

velocities of water in northern Chesapeake Bay estuary (16), but flocculation is still an important depositional mechanism which agglomerates individual clay- and silt-sized mineral grains to pelleted sediments in situ (29).

These findings fill a gap in an area where very little is known about either the arrangements of grains in agglomerated sediments or the environmental significance of these features (38). Although this information will be useful in the modeling of sediment transport processes in estuaries, it will be of little use in the study of fine-grained sedimentary rocks because the effects of compaction and postdepositional diagenetic changes make it almost impossible to recognize the original texture in ancient sediments.

CHRISTOPHER F. ZABAWA*

Department of Geology,
University of South Carolina,
Columbia 29208

References and Notes

- H. Van Olphen, *Introduction to Clay Colloid Chemistry* (Wiley, New York, 1963).
- D. W. Pritchard, in *Estuaries*, G. Lauff, Ed. (AAAS Special Publication 83, Washington, D.C., 1967), p. 3.
- W. Sakamoto, *Bull. Ocean Res. Inst. Univ. Tokyo No. 5* (1973), p. 1; N. O'Brien, *Clays Clay Miner.* **19**, 353 (1971); R. B. Krone, "Flume studies of the transport of sediment in estuarial shoaling processes—final report" (Hydraulic Engineering Laboratory and Sanitary Engineering Research Laboratory, University of California, Berkeley, 1962); *U.S. Army Corps Eng. Comm. Tidal Hydraul. Bull. No. 7* (1963); U. G. Whitehouse, L. M. Jeffrey, J. D. Derbrecht, in *Clays and Clay Minerals: National Conference on Clays and Clay Minerals, 7th, Proceedings*, A. Swineford, Ed. (Pergamon, New York, 1960), p. 1; B. Mattiat, *Geol. Jahrb.* **88**, 87 (1969).
- A. T. Ippen, in *Estuarine and Coastline Hydrodynamics*, A. T. Ippen, Ed. (McGraw-Hill, New York, 1966), p. 648.
- L. Van Straaten and Ph. Kuenen, *Geol. Mijnbouw* **19**, 329 (1958); E. Schultz and H. Simons, *U.S. Army Corps Eng. Comm. Tidal Hydraul. Bull. No. 2* (1957); M. Powers, *J. Sediment. Petrol.* **27**, 355 (1957); C. Duke, *ASCE J. Waterw. Harbors Div.* **87**, 29 (1961); J. Neihisel, *U.S. Army Corps Eng. Comm. Tidal Hydraul. Bull. No. 10* (1966); W. Anikouchine and R. Sternberg, *The World Ocean* (Prentice-Hall, Englewood Cliffs, N.J., 1973); B. D'Anglejan and E. Smith, *Can. J. Earth Sci.* **10**, 1380 (1973); L. Wright and J. Coleman, *Geol. J.* **82**, 751 (1974).
- H. Einstein and R. B. Krone, *J. Geophys. Res.* **67**, 1451 (1962).
- B. Gallenne, *Estuarine Coastal Mar. Sci.* **2**, 261 (1974).
- H. Luneberg, *Arch. Dtsch. Seewarte* **59**, 1 (1939); B. Nelson, in *International Oceanographic Congress Preprints* (AAAS, Washington, D.C., 1959), p. 640; M. Mathews, thesis, Northwestern University (1973).
- H. Postma and K. Kalle, *Dtsch. Hydrogr. Z.* **8**, 137 (1955); L. Glangeaud, *Bull. Soc. Geol. Fr.* **8**, 599 (1938).
- H. Postma, in *Estuaries*, G. Lauff, Ed. (AAAS Special Publication 83, Washington, D.C., 1967), p. 158.
- R. Meade, *Geol. Soc. Am. Mem.* **133** (1972), p. 91.
- J. R. Schubel, in *The Estuarine Environment*, J. R. Schubel, Ed. (short course lecture notes) (American Geological Institute, Washington, D.C., 1971).
- H. A. Einstein and R. B. Krone, *ASCE Hydraul. Div.* **87**, 51 (1961); A. Anderson, *J. Geophys. Res.* **67**, 1463 (1962).
- I. N. McCave, *J. Geophys. Res.* **75**, 4151 (1970).
- H. B. Simmons, in *Estuarine and Coastline Hydrodynamics*, A. T. Ippen, Ed. (McGraw-Hill, New York, 1966), p. 673.
- J. R. Schubel, *Science* **161**, 1013 (1968); *Chesapeake Bay Inst. Johns Hopkins Univ. Tech. Rep.* **35** (1968), reference 68-2.
- H. Moore, *J. Mar. Biol. Assoc. U.K.* **17**, 325 (1931); J. Verveij, *Arch. Neerl. Zool.* **10**, 171 (1952); D. Rhoads, *J. Sediment. Petrol.* **33**, 723 (1963); D. Haven and R. Morales-Alamo, *Sediment. Geol.* **2**, 141 (1968); R. Johnson, *J. Mar. Res.* **32**, 313 (1974).
- T. Smayda, *Limnol. Oceanogr.* **14**, 621 (1969).
- D. Lal, *Science* **198**, 997 (1977).
- D. Haven and R. Morales-Alamo, *Geol. Soc. Am. Mem.* **133** (1972), p. 121.
- V. La Mer, *J. Colloid Sci.* **19**, 291 (1964).
- R. Grim, *Clay Mineralogy* (McGraw-Hill, New York, 1968); C. Chang and J. Anderson, *Soil Sci. Soc. Am. Proc.* **32**, 23 (1968); A. P. Black, F. B. Birkner, J. J. Morgan, *J. Am. Water Works Assoc.* **57**, 1547 (1965).
- H. W. Paerl, *Science* **180**, 496 (1973); *Microb. Ecol.* **2**, 73 (1975).
- J. Ernissee and W. H. Abbott, in *Third Symposium on Recent and Fossil Marine Diatoms*, Kiel, Germany, 1974, R. Simonsen, Ed. (Occasional Publication 53 of *Nova Hedwigia*) (von Cramer, Bremerhaven, 1975), p. 241.
- C. Moon, *Earth Sci. Rev.* **8**, 303 (1972).
- H. Paerl and S. Shimp, *Limnol. Oceanogr.* **18**, 802 (1973); D. Jernigan and J. McAtee, *Clays Clay Miner.* **23**, 161 (1975); B. Lung, *J. Microsc. (Oxford)* **101**, 77 (1974); F. Anderson, *J. Sediment. Petrol.* **40**, 1128 (1970).
- K. Terzaghi, *Erdbaumchanik auf Bodenphysikalischer Grundlage* (Deutcher, Leipzig, 1925).
- F. A. Bowles, *Science* **159**, 1236 (1968); W. A. Pryor and W. Vanwie, *J. Sediment. Petrol.* **41**, 763 (1971).
- C. F. Zabawa, thesis, University of South Carolina (1978).
- J. Kraeuter and D. Haven, *Chesapeake Sci.* **11**, 159 (1970).
- J. R. Schubel and T. W. Kana, *Powder Technol.* **6**, 9 (1972).
- K. Marshall, R. Stout, R. Mitchell, *J. Gen. Microbiol.* **68**, 337 (1971); *Can. J. Microbiol.* **17**, 1413 (1971).
- J. Sieburth, *Microbial Seascapes* (University Park Press, Baltimore, 1975).
- W. Corpe, *Dev. Ind. Microbiol.* **11**, 402 (1970).
- R. L. Folk, *Petrology of Sedimentary Rocks* (Hemphill, Austin, Texas, 1968); D. Swift, J. R. Schubel, R. E. Sheldon, *J. Sediment. Petrol.* **42**, 122 (1972).
- G. A. Riley, *Limnol. Oceanogr.* **8**, 372 (1963); R. W. Sheldon, T. P. T. Evelyn, T. R. Parsons, *ibid.* **12**, 367 (1967); H. W. Paerl, *ibid.* **19**, 966 (1974); J. K. Edzwald, J. B. Upchurch, C. R. O'Melia, *Environ. Sci. Technol.* **8**, 58 (1974); J. E. Gillot, *J. Sediment. Petrol.* **39**, 90 (1969); W. von Engelhardt and K. Gaidia, *ibid.* **33**, 919 (1963); P. J. Stalder, *Geol. Mijnbouw* **52**, 217 (1973); R. A. Feely, *Mar. Geol.* **20**, M7 (1976); R. B. Krone, in *Estuarine Transport Processes*, B. Kjerfve, Ed. (Library in Marine Science Publication 7) (Univ. of South Carolina Press, Columbia, 1978), p. 177; M. W. Silver, A. L. Shanks, J. D. Trent, *Science* **201**, 371 (1978).
- I. Sherman, *Trans. Am. Geophys. Union* **34**, 394 (1953).
- H. E. Reineck and I. B. Singh, *Depositional Sedimentary Environments* (Springer-Verlag, New York, 1973).
- I thank J. R. Schubel, R. H. Meade, M. O. Hayes, and O. P. Bricker for reviewing this manuscript; N. Watabe and the staff of the SEM Laboratory, University of South Carolina, for their assistance; and P. van Slyck and D. Pendleton for their assistance with graphics. This work was supported by the Maryland Department of Natural Resources, through a grant to Westinghouse Corporation, Chesapeake Bay Institute, and the University of Maryland, to study chlorinated hydrocarbon pesticides and polychlorinated biphenyl contaminants in upper Chesapeake Bay. Additional support came from the Department of Geology and the SEM Laboratory, University of South Carolina.

* Present address: Coastal Zone Unit, Energy and Coastal Zone Administration, Maryland Department of Natural Resources, Tawes State Office Building B-3, Annapolis 21401.

9 February 1978; revised 25 April 1978

Larval Bivalve Shell Morphometry: A New Paleoclimatic Tool?

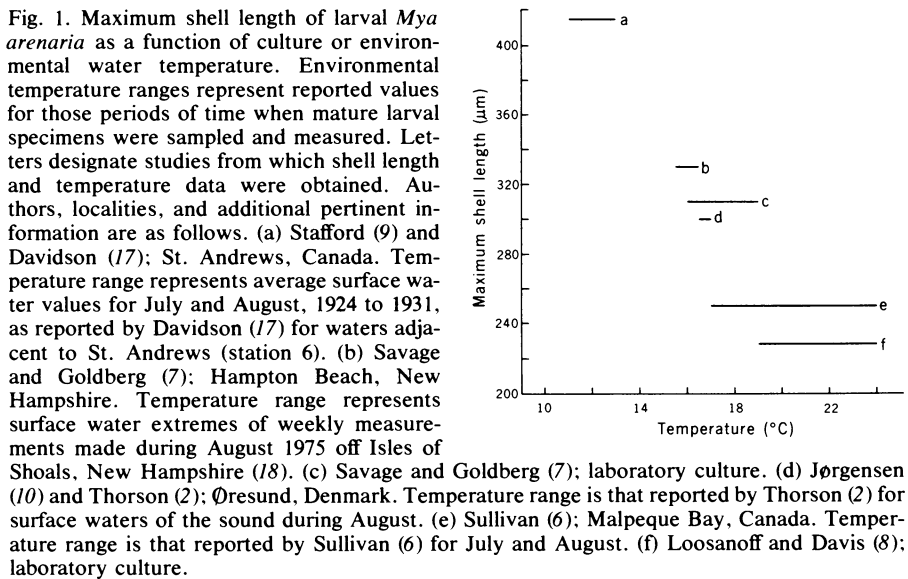
Abstract. *The shells of the pelagic larvae of bivalve mollusks may be useful as paleoclimatic indicators. An inverse relationship between temperature and maximum size of larval shells within a particular population is reported for a number of Recent species. Changes in the dimensions of the prodissoconch-dissoconch boundary on juvenile specimens may reflect changes in the ambient temperature of marine environments.*

Paleoclimatic investigations in marine sediments are based primarily on the fossil record of holoplanktic microorganisms: Foraminifera, Radiolaria, calcareous nannofossils, diatoms, and silicoflagellates. Established techniques rely heavily on interpretation of oscillations of cold- and warm-water assemblages. In this report, we present evidence for an inverse relationship between temperature and maximum size in another group of minute shelled organisms, larval bivalves, which may provide an additional interpretive tool in paleoclimatic studies.

The larvae of marine benthic invertebrates are an important constituent of both the coastal and the oceanic plankton. Such meroplanktic stages often serve as a means of long-range dispersal and population recruitment for organisms of otherwise low migratory capability (1). Of all pelagic larval forms, members of the class Bivalvia are by far

the most dominant, comprising more than 57 percent of the total invertebrate meroplankton in certain marine waters (2). In addition, the calcareous skeletons of these mollusks render such organisms useful in paleontological studies (3). During the past decade, various workers have alluded to the usefulness of such larval shells in paleoecological studies for defining population dispersal patterns (1, 3), in biostratigraphic studies for evaluating the potential of certain benthic species as index fossils (1), and in systematic studies for assessing evolutionary relationships (3). Here we discuss an additional paleontological application by illustrating how changes in the dimensions of shell features associated with larval metamorphosis may reflect changes in the ambient temperature of marine environments.

In mollusks, the term metamorphosis has often been used to describe the immediate changes that occur when the lar-



va exchanges a pelagic existence for a benthic or sessile mode of life. In bivalves, the term has been refined to signify the morphological changes that occur between the first secretion of the byssus and the appearance of the dissoconch shell (4). The ability of bivalve larvae to delay the process of metamorphosis has been well documented, and numerous experiments have been conducted in an attempt to define factors influencing the duration of this delay. Of all factors studied, temperature has received the most attention. Its effect appears to dominate that of other variables, and a highly significant negative correlation has been found between the temperature of larval cultures and the duration of the delay (4). At uniform temperatures, nonlethal variations in oxygen saturation, as well as the quality or quantity of food, appear to play a relatively minor role in the delay of metamorphosis. While there is some indication that salinity may be of some importance in influencing the delay, its effect has not been well defined and further experiments are needed, especially with regard to possible synergistic effects of temperature and salinity (4).

The effect of temperature on larval size at metamorphosis has been discussed by several authors. For the few species that have been examined in detail, strong negative correlations have been found between temperature and maximum larval shell size (4, 5). A compilation of data from detailed laboratory and field studies (5–10) of the soft-shell clam, *Mya arenaria*, provides a case in point (Fig. 1). The maximum reported size at metamorphosis of *M. arenaria* cultured at 19° to 24°C was 228 μm (8), while a maximum of 310 μm was found

at lower culture temperatures fluctuating between 16° and 19°C (7). A similar relationship between temperature and maximum size at metamorphosis of *M. arenaria* is apparent through examination of data from plankton studies conducted in various areas along the eastern and western Atlantic coasts. Sullivan (6), who worked with *M. arenaria* from Canadian waters, reported that larvae were “observed to settle at $235 \times 250 \mu\text{m}$ in Malpeque as compared with $315 \times 415 \mu\text{m}$ at St. Andrews” and attributed the difference to the much warmer (although unreported) summer temperatures at

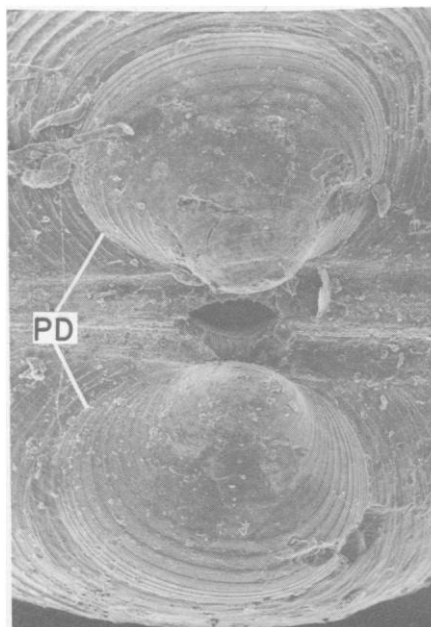


Fig. 2. Scanning electron micrograph of the umbonal region of *Striarca haddonfieldensis* from the Severn [formerly Monmouth (19)] Formation (Maestrichtian) near Brightseat, Maryland. Note the distinct prodissoconch-dissoconch boundary (PD) ($\times 170$).

Malpeque. Similarly, Savage and Goldberg (7) summarized morphometric findings of several authors that showed a negative correlation between temperature and size of *M. arenaria* at metamorphosis.

Several species of Mytilidae have also been examined in detail, and the results indicate a negative correlation between temperature and mean maximum size at metamorphosis similar to that found for *M. arenaria*. In laboratory studies of the larvae of two tropical mussels, *Perna perna* and *Perna* (= *Mytilus*) *viridis*, the maximum size attained during periods of delayed metamorphosis occurred at temperatures below those yielding the highest growth rates (5, 11). In these studies it was suggested that at higher temperatures, feeding stages are passed more rapidly and the velum is resorbed faster, both factors resulting in smaller maximum sizes at metamorphosis. In detailed studies of laboratory-reared *Mytilus edulis*, the maximum shell length of larvae was found to be a function of both the rate of growth during the delay of metamorphosis and the time available for growth (4). The positive correlation between maximum size and duration of the delay of metamorphosis of this species is highly significant. At high temperatures, the high rate of growth is apparently insufficient to compensate for the short time available for feeding, and this results in a smaller maximum size at higher temperatures (4, 12).

To the extent that initiation of deposition of the dissoconch shell marks the end of metamorphosis, the prodissoconch-dissoconch boundary provides an easily discerned morphological feature for distinguishing true juveniles from larval forms or metamorphosing post-larvae. Although no data are available on relationships between prodissoconch-dissoconch boundaries per se and ambient temperatures, the morphometry of this boundary, when defined for large numbers of juveniles within a population, should provide an accurate estimate of the maximum larval size at metamorphosis. It follows from the discussion in the preceding paragraphs that variations in the maximum size of the prodissoconch, as delimited by this boundary, should be largely a function of environmental temperature (13). The empirical observations reviewed above indicate that while such factors as individual genetic differences, food availability, and salinity contribute to the variation in larval size at metamorphosis, they do not mask the temperature effect.

Within the past few years, several workers have commented on the pres-

ence of larval and early postlarval bivalves in ancient sediments and have discussed methods of species-level identification (3, 14). Original aragonitic structures have been found to be extremely well preserved in some deposits as old as the Late Cretaceous (3). Prodissoconch-dissoconch boundaries of specimens from such sediments are readily distinguished (Fig. 2) and, when coupled with size distribution data for larval specimens, can be used in defining maximum sizes at metamorphosis. This approach should permit the reconstruction of both relative and absolute temperatures.

1) *Relative temperatures.* Detailed examination of changes in prodissoconch dimensions in a species through time at a single locality, or in a series of localities along a single horizon, should provide an indication of temporal or spatial temperature gradients for any interval containing adequately preserved faunas. Such paleotemperature gradient reconstructions should serve as an independent test of data derived from other microorganisms or stable isotope analyses.

2) *Absolute temperatures.* The long geologic duration of most bivalve species (15) suggests that absolute paleotemperature estimates might be achieved for Holocene, Pleistocene, and Pliocene environments by using regressions of prodissoconch length on temperature for a variety of extant species. However, as with other quantitative paleoclimatic techniques (16), the assumption of evolutionary stasis within species with regard to physiological processes may not be entirely warranted, and should be used with caution.

RICHARD A. LUTZ

DAVID JABLONSKI

Department of Geology and
Geophysics, Yale University,
New Haven, Connecticut 06520

References and Notes

1. R. S. Scheltema, *Biol. Bull. (Woods Hole, Mass.)* **140**, 284 (1971); in *Concepts and Methods of Biostratigraphy*, E. G. Kauffman and J. E. Hazel, Eds. (Dowden, Hutchinson & Ross, Stroudsburg, Pa., 1977), p. 73; E. G. Kauffman, *Geol. Assoc. Can. Spec. Pap.* **13**, 163 (1975).
2. G. Thorson, *Medd. Dan. Fisk. Havunders.* **4**, 1 (1946).
3. M. LaBarbera, *J. Paleontol.* **48**, 265 (1974); R. A. Lutz and D. Jablonski, *Science* **199**, 439 (1978); D. Jablonski and R. A. Lutz, *Geol. Soc. Am. Abstr. Programs* **10**, 49 (1978); J. Thiede, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **15**, 267 (1974).
4. B. L. Bayne, *Ophelia* **2**, 1 (1965); in *Fourth European Marine Biology Symposium*, D. J. Crisp, Ed. (Cambridge Univ. Press, London, 1971), p. 259.
5. S. E. Siddall, *FAO Aquaculture Bull.* **8** (No. 2), 12 (1977); in *Proceedings of the Ninth Annual Meeting, World Mariculture Society* (Louisiana State Univ. Press, Baton Rouge, in press).
6. C. M. Sullivan, *Bull. Fish. Res. Board Can.* **77**, 1 (1948).
7. B. B. Savage and R. Goldberg, *Proc. Natl. Shellfish. Assoc.* **66**, 42 (1976).

8. V. L. Loosanoff and H. C. Davis, *Adv. Mar. Biol.* **1**, 1 (1963).
9. F. Stafford, *Contrib. Can. Biol.* 1906-1910 (1912), p. 221.
10. C. B. Jørgensen, *Medd. Dan. Fisk. Havunders.* **4**, 277 (1946).
11. S. E. Siddall, *Proc. Natl. Shellfish. Assoc.*, in press.
12. This apparent decoupling of rates of somatic growth and ontogenetic change [S. J. Gould, *Ontogeny and Phylogeny* (Harvard Univ. Press, Cambridge, Mass., 1977)] is of considerable interest in a group of organisms in which paedomorphosis has played a significant evolutionary role [S. M. Stanley, *Annu. Rev. Earth Planet. Sci.* **3**, 361 (1975)].
13. A relationship may well exist between mean size at metamorphosis and temperature, but no data are available at this time.
14. H. R. Kudrass, "Meteor" *Forschungsergeb. Reihe C* **13**, 1 (1973).
15. S. M. Stanley, in *Patterns of Evolution*, A. Hallam, Ed. (Elsevier, Amsterdam, 1977), p. 209.
16. J. Imbrie and N. G. Kipp, in *The Late Cenozoic Glacial Ages*, K. K. Turekian, Ed. (Yale Univ.

- Press, New Haven, Conn., 1971), p. 71; CLIMAP Project Members, *Science* **191**, 1131 (1976); H. M. Sachs, T. Webb III, D. R. Clark, *Annu. Rev. Earth Planet. Sci.* **5**, 159 (1977).
17. V. M. Davidson, *Contrib. Can. Biol. Fish.* **8**, 357 (1933).
18. R. A. Lutz, unpublished data.
19. J. P. Minard, N. F. Sohl, J. P. Owens, *U.S. Geol. Surv. Bull.* **1435-A** (1977), p. 132.
20. We thank R. D. Turner, M. R. Carriker, D. C. Rhoads, D. F. Schnitker, T. W. Dignes, S. E. Siddall, D. M. Rye, T. Hansen, and G. R. Clark for critical reviews of the manuscript; T. R. Waller for helpful discussions; A. S. Pooley and E. Tveter Gallagher for technical assistance with the scanning electron microscopy; G. Mercer for graphic illustrations; and W. K. Sacco for assistance with photographic reproductions. Supported in part by NOAA grants 04-6-158-44056, SGI-77-17, and 04-7-158-44034, EPA grant R804-909-010, and a grant-in-aid of research from the Society of Sigma Xi. Contribution 120 from the Ira C. Darling Center, University of Maine, Walpole.

30 May 1978; revised 6 July 1978

Genetically Determined Sex-Reversal in 46,XY Humans

Abstract. Evidence is presented for the existence of a gene, probably on the X chromosome, which prevents testis differentiation when present in 46,XY human embryos. Affected 46,XY women are not completely normal because of premature ovarian involution, as a result of which they have "streak gonads" similar to those of 45,X women.

In most mammals the XY and XX sex chromosome complements determine male and female sex, respectively. A genetic determinant on the Y is responsible for differentiation of the indifferent embryonic gonad into testis, which otherwise becomes ovary. The testis, in turn, produces substances that suppress Müllerian and promote Wolffian ductal development and masculinize the indifferent external genital structures. In the absence of a testis, Müllerian ducts differentiate, Wolffian ducts fail to differentiate, and the external genitalia are not masculinized.

It is well known that sex-chromosome imbalance can interfere with normal sexual development. In fact, the delineation of the various clinical syndromes which result from human sex-chromosome imbalance has played a pivotal role in clarifying normal mechanisms of sexual differentiation. Less widely recognized but no less interesting, and potentially more informative, are single genes that also are capable of disturbing these mechanisms (1, chaps. 5, 6, and 8).

By 1971 (2), indirect evidence had accumulated pointing to the presence of a human gene in this class, one that was capable of preventing differentiation of the testis in individuals with the chromosome complement 46,XY (and thus, secondarily, of male external genitalia, as was mentioned above). The phenotype predictable for the 46,XY individual carrying such a gene would have just been that of the female. This prediction has

been correct, except that the gonad of 46,XY females thought to carry the gene has been not the functional ovary predicted for phenotypic females; instead, it has been the so-called streak gonad, a structure devoid of germ cells and indistinguishable from the structure found in adult 45,X females, who have Turner's syndrome (1, pp. 259-293). (Occasionally the streak in XY gonadal dysgenesis is replaced by a neoplasm such as gonadoblastoma or dysgerminoma.) The clinical syndrome—streak gonads in a 46,XY female—is best termed XY gonadal dysgenesis, replacing the earlier "pure gonadal dysgenesis" which refers to several entities [see (2) for the argument]. Normal female internal and external genitalia are found in both XY gonadal dysgenesis and 45,X gonadal dysgenesis (Turner's syndrome). The major clinical difference between these two conditions is a normal height in XY gonadal dysgenesis and shortness in Turner's syndrome. In addition, in XY gonadal dysgenesis certain other anatomical defects characteristic of Turner's syndrome besides short stature usually are absent.

The foregoing comparison makes it easy to understand why the presence of an undetected monosomic cellular component (45,X) has always loomed high as a possible explanation for the gonadal streaks found in 46,XY females. But we and our colleagues have been impressed by the occasional familial clustering of 46,XY individuals with gonadal streaks