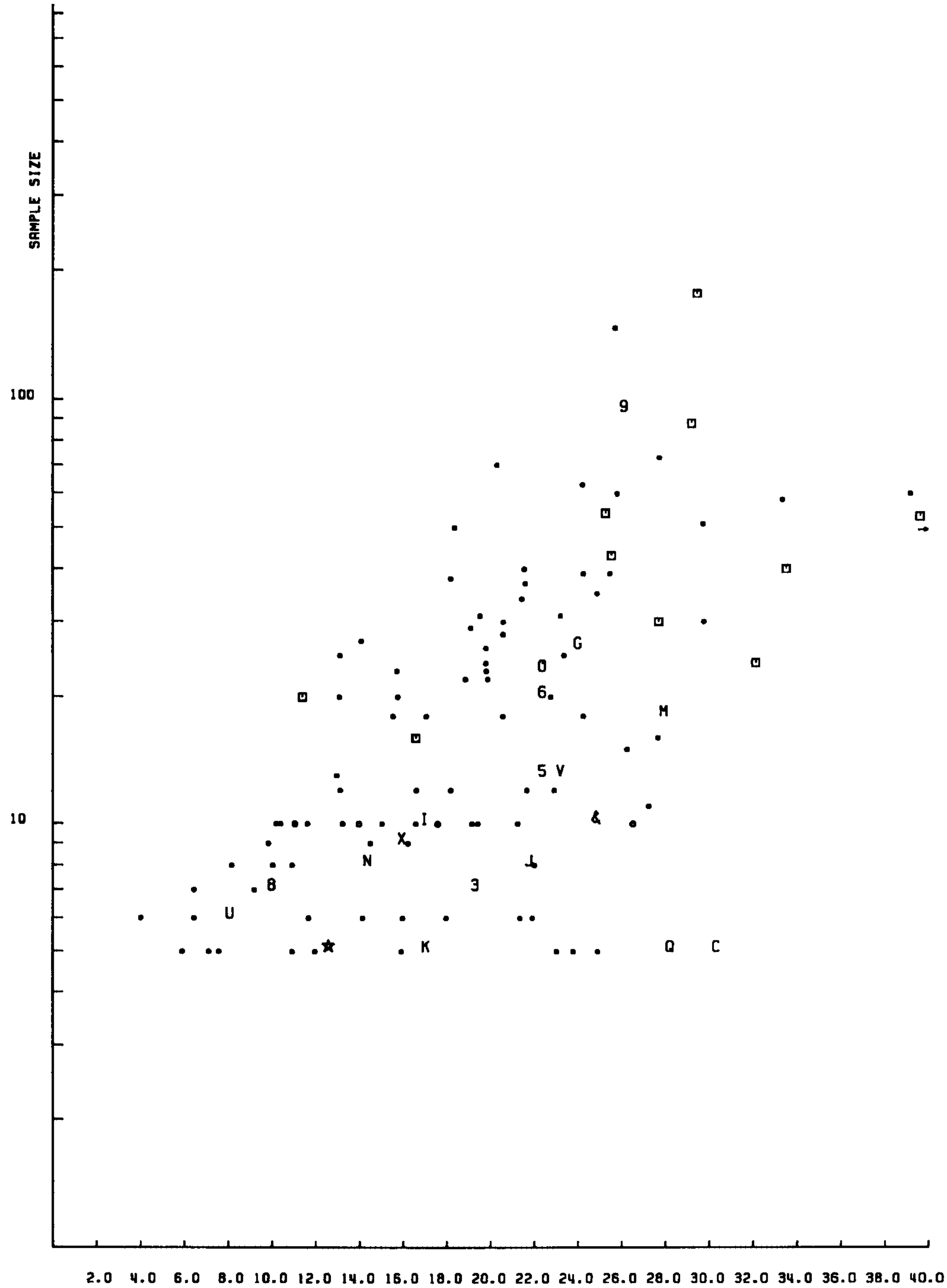

Fig. 9. Relation of V' and sample size for length of M_3. Vertical scale is logarithmic. The ★ indicates the position of the symbols D and H (*Apodemus dominans* from Wèze and *Apodemus flavicollis* from Cueva de las Graderas).

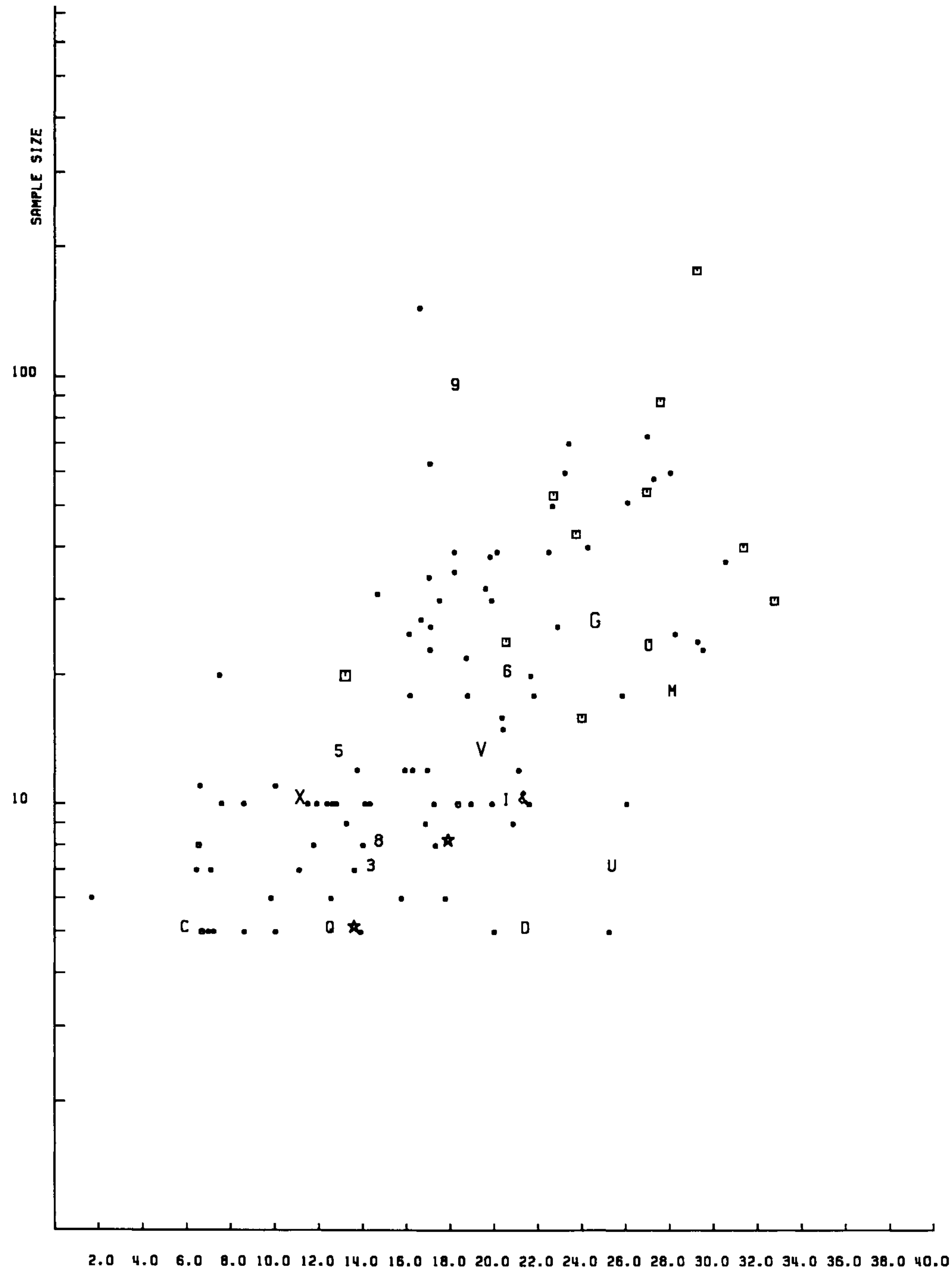

Fig. 10. Relation of V' and sample size for width of M_3. Vertical scale is logarithmic. The upper ★ indicates the position of the symbols J and N (*Apodemus gudrunae* from Salobreña and *Apodemus sylvaticus* from Prince à Grimaldi); the lower ★ indicates the position of the symbols H and K (*Apodemus flavicollis* from Cueva de las Graderas and *Apodemus mystacinus* from Cueva Victoria).

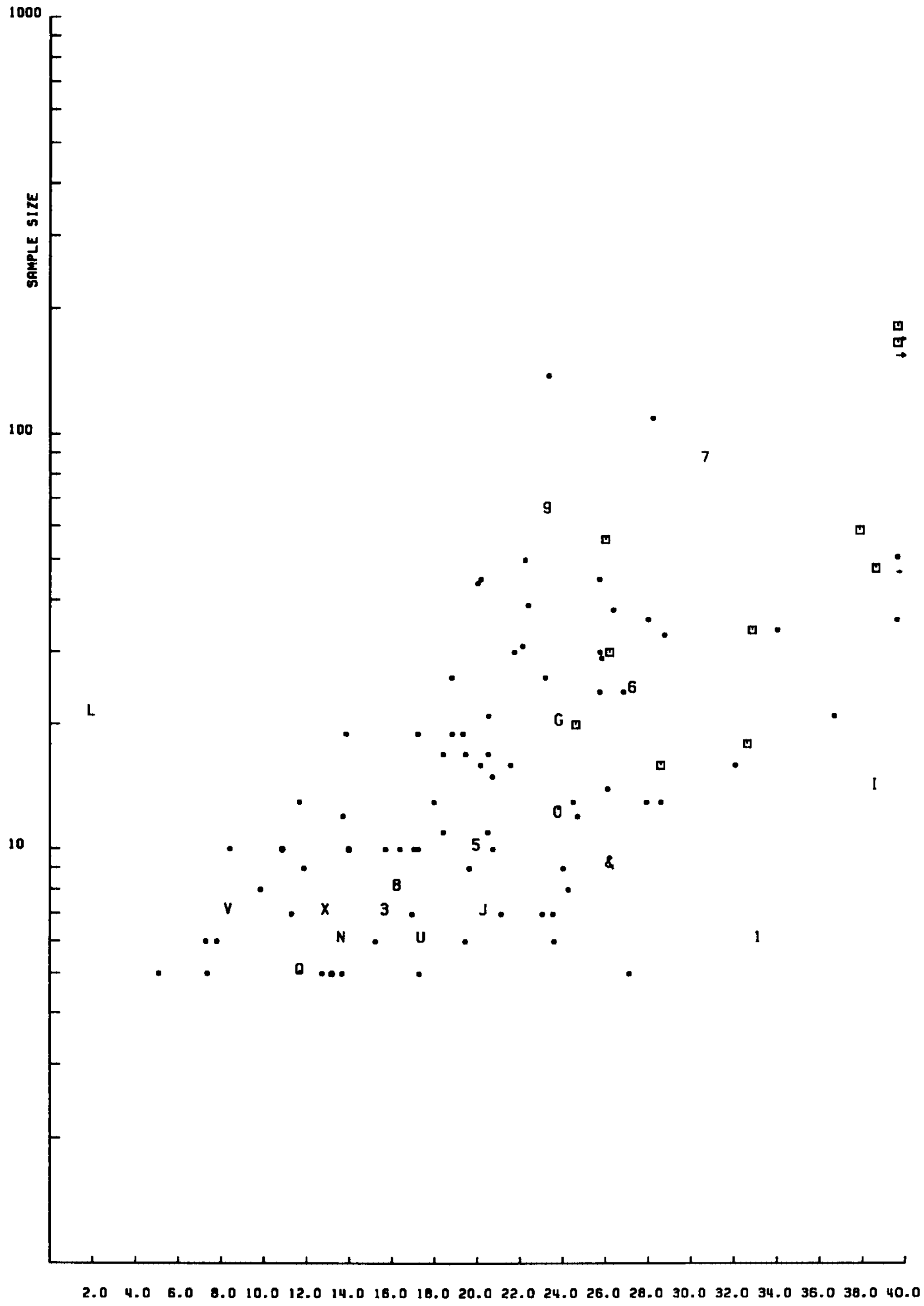

Fig. 11. Relation of V' and sample size for length of M^3. Vertical scale is logarithmic.

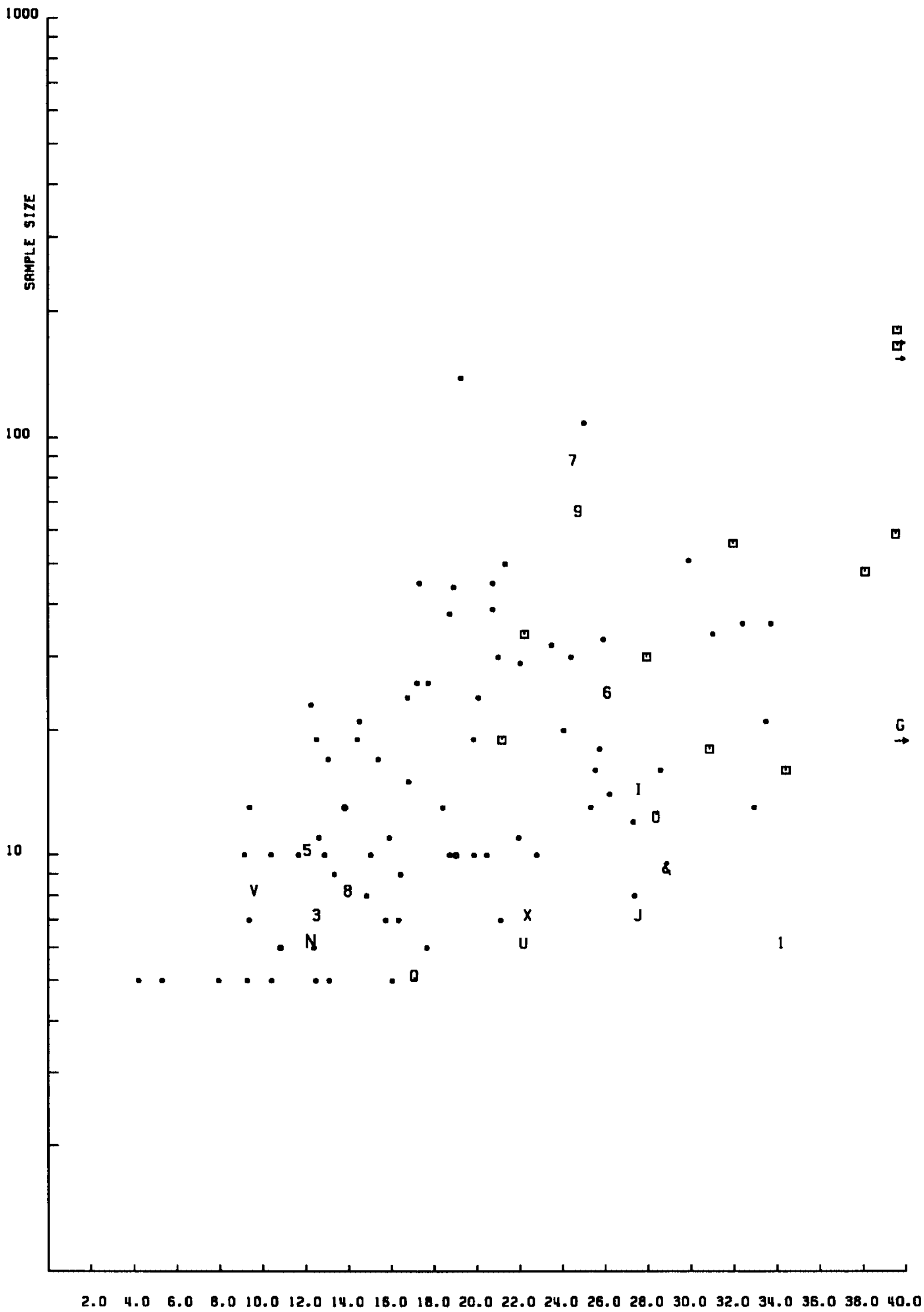

Fig. 12. Relation of V' and sample size for width of M^3. Vertical scale is logarithmic.

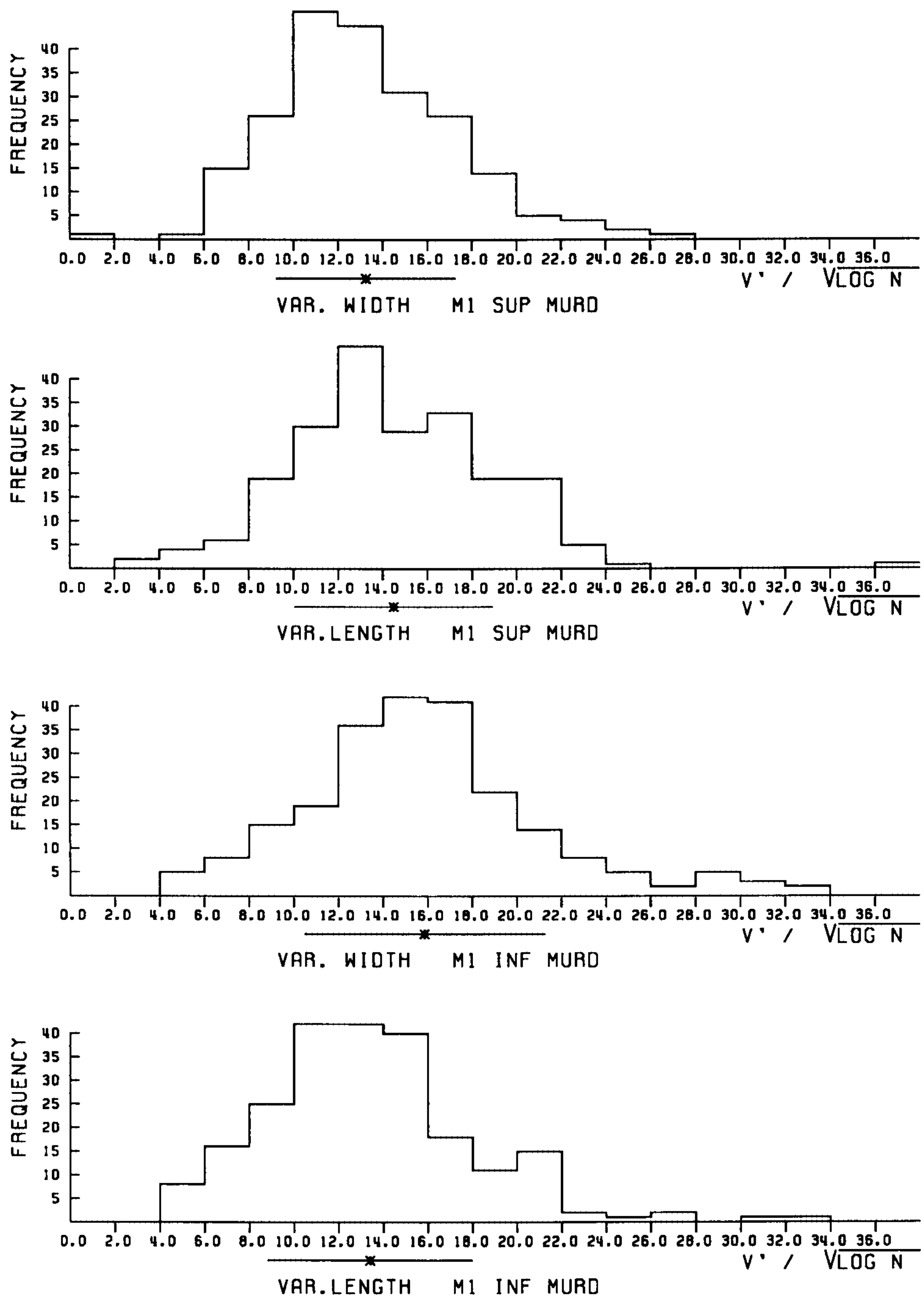

Fig. 13. Histograms of V'/√log N for the first molars of Muridae. The line under each histogram represents 2 standard deviations, the ✻ indicates the mean value.

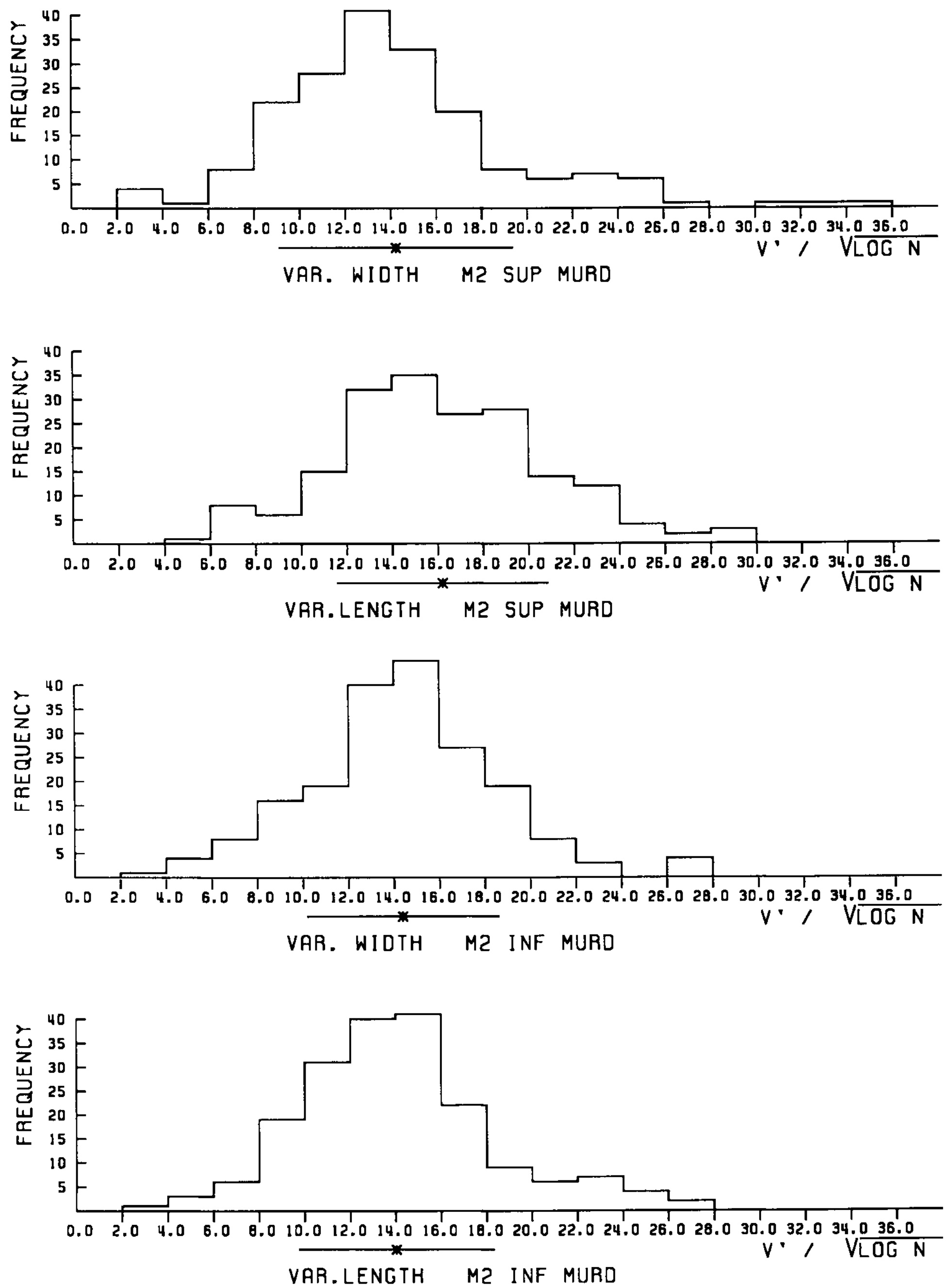

Fig. 14. Histograms of $V'/\sqrt{\log N}$ for the second molars of Muridae. The line under each histogram represents 2 standard deviations, the * indicates the mean value.

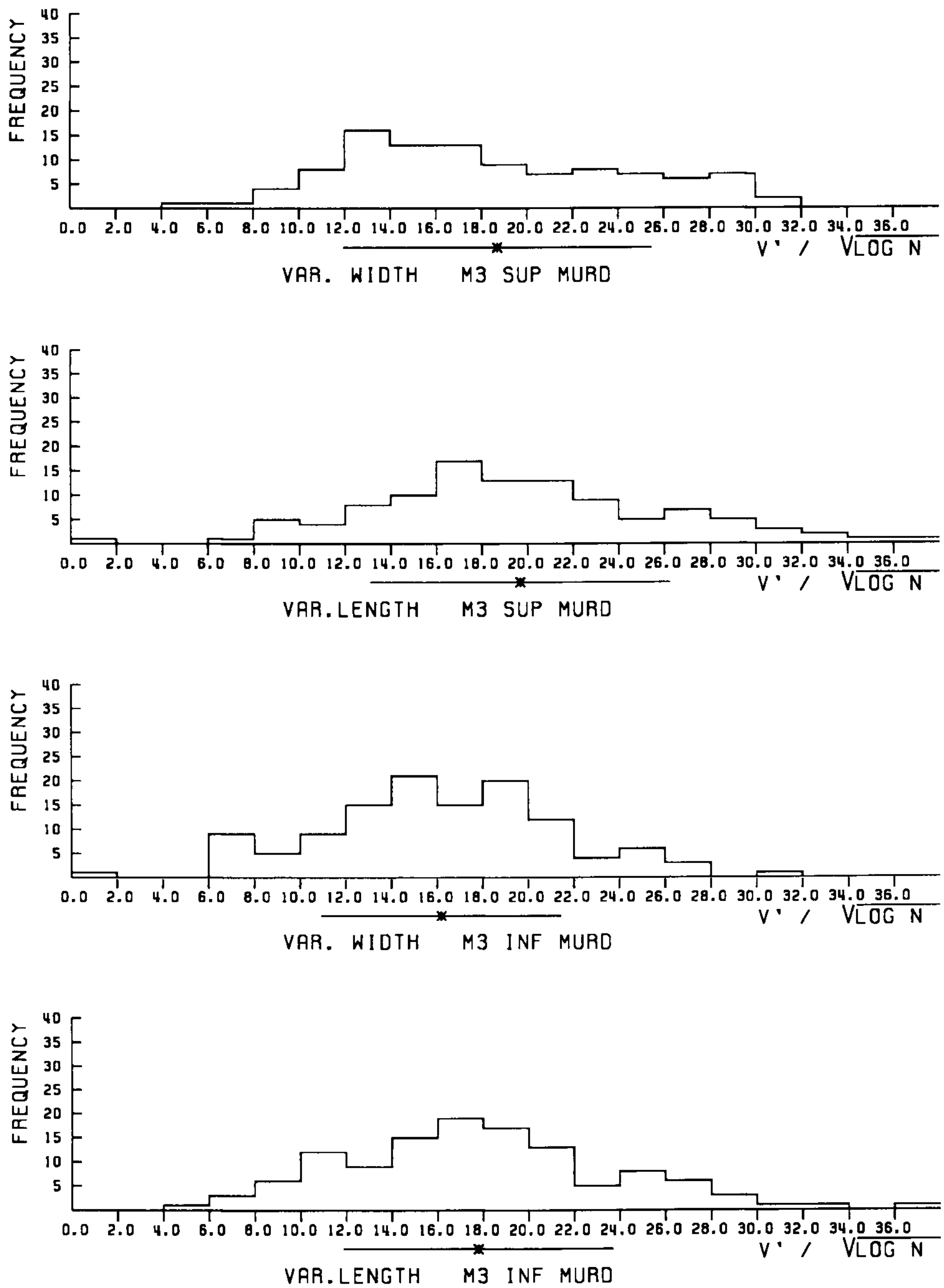

Fig. 15. Histograms of $V'/\sqrt{\log N}$ for the third molars of Muridae. The line under each histogram represents 2 standard deviations, the ✱ indicates the mean value.