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STROPHY: A POORLY-KNOWN MODE OF COILING IN GASTROPODS

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There has long been a fascination with one type of coiling abnormality in gastropods, and that is reversal of the direction of coiling or CHIRALITY, which often goes under the nontechnical term "handedness". Tangled in with this is an independent and unrelated mode of coiling, strophy, which is generally misunderstood, even by the molluscan authorities; this involves not the direction of coiling, but the direction of the TREND of coiling.

DEFINITIONS

AMBIDEXTROUS – Also, and perhaps more precisely, termed amphidromine after the amphidromine landsnail *Amphidromus*. Species which normally coil both dextrally and sinistrally within a population.

ANTERIAD – Directed toward the anterior end.

CHIRALITY - Direction of coiling around the coiling axis; beginning from the protoconch in coiled forms, the direction never changes in a given normal specimen, even those with irregular coiling or those with heterostrophic protoconchs. Chirality is an absolute; there are no halfsinistral or halfdextral shells; they can only be one or the other, with no gradation between the two. Independent of strophy.

COILING AXIS - An imaginary line around which the shell "revolves" as it grows; normally absolutely straight in most taxa, but in some curved (many EULIMIDAE) wandering (*Vermicularia*, SILIQUARIIDAE, VERMETIDAE) or even disappearing (late growthstage of muricid *Magilus*).

DEXTRAL CHIRALITY - "Righthanded". Coiling in clockwise manner when viewed from posterior (apical end in orthostrophic forms, basal in hyperstrophic). By far the most common chirality, both in the past and today.

GENERATING CURVE - Geometric curve defining the rate of increase of distance of the center of the aperture from the coiling axis during growth, clearly visible in apical view. Generally the generating curve is constant, producing a regular coil; however it may increase or decrease normally in some taxa (inevitably this involves changes in the rate of translation also). Tightening of curve can cause changes in spire-outline eg *Babylonia perforata*, *Urocoptis*, *Cerion*. Changes are inextricably linked to proportional changes in rate of translation along coiling axis; tightening of generating curve results in increase in rate of translation (or vice-versa). Only in the extinct bellerophontoids is the curve truly logarithmic; in all other gastropods the curve is pulled out into a helicone by translation along the coiling axis.

HETEROSTROPHY - Shells in which a change in strophy occurs. This is normal in such groups as MATHILDIDAE, ARCHITECTONICIDAE, PYRAMIDELLIDAE, opisthobranchs (including pteropods) and ELLOBIIDAE (and other archaeopulmonates). The protoconch is in part or entirely hyperstrophic, altering to orthostrophic just prior to initiation of deposition of the teleoconch ("adult" shell). The superficial appearance given is that of a dextral shell with sinistral protoconch, and this is the incorrect definition used in almost all literature. In fact the entire shell is dextral (except in the case of the one known genus containing sinistral species, the ellobiid *Blauneria*).

HYPERSTROPHY - Translation of growth along coiling axis toward posterior (posteriad translation). In entirely-hyperstrophic shells what appears to be a columella is in fact the parietal wall, which can be termed pseudocolumella. Some shells are unusual and appear to have components of orthostrophy, isostrophy and hyperstrophy in one shell (so-called bubble shells eg Atys, Bulla, Volvulella, which normally have a pseudocolumella in addition to a columella); however they are actually orthostrophic, and a hyperstrophic abnormality could occur in these forms. Hyperstrophy is NOT a mirror-image of orthostrophy. Hyperstrophic dextral shells often called "ultradextral" or "hyperdextral", hyperstrophic sinistral shells ""ultrasinistral" or "hypersinistral".

ISOSTROPHY - No translation whatsoever of growth along coiling axis. Growth is truly logarithmic. Shell is perfectly bilaterally-symmetrical; planispiral. Does not occur in modern gastropods but was normal in extinct bellerophontids.

ORIENTATION OF SHELL - Standard orientation of a gastropod shell is anterior (base)-down, posterior (apex)-up; this orientation is invalid in the case of hyperstrophic shells, as in such specimens the "apex" if any is actually at the anterior. In any case, if there is a siphonal canal, this is always anterior. Therefore in illustration a dextral orthostrophic shell should have the aperture located at lower-right; a dextral isostrophic shell at center-right; a dextral hyperstrophic shell at upper-right. That is, any specimen should be oriented with the aperture to the correct side for its chirality. Note that in the past such standards were not always practiced, and even today the French and Indians often persist in illustrating shells "upside-down".

ORTHOSTROPHY - Translation of growth along coiling axis toward anterior (anteriad translation). The normal mode for the vast majority of gastropod genera over geologic time.

POSTERIAD – Directed toward the posterior.

RATE OF EXPANSION - As a shell grows the aperture increases in area, producing a tube in the form of a shelly cone. This tube in most taxa rotates around an axis to produce a coiled shell. The rate of expansion defines the rate at which the width of the cone increases per distance from the protoconch, and can be expressed as a ratio (diameter:length). Rate of expansion controls presence and diameter of any umbilicus; the greater the rate for a given generating curve, the narrower the umbilicus. The higher the rate of expansion, the more rapid the increase in diameter of the cone. Species with a low rate of expansion produce a long narrow gradually-tapering cone; when wound around the axis this tends to form a high-spired shell of many whorls (eg *Terebra*). Species with a high rate of expansion produce a shorter more rapidly-tapering cone, which when coiled produces a short broad spire of fewer whorls (eg *Turbo*). Intermediates take the form of "semilimpets" such as *Capulus* and *Amathina*, which have a distinct but small spire and at least a hint of translation. Taken to an extreme of expansion, there is insufficient length of cone to produce whorls, much less translation, and a patelliform (limpetlike) shell results. Changes of rate in a single individual can create concave or convex spire-outlines (eg concave or convex upper spires in some *Calliostoma* and *Perotrochus* and in Clausiliidae). Independent of chirality, strophy and rate of translation.

SINISTRAL CHIRALITY - "Lefthanded"..Coiling in anticlockwise manner when viewed from posterior. Mirror-image or reversed geometry of dextral. A sinistral shell of a given species is an exact mirror-image of a dextral specimen of the same species; the animal itself is also a mirror-image.

STROPHY - Defined by direction of translation. The direction in most forms does not change in a given specimen, but in certain "higher" groups of gastropods a reversal is normal (Heterostropha, Opisthobranchia, Archaeopulmonata). Strophy is not an absolute; there is a full range of potential gradation between the endpoints (orthostrophy and hyperstrophy). Independent of chirality.

TRANSLATION - In geometry/mathematics, a movement from one place to another, without altering shape or orientation. As an orthostrophic or hyperstrophic shell grows by accretion along the apertural margin, the aperture moves not only in a rotation of increasing diameter, but also in a direction away from the protoconch. Translation produces the helical component of coiling present in most gastropods. In some taxa the rate of translation may change during growth, generally in individuals approaching maturity; this inevitably changes the generating curve, increases tightening it (causing the suture to suddenly descend more steeply, displacing the anterior whorl/whorls anteriad eg *Babylonia perforata*, CLAUSILIIDAE, UROCOPTIDAE); decreases loosening it. Isostrophic shells have zero translation, and only occur in the long-extinct and problematic bellerophontids. Changes in a single specimen can create concave or convex spire-outlines. Independent of chirality and strophy; dependent on or in part controlling rate of expansion and generating curve.

DISCUSSION

NOTES - Chirality is useless as a taxonomic character at above specific level, as an abnormally reversed specimen would "by definition" often have to be placed in a different genus. This renders *Sinistrofulgur*, a subgenus of *Busycon*, nonsense, as a dextral abnormality of a specimen of *Sinistrofulgur* then by definition MUST be placed in a different subgenus ie *Busycon* sensu stricto. One species absolutely cannot be placed in more than one supraspecific taxon. At specific level chirality becomes more important taxonomically, as the vast majority of species display only one direction; however abnormal specimens do occur in many families. A number of species and genera are ambidextrous (*Pyrulofusus harpa*; *Busycon perversum*; several species of *Marginella* and *Ancilla* occurring at Jeffrey's Bay, South Africa; *Amphidromus* spp).

- It is worthy of note that while it is possible for any gastropod species to produce an abnormal specimen of reversed chirality, the tendency to abnormal sinistrality in marine gastropods clusters in a few families (BUCCINIDAE, OLIVIDAE, MARGINELLIDAE, VOLUTIDAE). Despite the number of species and specimens occurring, in only one of these familes have sinistrality genes become fixed, giving rise to sinistral species in addition to the numerous species displaying abnormal sinistrality, and that is BUCCINIDAE (with sinistral species in Busycon, Neptunea, Prosipho, Pyrulofusus, Sinistralia).

- It is also worthy of note that abnormal hyperstrophy tends to be restricted to two families: Turbinidae and Architectonicidae. In the former the cause is uncertain, but the shells generally are somewhat irregular. In the latter it is due to failure of coiling to change to orthostrophic before commencement of production of teleoconch whorls, and the everted umbilicus is far "taller" than the spire of a normal specimen...

- Cephalopds such as ammonoids and nautiloids can have heliconic shells which superficially resemble those of gastropods, but their coiling is of a different order to those of gastropods, and application of some of the terms defined above to them is problematic and best avoided.

- It would be best to avoid the usage of "righthanded" and "lefthanded", as these confuse chirality with strophy.

It is believed by some that the shell twists the animal... and also that a hyperstrophic dextral shell (*Lanistes*, *Limacina*, protoconchs of pyramidellids, other opisthobranchs and architectonicids) is truly sinistral because it LOOKS superficially sinistral (Planorbidae are sinistral equivalents... though they look dextral, they are in fact hyperstrophic sinistral).

In this case the animal is uncharacteristic and "puts a new twist on" the shell, though this has been going on at least since the Devonian. In thse taxa the animal is a normal (usually dextral) but has a deformity, you could say... the viscera "drops below" the head-foot instead of standing "above" it (using normal orientation eg as used in photography). This means that instead of coiling toward the animal's anterior, growth is toward the posterior... so the shell apex is on the outer lip (labrum) and the apparent "apex" is in fact the extruded base.

Almost all living gastropods are orthostrophic; they grow from the apex toward the anterior direction, "dropping downward" along the coilng axis (geometrically an anteriorward translation). This goes for both sinistral and dextral species, both normally and abnormally so. A tiny minority of species today are hyperstrophic, that is, they translate POSTERIORAD; such shells were far more common in the Ordovician, such as Macluritoidea. No gastropod after the Triassic is truly isostrophic, that is, coiling in one exact plane, so producing a shell much like that of modern Nautilus (only the problematic Bellerophontoidea were truly isostrophic).

INFORMALLY SPEAKING

Let's have another go at explaining this LESS FORMALLY... see if I can confuse you enough to get you to send me all of your collections for free.

To visualize a hyperstrophic shell, think of a freshwater pilid apple snail (familial name PILIDAE has chronologic precedence over AMPULLARIIDAE) such as *Ampullaria*, say one found introduced in a Florida stream. Now, I have never heard of a sinistral pilid species, despite sinistral abnormalities of *Pila* being not rare... ALL pilid species, no matter what they look like, are normally dextral, though abnormal sinistral specimens of *Pila* do occur.

You could try the "experiment" below using plasticene. Make sure you don't stick the whorls together where they contact, so they can slip past one another…

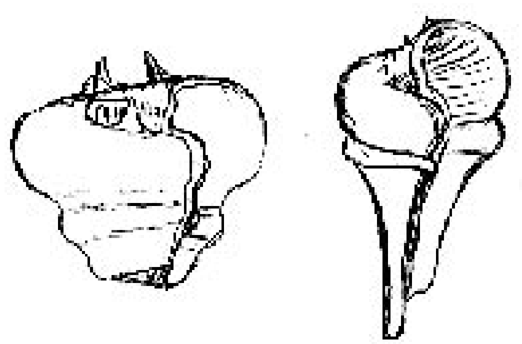
OK, take a *Pila* shell that's been softened by soaking in Palmolive dishwashing detergent (softens your hands while you do dishes)… don't make it too concentrated or the shell may turn to mush! Slip a thin wire tipped with a drop of superglue up the narrow umbilicus until it sticks to the underside of the protoconch and sets. Now, gently pull the wire down along its axis... you'll see the shell's spire become lower (it's been softened, remember) as it's pulled in, and the whorls slip apart a bit and slide over one another's surfaces (ie increasing the rate of expansion of the generating curve)... eventually the shell becomes broad and almost flat, when the protoconch has been pulled down far enough to be level with the middle of the aperture; the umbilicus has had to open up, as the whorls will not become laterally compressed. The shell is now as close as possible to isostrophic, as is the case in pilid genus *Marisa*, which is also found introduced in Florida streams. *Marisa*'s spire is extremely low, but not quite flat, and the shell can be seen to still be dextral. Now resume pulling on the wire. The spire begins to sink below the level of the center of the aperture and the shell begins to LOOK sinistral... keep pulling and the whorls slide across one another further, closing back up on the UPPER surfaces, producing what LOOKS like a wide umbilicus above as what LOOKS like a spire appears on the bottom of the shell, where a narow umbilicus was before. Continued pulling deepens the sunken spire's pseudoumbilicus above, and the everting umbilicus below grows into a steeper "spire"... eventually the shell comes to look like an upsidedown sinistral pilid. It now can be called *Lanistes*. But it is NOT sinistral... no reversal of direction of coiling rotation has occurred (this would be a lot easier to demonstrate, and for most to understand, if done in a computer-generated "movie"... do we have any computer-graphics people on the list??).

Think of the individual whorl as it moves in relation to other whorls. The parietal shield, at the top of the inner lip, is originally adpressed to the midpart of the previous whorl. With increasing depression of the spire the parietal shield slips higher on the previous whorl, until eventually it rolls a bit inward and becomes located at the upper surface of the previous whorl, and forms the side of the pseudoumbilicus, now resembling a columella. The columella and base of the lip slides upward also, until in the extreme form it is attached to the midlevel of the previous whorl, coming to look like the parietal shield of a sinistral shell (more new terminology is needed, such as "pseudoparietal shield").

Pilids generally do not have any characters which can give obvious clues to orientation; no labral sinus, no siphonal canal, in most cases no sharp shoulder-angle, no umbilical cords; the exceptions are some species of Lanistes, which have a carinate umbilical angle which is expressed as a "shoulder" angulation. However some dextral shells do occasionally have a hyperstrophic abnormality; to my knowledge this is known in at least 3 genera of Turbinidae (eg *Dinassovica smaragdus* of NZ, *Subninella undulata* of SE Australia, *Sarmaturbo sarmaticus* and *"Turbo" natalensis* of South Africa) and to in two species of architectonicid genus *Heliacus*. These shells DO have characters which show the shell's orientation; they also have coiled opercula, and as the operculum is not affected by the strophic abnormality, its coiling remains to show the shells to be dextral (in reversed coiling the operculum's coiling is also reversed; note that pilids do not have coiled opercula, so hyperstrophic or sinistral specimens could not be differentiated by the opercula). Turbinids generally have a faint anterior canal, and in the hyperstrophic specimens this can be seen to be distorted and plastered against the side of the previous whorl; likewise *Heliacus*. The shell's sculpture will also give the orientation away ie position of certain spiral ribs etc which are specific to certain parts of the whorl's surface, which in the case of hyperstrophy will be displaced. The abnormal turbinids also tend to be rather irregular in growth, indicating that something was wrong with the animal, apart from the change in growth direction; the condition may well be pathological rather than genetic in these shells.

Note that some groups combine normal orthostrophy with what appears to be partial hyperstrophy. Many opisthobranchs (Bulla etc) have spires sunken to produce a pseudoumbilicus as the posterior parts of the shell grow "upward" while the anterior end grows normally in an anteriorward diretction.

I tried to work out what a hyperstrophic specimen of a species with a long siphonal canal would look like. I chose my old favorite *Busycon perversum*. What we get is still somewhat turnip-shaped, but wierd. The shoulder inclines "upward" instead of "downward"; the bodywhorl is rounded, as the peripheral keel is rolled over/inward toward the sunken apex; the peripheral spines likewise roll in toward the sunken apical pit (pseudoumbilicus) and surround it. The swollen ridge around the canal base runs slightly upward, around the middle of the shell or a bit "above"; I can't quite decide what the canal does, but I suppose that it will grow thicker than normal as it coils around itself; it will continue to grow anteriad, but to a lesser degree than normal.



Two possible alternative hyperstrophic busycon perversum.

There exists a diagram called Strophy.jpg hiding on the web. It shows quite well the differences between dextral & sinistral orthostrophy & hyperstrophy. It also shows heterostrophic protoconchs (in these shells the early part of the protoconch is hyperstrophic, changing to orthostrophic before the adult shell begins to form eg *Odostomia*, *Architectonica*, *Amphibola*); note that, despite what you will read everywhere, there is NO SUCH THING as a sinistral protoconch on a dextral adult shell. This diagram shows a "hypothetical" sinistral heterostrophic protoconch, claiming that it is an unknown possibility; this is inaccurate, as there is ONE known sinistral heterostrophic species, the previously-mentioned ellobiid *Blauneria heteroclita*.

Always remember: The animal shapes the shell, not the other way around. After all, the animal MAKES the shell. A chirally reversed animal will make a reversed shell. So the entire animal and shell are exact mirror-images of a normal specimen. A dextral animal cannot produce a sinistral shell.

Some gastropods have come close to uncoiling, and these shells are often called “limpets”, though only a few of these families should be called such. To the best of my current knowledge all are normally dextral, though some eg the archaeopulmonate Siphonariidae and Trimusculidae show heterostrophic protoconchs. The protoconch is small and in larger forms is inconspicuous and often eroded away; the teleoconch becomes almost a straight cone, though the shortening of either the anterior (Acmaeidae) or posterior (Fissurellidae) gives a hint of the original coiling; some have a central protoconch eg Addisonia.

SOME NORMALLY-SINISTRAL TAXA
Calliostoma incertum
TRIPHORIDAE: all members of subfamily TRIPHORINAE
Acirsa antarctodelicata (Stilwell & Zinsmeister 1992) (Eocene Antarctic fossil)
Antistreptus spp
Busycon perversum (Linné 1758) (ambidextrous)
Neptunea contraria
Neptunea laeva
Prosipho spp
Pyrulofusus harpa (ambidextrous)
Sinistralia spp
Antiplanes several spp (genus ambidextrous)
Conus adversarius (Plio-Pleistocene US fossil)
Sinistrella spp
Terebra inversa (Miocene European fossil)
Blauneria heteroclita
PHYSIDAE
Vertigo spp
Clausiliidae most spp
Amphidromus several spp (genus ambidextrous)

SOME NORMALLY-HYPERSTROPHIC TAXA
MACLURITOIDEA (dextral Ordovician fossil)
Lanistes all spp (dextral)
Limacina all spp (dextral)
PLANORBIDAE (all sinistral) excepting *Glyptophysa* (orthostrophic)

SOME HETEROSTROPHIC TAXA
ARCHITECTONICIDAE
Mathildidae spp
PYRAMIDELLIDAE
AMATHINIDAE ??
OPISTHOBRANCHIA in general
AMPHIBOLIDAE
TRIMUSCULIDAE
SIPHONARIIDAE
ELLOBIIDAE
CARYCHIIDAE ??

CONTACT DETAILS
I am interested in obtaining specimens of both abnormal chirality and strophy, and can be contacted at these addresses:

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Thanks to Harry Lee (28-7-2005) for looking over this note and making suggestions, most of which have been incorporated here.

NONREFERENCES
I cannot give references, as all of my (unindexed!) literature on abnormal coiling disappeared when moving house last year (I suspect that one of my helpers managed to misfile a couple of boxes into the trash trailer). However Robert Robertson’s papers certainly are important. Harry Lee’s section in the Jacksonville Shell Club’s website (homepage www.jaxshells.org) is an important item, and includes a note on abnormal hyperstrophy in *Heliacus* added since I began this note.