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Gustaf Retzius and spermatology

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Gustaf Retzius (1842-1919) began his investigations of animal sperm when he was in his sixties and thus had reached an age when creativity is claimed to be decreased (Fig. 1). His ambitions and energy were undiminished, however, and his spermatological contributions were to become the standard towards which other scientists would strive.

The eleventh volume of Biologische Untersuchungen, Neue Folge, from the year 1904 is the first volume to contain several papers on sperm structure. In its preface, Retzius states the aim of his studies (translated from the original): In order to understand the fertilization process it is necessary to undertake a detailed investigation of the two parties at fertilization – the spermatozoon and the oocyte. He also claimed it to be necessary to study spermiogenesis in order to be able to interpret the homologies.

He never came to study the fertilization process, however, and the species in which he examined the spermiogenetic events were few. The strength of his work resides in two other features. One was the technical excellence. His investigations were at the top of what could and can be achieved by light microscopy (Figs. 2-6). Wherever possible he took his material from freshly killed animals, fixed their spermatozoa with osmium tetroxide or Zenker's fixative and performed the examination with a good Zeiss microscope provided with apochromatic lenses (numerical apertures 1.3 or 1.4). As source of light he preferred to use sun rays and was thus dependent of favorable weather for his work. According to some contemporary witnesses, he used every moment of daylight with hectic activity.

The other feature is more unique. He was able to procure material from nearly all major animal groups and from numerous animal species that from one point or another can be regarded as interesting. He thus examined the contents of the epididymal ducts or the seminiferous tubes or the isolated spermatozoa from over 400 animal species, out of which nearly half were vertebrates. A list of the species examined by him (with their scientific names updated) is given in the Appendix. The animals came from all six continents and many were bought from animal dealers in Sweden, Germany, or elsewhere. Other specimens were obtained from zoologists, hunters, or collectors for the natural history museums. It is certain that nobody before him had ever studied spermatozoa from such a wide range of animal species. Likewise it appears certain that no investigator in the future will be able to study fresh material from so many rare game animals. Nowadays it is technically hardly possible, nor ethically justifiable, to purchase an Australian echidna, a Thai gibbon, a Madagascan lemur, and a Japanese giant salamander in order to kill it and to study its testicular or epididymal contents. Nor would many investigators be able to afford the expenses involved in buying the animals paying from one's own pocket. It is fortunate that this unique investigation, which never is to be repeated, was performed with the best technique available and with a meticulous accuracy. He published Biologische Untersuchungen at his own expense and used the best methods for reproduction at the time. He was married to a rich woman, Anna Hierta Retzius, daughter to the founder of the biggest newspaper in Sweden, a woman who also had very high ambitions for her husband (Afzelius, 1980).

Primate spermatozoa

It seems that his intentions were to sum up all available sperm data in the last volume of Biologische Untersuchungen and to present such conclusions as could be drawn from the data. He never came to perform this task. A few examples of Retzius' achievements will now be presented. All groups of anthropoid apes were investigated by him, gorilla, chimpanzee, orang-utan, and gibbon. Retzius found a notable intraspecific variation in sperm size and shape in the case of the gorilla and the gibbon,

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Fig. 1. Gustaf Retzius (1842-1919) *was professor of Histology and Anatomy at the Karolinska Institute in Stockholm from 1877 until 1890, when he withdrew from his academic position in protest for the promotion on a colleague. From that date he undertook his studies in gross anatomy and microscopic anatomy either in his home in Stockholm or at the Kristineberg zoological station, Fiskebäckskil, Sweden. He was exceedingly productive; all the large volumes seen on his right side in the photograph were written and illustrated by him. This photograph was taken in 1907, a year in which he was engaged in comparative spermatology. His works on the sensory organs and the nervous system are particularly famous.*

just as it had been described both by him and by others in the case of the human ejaculate. This fact is important when discussing the possible reasons for the poor semen quality in our species. It is likely that the sperm variability is a fairly unimportant characteristic of the human (or gorilla) species rather than an effect of drugs, X-ray, stress, or tight clothing, as has also been suggested. It is to be noted that the gorilla, from which the spermatozoa were obtained, was one that was shot in its natural habitat in Cameroon, rather than one that had been obtained from a primate research center, a zoo, or a circus as were the gorillas that have been examined in this respect by other investigators.

Retzius noted with some surprise that the small chimpanzee had larger testes than those of man and that the huge gorilla, on the contrary, had smaller testes than man. He could give no explanation of this. During the last few decades an interpretation has been offered. The chimpanzee has promiscuous mating habits: a female in estrus mates with several males and the chimpanzee species as a consequence has developed a trait that is called 'sperm competition' (Short, 1976; Mannig and Chamberlain, 1994). The male who introduces most spermatozoa in the female genitals during her estrus, is the one who runs the greatest chance to father the baby that is conceived at this period. The gorilla, on the other hand, is a monogamous species in which the dominant male keeps a harem, and the male hence will need only few spermatozoa to ensure fertilization. The assurance of paternity is in the behavioral pattern. The intermediate testis size of our own species has been interpreted as a sign of mating habits that are intermediate between those of the monogamous gorilla and the promiscuous chimpanzee.

Game animals

One of his sperm investigation deals with the large African game collected for him by his friend Dr. Einar Lönnberg. Retzius noted in this study that animals such as the elephant, giraffe, gnu, and Cape buffalo had unusually small spermatozoa. Later investigators have also been puzzled over the inverse relation between sperm size and body size. Actually no other instance of such inverse relation is known. Cummins, who in 1983 published a literature survey on mammalian sperm dimensions, noted that

Fig. 2. A drawing of the mouse sperm head made by Gustaf Retzius in 1909 (A) and an electron micrograph taken by D. M. Phillips (B). *(Fig. 2B reproduced with kind permission from Phillips, 1974).*

indeed there is an inverse relation between these two parameters and that it occurs in all ten examined mammalian orders except that of the bats (Fig. 5). Cummins also suggested that two different trends can be recognized in the mammals. The larger mammals have developed an intersexual competition favoring the male that delivers the most gametes, whereas in small mammals fertilization is effected by the first spermatozoon to enter the ampulla, which will favor relatively large and rapid spermatozoa. Retzius' investigations also included a whale, which in agreement with these ideas, was found to have small spermatozoa with a very short sperm midpiece. Such short midpieces were seen only in four other mammalian species, namely sloth, porcupine, gorilla and man.

Phylogenetic implications

Perhaps the most important conclusion from Retzius' sperm data is the fact that related species tend to have spermatozoa of similar structure. This finding could then be used in reverse: from the appearance of the spermatozoa it is possible to draw phylogenetic conclusions. Within the mammalian class there are three or four types of spermatozoa. Most eutherian species have a characteristic sperm shape, somewhat similar to that of human or bovine spermatozoa. Within the rodent order, hook-shaped sperm heads have developed. The marsupial spermatozoon has its particular morphology. Two mammalian groups have spermatozoa that are threadlike and of the same shape and organization as in reptiles or primitive birds (for instance the ostrich, also examined by Retzius); Retzius termed them sauropsid spermatozoa. The two groups are the monotremes (the echidnas and platypus) and the pangolins (order Pholidota). The implications of this are: (a) that the monotremes are to be regarded as the most primitive mammals, (b) that the pangolins are the most primitive extant eutherian mammals, and (c) that the eutherian infra-class is likely to have branched off the main mammalian stem before the appearance of the

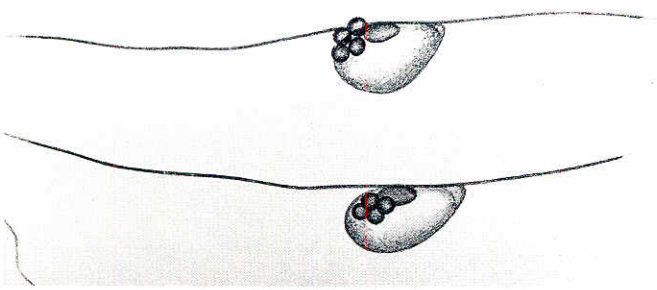

Fig. 3. Two spermatozoids of the brown alga *Fucus vesiculosus*.

marsupials. (Whether the aardvark shares this property with the pangolins is unknown; spermatozoa of this animal have not yet been examined; even Retzius was unable to obtain a specimen of this animal. Nor actually did he examine the pangolin sperm, which however had been examined by his peer Emil Ballowitz).

Retzius' hesitation to speculate is evident in his sperm investigations. Only in a few cases did he make specific claims of phylogenetic relationships. He thus finds that the avian family Laniidae is apparently close to family Corvidae, as can be judged from sperm data. Other examples are that the two most primitive taxa within the crustacean class are the branchiurans and the cirripeds and that the crustacean order Cumacea must be closely related to the orders Isopoda, Mysidacea and Amphipoda.

Perhaps his most successful hypothesis in this field is the concept of the primitive spermatozoon (Fig. 4). This is a sperm cell with a characteristic appearance: a short roundish nucleus, a short midpiece that usually contains four or five mitochondria, and a long and thin tail flagellum. This is the sperm type found in most animal groups that have a position close to the base of the evolutionary tree. Retzius even proposed the term 'Protospermia' for the cohort of primitive spermatozoa and this fact seems to reflect a concept that the spermatozoa have undergone an evolutionary process of their own, in parallel and partly independent from the evolution of the animal soma.

An important enlargement of the concept 'primitive spermatozoon' came long after the days of Retzius, namely when in 1956 Åke Franzén showed that this type of spermatozoon is found only in such animal species, where the semen is discharged in the ambient water, usually (but not always) for external fertilization. With this enlargement of the concept, emphasis has shifted from phylogeny to the mode of fertilization. It seems that Retzius did not note the correlation between sperm shape and fertilization biology and actually did not pay much attention to the mode of fertilization, in spite of the fact that he claimed this to be an aim of the investigation of spermatozoa.

The fertilizing spermatozoon

Furthermore, because he did not perform any investigations on the behavior of the spermatozoa during fertilization, he did not see the changes that most kinds of sperm cells undergo in the vicinity of the egg. Their so-called acrosome reaction was thus not discovered until the 1950ies by Jean Dan. Retzius, however, depicted a few cases of spermatozoa that seemingly have undergone the acrosomal reaction. One case was a marine snail, *Astralium (Turbo) rugosum*, that was examined by him at a marine station at Trieste; others can be seen in Fig. 6C. After a loss of the acrosomal vesicle a short acrosomal filament appears. Another case is the very long and thin preformed acrosomal filament that appears soon after ejaculation in the lamprey sperm; it was described by him as a very curious and unique feature.

From all this, it is evident that Retzius' sperm investigations will continue to function as a treasure of information to serve us for as long as biology is studied. The artistic quality of the drawings adds to our fascination of the Biologische Untersuchungen. The reader feels that Retzius worked on these books with all the dedication that a man could give. So, how did Retzius himself regard his sperm investigations? This is a question to which we will never get the answer. It is surprising, however, to find that he spent only half a page in his memoirs to his sperm investigations, which means about ten percent of the space. This to be compared with well over ten percent of the space in the Biologische Untersuchungen.

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APPENDIX

ANIMAL SPECIES EXAMINED BY GUSTAF RETZIUS WITH RESPECT TO SPERM STRUCTURE

(One or more up-dated scientific names are given within the parentheses. Numbers 11-19 refer to volumes XI-XIX of Biologische Untersuchungen N.F.)

Cnidaria

12 *Tubularia larynx*
12 *Clava squamata*
12 *Sertularia pumila*
12 *Halecium* sp.
12 *Sagartia viduata*
12 *Alcyonium digitatum*
11 *Tealia crassicornis*
11, 15 *Cyanea capillata*
14, 15 *Aurelia aurita*

Platyhelminthes, Turbellaria

12 *Turbellaria* species A
12 *Turbellaria* species B
13 *Turbellaria* species C
13 *Turbellaria* species D
15 *Turbellaria* species X
13, 15 *Prostheceraeus vittatus*

Platyhelminthes, Digenea

14 *Hemiurus communis*

Platyhelminthes, Cestodaria

14 *Amphiptyches urna*

Platyhelminthes, Cestoda

14 *Tetrarhynchus tetrabothrius* (=*Gilquinia tetrabothrium*)
14 *Tetrarhynchus* (=*Grillotia*) *erinaceus*

Nemertina

13 *Cerebratulus marginatus*
13 *Oxypolella alba*
13 *Carinella annulata* (=*Tubulanus annulatus*)
11 *Malacobdella grossa*

Nematomorpha

15 *Gordius aquaticus*

Nematoda

15 *Thoracostoma acuticaudatum*
15 *Cylicolaimus magnus*
15 *Oncholaimus vulgaris* (=*Pontonema vulgare*)
16 *Ascaris* (=*Parascaris*) *megalocephala* (=*equorum*)

Bryozoa (=Polyzoa)

12 *Flustra foliacea* (=*foliacea*)
13 *Alcyonella* (=*Plumatella*) *fungosa*

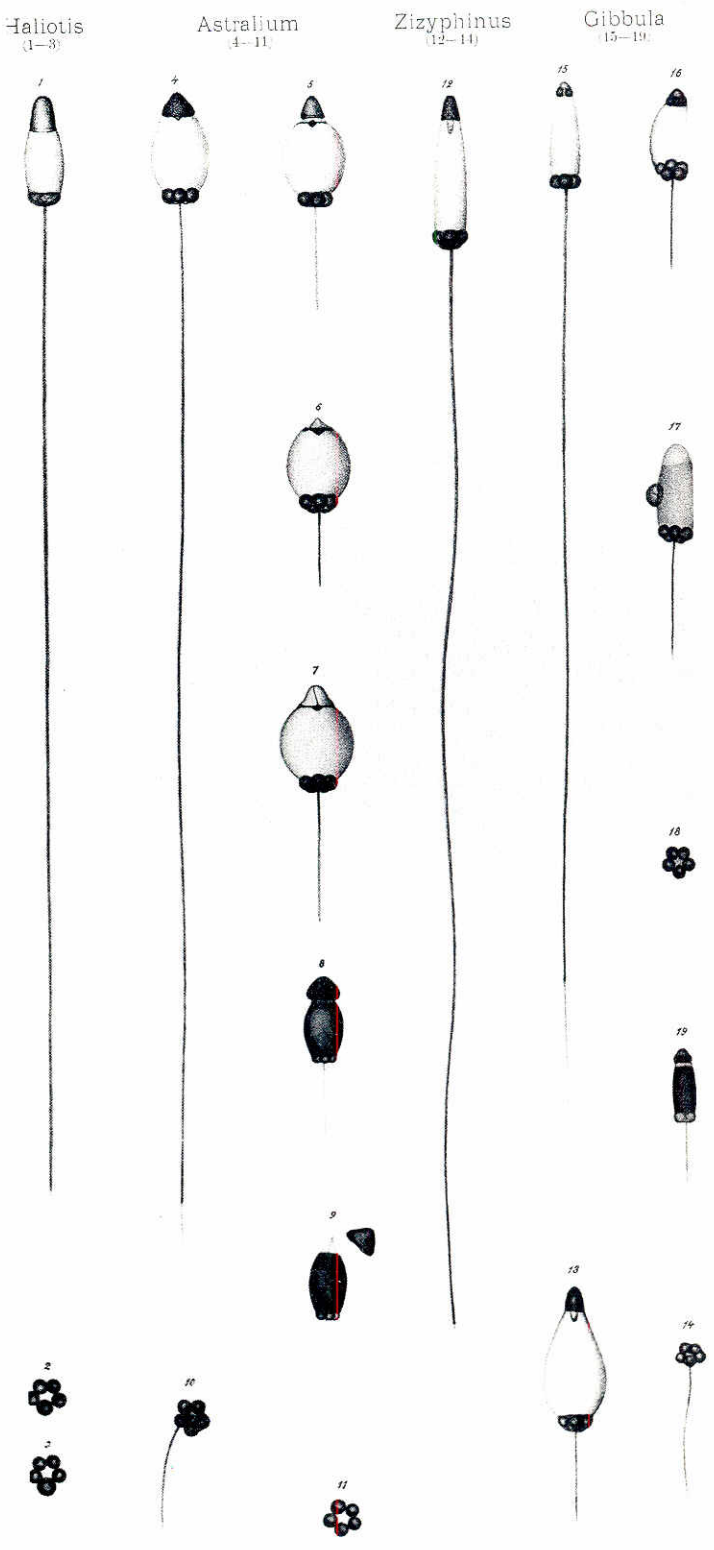
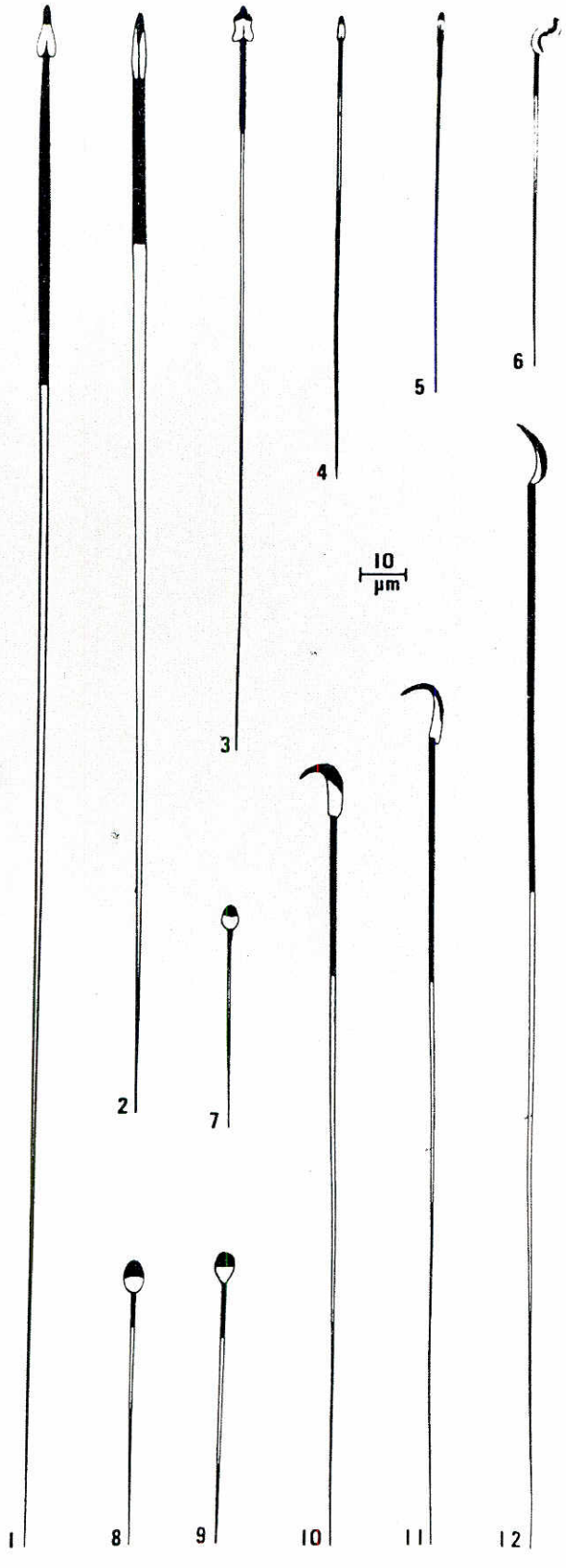


Fig. 4. The primitive marine gastropods are among the animal groups that have so-called primitive spermatozoa.



13 *Triticella Korenii* (=*korenii*)
14 *Scrupocellaria reptans*
11, 15 *Alcyonidium gelatinosum*

Brachiopoda

11 *Terebratula* (=*Terebratulina*) *caput serpentis*

Mollusca, Polyplacophora

11 *Chiton* sp
12 *Chiton* sp
15 *Chiton* sp

Mollusca, Aplacophora

11 *Chaetoderma nitidulum*

Mollusca, Gastropoda

11 *Patella* sp.
12 *Emarginula crassa*
12 *Nacella* (=*Ansates*) *pellucida*
12 *Puncturella noachina*
13 *Neretina* (=*Theodoxus*) *fluviatilis*
13 *Haliotis tuberculata*
13 *Astralium* (=*Turbo*) *rugosum* (=*Bolma rugosa*)
13 *Zizyphinus Linnei* (=*Trochus zizyphinus* = *Calliostoma conuloide*)
13 *Gibbula albida*
13 *Vermetus* sp.
13 *Eulima intermedia*
13 *Cypraea europaea* (=*Trivia arctica*)
13 *Natica Montagui*
13 *Scalaria communis*
13 *Bythinia* (=*Bulimus*) *tentaculata*
13 *Apporais pes pelicani* (=*Aporrhais pespelicani*)
13 *Turritella terebra* (=*communis*)
13 *Littorina littorea*
13 *Rissoa* sp.
13 *Cyclostoma* (=*Pomatias*) *elegans*
13 *Velutina haliotoidea*

12 *Paludina vivipara* (=*Viviparus*)
13 *Purpura* (=*Nucella*) *lapillus*
13 *Conus mediterraneus*
13 *Murex trunculus*
13 *Fusus despectus* (=*Neptunea antiqua*)
13 *Buccinum undatum*
14 *Nassa reticulata*
13 *Bulimus* sp.

13 *Aplysea punctata* (=*rosae*)
13 *Acera* (=*Akera*) *bullata*
13 *Philine aperta*
13 *Doridopsis* (=*Dendrodoris*) *limbata*
13 *Doris* sp
13 *Aeolis* sp.

Fig. 5. Drawing by Cummins of spermatozoa from mammals. *The spermatozoa are drawn to scale and show the great difference in size between various marsupial spermatozoa from the small honey possum (1) to the relatively large koala (6) and between eutherian spermatozoa from man (7) to Chinese hamster (12). (With kind permission from Dr. Cummins).*

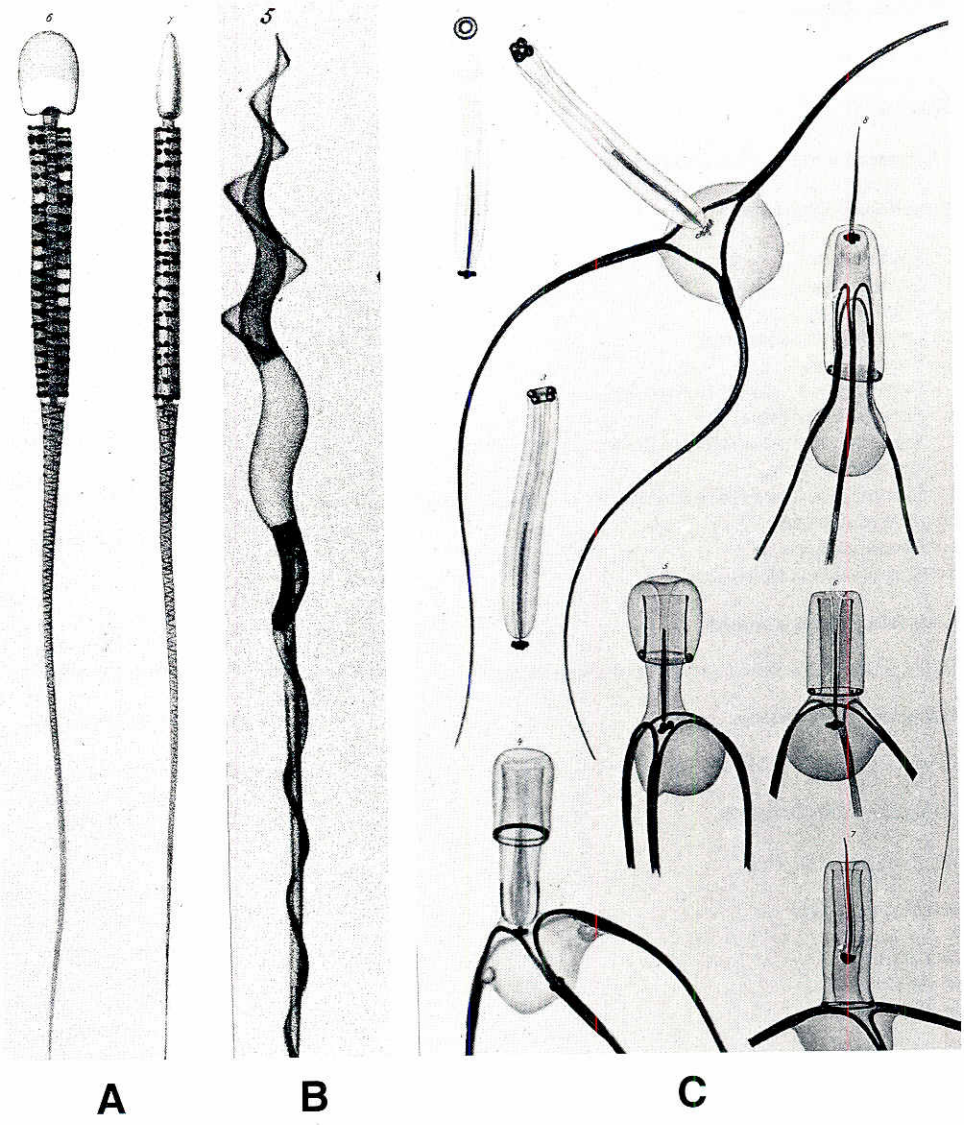


Fig. 6. Two spermatozoa from a pipistrelle bat, seen from different angles (A), one from the rock pipit (a passerine bird) (B), and some from the marine crustacean, *Nephrops norvegicus* (C).

13 *Succinea* sp.
13 *Helix pomatia*
13 *Helix* (=*Cepea*) *hortensis*
13 *Limax agrestis* (=*Deroceras agreste*)
13 *Physa fontinalis*
13 *Planorbis* (=*Planorbarius*) *corneus*
13 *Limnaeus* (=*Lymnaea*) *stagnalis*
13 *Ancylus lacustris*

Mollusca, Scaphopoda

12 *Dentalium entalis*

Mollusca, Bivalvia

11 *Nucula nucleus*
11 *Leda minuta*
11 *Pecten septemradiatus*
11 *Mytilus edulis*
11, 12, 15 *Modiola* (=*Modiolus*) *modiolus*
12 *Anomia* sp.
12 *Lima* (=*Limatula*) *elliptica*
11 *Anodonta anatina* (=*piscinalis*)
11 *Lucina borealis*
11, 12 *Cyprina islandica*
11 *Venus gallina*
12 *Modiolaria marmorata* (=*Musculus marmoratus*)
12 *Tapes* (=*Venerupis*) *pullastra*
12 *Mactra* (=*Spisula*) *elliptica*
12 *Cardium edule*

11 *Corbula* (=*Aloidis*) *gibba* (=*gallicana*)
12 *Saxicava* (=*Hiatella*) *rugosa* (=*pholadis*)
12 *Cultellus* (=*Phaxas*) *pellucidus*
12 *Teredo navalis*

11 *Syndosmya nitida* (=*Abra nitida*)
11 *Axinus Sarsii* (=*Thyasira sarsii*)
12 *Psammobia ferroensis*
12 *Lyonsia norvegica*
12 *Neaera* (=*Cuspidaria*) *cuspidata*

Mollusca Cephalopoda

11 *Rossia* sp.

Sipuncula

11 *Phascolosoma* (=*Phascolion*) *strombi*

Annelida, Polychaeta

11 *Nephthys* sp.
11 *Glycera alba*
11 *Glycinde* sp.
11 *Lepidonotus squamatus*
11 *Brada villosa*
11 *Ophiodromus vittatus* (=*flexuosa*)
11 *Sabellaria spinulosa*
11 *Ammotrypane aulogaster* (=*Ophelina acuminata*)
11 *Arenicola marina*
11 *Notomastus latericius* (=*latericeus*)
12 *Ditrupa arietina*
14 *Nereis pelagica*
14 *Nereis* (=*Hediste*) *diversicolor*

Annelida, Myzostomaria

15 *Myzostoma cirrifera* (=*Myzostomum cirriferum*)

Annelida, Oligochaeta

12 *Allolobophora* (=*Eisenia*) *foetida*

Annelida, Archiannelida

12 *Polygordius lacteus*

Insecta, Odonata

14 *Lestes* sp.
14 *Aeschna* sp.
14 *Libellula* sp.

Insecta, Dermaptera

15 *Forficula auricularia*

Insecta, Orthoptera

14 *Locusta* (=*Tettigonia*) *viridissima*
14 *Gomphocerus* sp.

Insecta, Hemiptera

14 *Pilaenus spumarius*
14 *Capsus* sp. (by Retzius classified among Coleoptera)

Insecta, Coleoptera

14 *Carabus* sp.
14 *Dytiscus* sp.
14 *Ilybius fenestratus*
14 *Phyllodecta* sp.
14 *Cryptocephalus* sp.
14 *Lagria* sp.

Crustacea, Branchiopoda

14 *Podon intermedia*
14 *Daphnia pulex*

Crustacea, Ostracoda

14 *Loxoconcha rhomboidea*
14 *Cytherura* (=*Semicytherura*) *nigrescens*
14 *Paradoxostoma variabile*
14 *Cytheridea dentata*
14 *Cytheridea* sp.
14 *Notodromas monacha*
14 *Candona candida*

Crustacea, Copepoda

14 *Paracalanus parvus*
14 *Eurytemora velox*
14 *Antheacheres Dübenii*

Crustacea, Branchiura

14 *Argulus foliaceus*

Crustacea, Cirripedia

14 *Lepas* sp.
14 *Balanus* sp.
15 *Balanus balanus*
15 *Balanus balanoides*

Crustacea, Peracarida

14, 15 *Mysis oculata*
14 *Mysidacea* sp.
14 *Diastylis tumida*
14 *Leucon nasicus*

14 *Idothea viridis* (=*Idotea chelipes*)
14, 15 *Asellus aquaticus*
14, 15 *Oniscus* sp.
14 *Porcellio* sp.
14, 15 *Bopyrus squillarum*
14, 15 *Gammarus* sp.
14 *Phronima* sp.
14 *Caprella linearis*
14 *Corophium grossipes*
15 *Hyperia medusarum*

Crustacea, Decapoda

14, 15 *Palaemon* (=*Leander*) *squilla*
14 *Crangon vulgaris* (=*crangon*)
14, 15 *Nephrops norvegicus*
14 *Homarus vulgaris* (=*gammarus*)
14 *Calocaris Mac Andreae* (=*macandreae*)
14 *Astacus fluviatilis* (=*Potamobius astacus*)
14, 15 *Eupagurus* (=*Pagurus*) *bernhardus*
14, 15 *Galathea squamifera*
14 *Porcellana longicornis*
14 *Lithodes Maja* (=*maja*)
14 *Stenorhynchus rostratus*
14 *Hyas coarctatus*
14 *Eurynome aspera*
14 *Carcinas moenas* (=*maenas*)
14 *Cancer pagurus*
14, 15 *Portunus* (=*Liocarcinus*) *depurator*
14 *Portunus* (=*Liocarcinus*) *pusillus*
14 *Ebalia tumefacta*
15 *Pandalus borealis*

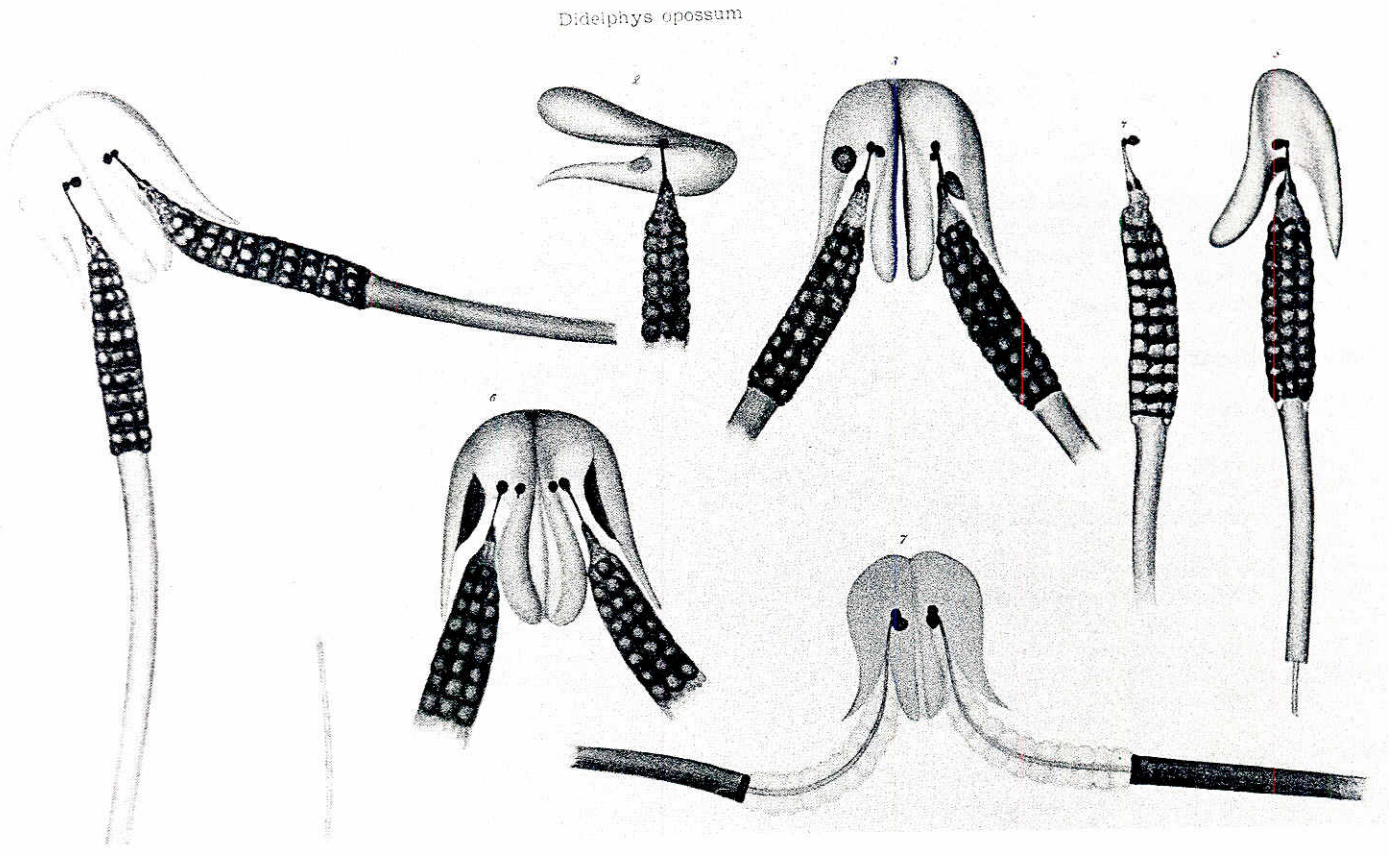


Fig. 7. The twin spermatozoa of an American opossum.

Pycnogonida

14 *Nymphon Strömii* (=*strömii*)

Chaetognatha

14, 15 *Sagitta bipunctata*

Echinodermata, Crinoidea

12 *Antedon petasus*

Echinodermata, Holothuroidea

12, 15 *Mesothuria intestinalis*
15 *Stichopus tremula* (=*tremulus*)

Echinodermata, Echinoidea

15 *Echinus esculentus*
11, 15 *Echinus* (=*Psammechinus*) *miliaris*
11 *Echinus neglectus* (=*Strongylocentrotus droebachiensis*)
15 *Strongylocentrotus droebachiensis*
15 *Arbacia punctulata*
15 *Paracentrotus* (=*Arbacia*) *lividus*
15 *Parechinus microtuberculatis*
15 *Sphaerechinus granularis*
15 *Echinocyamus pusillus*
12, 15 *Brissopsis lyrifera*

Echinodermata, Asteroidea

15 *Asteropecten irregularis*
15 *Solaster papposus*
15 *Cribrella* (=*Henricia*) *sanguinolenta*
15 *Asterias rubens*

Echinodermata, Ophiuroidea

15 *Ophiura* sp.
15 *Ophiura ciliata*
11, 15 *Ophiothrix fragilis*

Enteropneusta

13 *Ptychodera clavigera* (=*Balanoglossus clavigerus*)

Urochordata (=Tunicata)

12 *Oikopleura dioica*
15 *Cione intestinalis*
15 *Clavelina lepadiformis*
12 *Botrylloides rubrum* (=*leachi*)

Cephalocordata

12 *Amphioxus lanceolatus* (=*Branchiostoma lanceolatum*) (lancelet)

Cyclostomata

19 *Myxine glutinosa* (Atlantic hagfish)
19 *Petromyzon* (=*Lampetra*) *fluviatilis* (lamprey)

Pisces, Selachii

10, 13 *Acanthias vulgaris* (=*Squalus acanthias*) (spiny dogfish)
13 *Etmopterus spinax* (=*Spinax niger*) (black centrina)
15 *Scyllium canicula* (=*Scyliorhinus caniculus*) (spotted dogfish)
13 *Raja clavata* (thornback)
13 *Chimaera monstrosa* (chimaera)

Pisces, Osteichtyes

12 *Amia calva* (bowfish or amie)
12 *Clupea harengeus* (common herring)
12 *Salmo salar* (Atlantic salmon)
12 *Esox lucius* (European pike)
12 *Cyprinus* (=*Carassius*) *carassius* (Crucian carp)
12 *Lota vulgaris* (=*lota*) *(burbot)*
12 *Pleuronectes* (=*Platichtys*) *flesus (plaice)*
15 *Nerophis ophidion* (straight nosed pipefish)
12 *Perca fluviatilis* (river perch)
12 *Zoarces viviparus* (eelpout or blenny)
12 *Gobius niger* (black goby)
15 *Lophius piscatorius* (angler)

Amphibia, Urodela

13 *Siredon pisciformis* (=*Ambystoma mexicanum*) (Mexican axolotl)
13 *Molge* (=*Triton*=*Triturus*) *viridescens* (East American newt)
13 *Molge* (*Triton*) *cristata* (=*Triturus cristatus*) (crested newt)
13 *Molge* (=*Triton*=*Triturus*) *alpestris* (Alpine newt)
13 *Molge* (=*Triton*=*Triturus*) *pyrrhogaster* (Japanese red-bellied salamander)
13 *Molge* (=*Triturus*) *vulgaris* (smooth newt)
13 *Salamandra maculosa* (=*salamandra*) (common European salamander)
13 *Pleurodeles waltl* (=*waltlii*) (ribbed or Spanish newt)
13 *Spelerpes fuscus* (*Hydromantes genei*) (Sardinian cave salamander)

Amphibia, Anura

13 *Alytes obstetricans* (midwife toad)
13 *Bombinator igneus* (=*Bombina bombina*) *(fire-bellied toad)*
13 *Pelobates fuscus* (garlic frog)
13 *Bufo vulgaris* (=*bufo*) (common toad)
13 *Rana esculenta* (edible frog)
13 *Hyla arborea* (European tree frog)
13 *Callula* (=*Kaloula*) *pulchra* (Malayan bullfrog)

Reptilia

13 *Testudo graeca* (Greek tortoise)
13 *Platydactylus mauretanicus* (=*Tarentola mauretanica*) (common gecko)
13 *Anguis fragilis* (slow worm or blind worm)
13 *Chamaeleon vulgaris* (Mediterranean chameleon)

Aves

16 *Struthio molybdophanes* (=*camelus*) (Somalian ostrich)
14 *Anas boschas* (=*platyrhyncha*) domestica (domestic duck)
14 *Fuligula* (=*Aythya*) *fuligula* (tufted duck)
14 *Uria Troile* (=*aalge*) (common guillemot)
14 *Fulica atra* (common coot)
14 *Gallus gallus* (domestic rooster)
14 *Crex crex* (corncrake)
14 *Larus fuscus* (lesser black-backed gull)
14 *Vanellus vanellus* (lapwing)
14 *Tringa* (=*Calidris*) *alpina* (dunlin)
14 *Totanus* (=*Tringa*) *ochropus* (green sandpiper)
14 *Scolopax rusticola* (woodcock)
14 *Pavoncella* (=*Philomachus*) pugnax (ruff)
14 *Columba livia domestica* (domestic pigeon)
14 *Psittacus* sp. (a parrot species)
14 *Syrnium* (=*Strix*) *aluco* (tawny owl)
14 *Dendrocapus* (=*Picoides*) *major* (great spotted woodpecker)
14 *Corvus cornix* (=*corone corvus*) (hooded crow)
17 Corvus frugilegus (rook)
17 *Perisoreus infaustus* (Siberian jay)
16 *Coloeus* (=*Corvus*) *monedula* (jackdaw)
16 *Lanius collurio* (red-backed shrike)
14 *Pica pica* (magpie)
14 *Sturnus vulgaris* (starling)
14 *Turdus musicus* (redwing)
14 *Aedon* (=*Luscinia*) *luscinia* (thrush nightingale)
14 *Muscicapa atricapilla* (=*Ficedula hypoleuca*) (pied flycatcher)
14 *Phylloscopus sibilator* (=*sibilatrix*) (wood warbler)
14 *Alauda arvensis* (sky lark)
14 *Anthus obscurus* (=*spinoletta*) (rock pipit)
14 *Fringilla coelebs* (chaffinch)
14 *Chrysomitris* (=*Carduelis*) *spinus* (siskin)
14 *Chloris* (=*Carduelis*) *chloris* (greenfinch)
14 *Passer domesticus* (house sparrow)
14 *Emberiza citrinella* (yellowhammer)

Monotremata

13 *Echidna hystrix* (=*Tachyglossus aculeatus*) (shortnosed echidna)

Marsupialia

14 *Didelphis virginiana* (Virginian opossum)
13 *Bettongia cuniculus* (=*gaimardi*) (Eastern bettong)
13 *Macropus billardieri* (=*Thylogale billardierii*) (Tasmanian wallaby)
13 *Petrogale penicillata* (brush-tailed rock wallaby)
13 *Onychogale lunata* (crescent nailtail wallaby)
13 *Phalangista vulpina* (*Trichosurus vulpecula*) (brushtail opossum)

Edentata

14 *Bradypus cuculliger*(=tridactylus) (pale-throated sloth)
13 *Dasypus* (*Euphractus*) *villosus* (larger hairy armadillo)

Insectivora

14 *Talpa europaea* (European mole)
14 *Erinaceus europaeus* (Western European hedgehog)
16 *Macroscelides pulcher* (=*Elephantulus rufescens*) (elephant shrew)
18 *Ericulus* (=*Setifer*) *setosus* (greater hedgehog tenrec)
18 *Centetes* (=*Tenrec*) *ecaudatus* (tail-less tenrec)

Chiroptera

13 *Vesperugo* (=*Pipistrellus*) *pipistrellus* (common pipistrelle)

Lagomorpha

14 *Lepus* (=*Oryctolagus*) *cuniculus* (European rabbit)

Rodentia

14 *Sciurus vulgaris* (red squirrel)
14 *Cynomys ludovicianus* (black-tailed prairie dog)
16 *Xerus rutilus* (unstriped ground squirrel)
14 *Dipus aegypticus* (=*Allactaga tetradactyla*) (four-toed jerboa)
14 *Myoxis* (=Glis) *glis* (edible dormouse)
14 *Mus musculus* (house mouse)
14 *Mus* (=*Apodemus*) *agrarius* (striped field mouse)
14 *Mus* (=*Apodemus*) *sylvaticus* (wood mouse)
16 *Mus* (=*Rattus*) *norvegicus* (brown rat)
14 *Microtus terrestris* (=*Arvicola terrestra*) (ground vole)
14 *Lemmus lemmus* (Norway lemming)
14 *Hystrix cristata* (African porcupine)
14 *Cavia cobaya* (=porcellus) (domestic guinea gig)
14 *Myopotamus* (=Myocaster) *coypus* (nutria)

Proboscidea

16 *Elephas africanus* (=*Loxodonta africana*)(African elephant)

Hyracoidea

16 *Procavia pumila* (hyrax)

Cetacea

14 *Globicephalus* (=Globicephala) *melas* (melaena) (long-finned pilot whale)

Carnivora

14 *Canis familiaris* (dog)
14 *Canis lupus* (gray wolf)
14 *Vulpes vulpes* (red fox)
16 *Felis* (=Panthera) *leo* (lion)
14 *Felis domestica* (domestic cat)
16 *Cynailurus* (=*Acinonyx*) *jubatus* (cheetah)
14 *Herpestes ichneumon* (Egyptian mongoose)
14 *Meles meles* (European badger)
18 *Cryptoprocta ferox* (fossa)
18 *Eupleres goudotii* (falanouc) (by Retzius classified as an insectivore)

Perissodactyla

14 *Equus caballus* (domestic horse)
16 *Equus grevyi* (Grevy's zebra)

Artiodactyla

14 *Sus scrofa* (domestic boar)
14 *Dicotyles* (=*Tayassu*) *tajacu* (collared pecary)
14 *Cervus elaphus* (red deer)
14 *Alces alces* (moose)
14 *Rangifer tarandus* (reindeer)
14 Capra (hybrid) (goat)
14 *Ovis aries* (domestic sheep)
14 *Bos taurus* (domestic cattle)
16 *Giraffa reticulata* (=*camelopardalis*) (reticulated giraffe)
16 *Connochaetes albojubatus* (=gnou) (white-tailed gnu or black wildebeest)
16 *Cephalophus abyssinicus* (=*Sylvicapra grimmia*) (grey duiker)
16 *Gazella granti* (Grant's gazelle)
16 *Rhynchotragus* (=*Madoqua*) *guentheri* (Günther's dikdik)
16 *Aepyceros melampus* (impala)
16 *Lithocranius* (=*Litocranius*) *walleri* (gerenuk)
16 *Oryx beisa* (=gazella) (gemsbok)
16 *Cobus* (=Kobus) *ellipsiprymnus* (waterbuck)
16 *Buffelus* (=*Bubalus*=*Synceros*) *caffer* (African buffalo)

Pinnipedia

14 *Halichoerus grypus* (grey seal)

Primates

14 *Lemur catta* (ring-tailed lemur)
18 *Lemur mongoz* (mongoose lemur)
18 *Lepilemur* sp. (sportive lemur)
18 *Chiromys* (=*Daubentonia*) *madagascariensis* (aye-aye)
19 *Chrysothrix sciurea* (=*Saimiri sciureus*) (squirrel monkey)
14 *Hapale* (=Callithrix) *jacchus* (common marmoset)
14 *Inuus ecaudatus* (=*Macaca ecaudata* =*M. sylvanus*) (Barbary macaque)
17 *Macacus sinicus* (=*Macaca sinica*) (toque macaque)
18 *Macacus cynomolgus* (*Macaca irus*=fascicularis) (crab-eating macaque)
17 *Maimon maimon* (=*Papio papio*) (Guinea baboon)
17 *Papio* (=*Mandrillus*) *sphinx* (mandrill)
18 *Cercocebus fuliginosus* (=*Torquatus atys*) (white mangabey)
18 *Cercopithecus pygerythraeus* (=*aethiops*) (green monkey)
19 *Hylobates lar* (common gibbon)
14 *Hylobates agilis* (=*Hylobates lar agilis*) (agile gibbon)
16 *Simia satyrus* (=*Pongo pygmaeus*) (orangutan)
18 *Gorilla gorilla* (gorilla)
16 *Anthropopithecus* (=*Pan*) *troglodytes* (chimpanzee)
14, 16 *Homo sapiens* (man)