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Standardized Descriptions of Primate Locomotor and Postural Modes

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ABSTRACT. As quantitative studies on primate positional behavior accumulate the lack of a standard positional mode terminology is becoming an increasingly serious deficiency. Inconsistent use of traditional terms and inappropriate conflation of mode categories hamper interspecific and interobserver comparisons. Some workers use common terms without definition, allowing at least the possibility of misunderstanding. Other researchers coin neologisms tailored to their study species and not clearly enough defined to allow application to other species. Such neologisms may overlap, may completely encompass, or may conflate previously defined labels. The result is, at best, the proliferation of synonyms and, at worst, the creation of confusion where clarity had existed. Historical precedents have sometimes resulted in "catch-all" terms that conflate any number of kinematically different behaviors (e.g. "brachiation," "climbing," and "quadrumanous climbing"). We recognize three areas where distinction of positional modes has some current importance: (1) Modes that require humeral abduction should be distinguished from adducted behaviors; (2) locomotor modes that involve ascent or descent should be distinguished from horizontal locomotor modes; and (3) suspensory modes should be distinguished from supported modes. We recommend a nomenclature that is not dedicated to or derived from any one taxonomic subset of the primates. Here we define 32 primate positional modes, divided more finely into 52 postural sub-modes and 74 locomotor sub-modes.

Key Words: Locomotion; Posture; Positional mode.

INTRODUCTION

Thirty years ago PROST (1965) wrote "primate locomotor classification is in a state of disorder." He specified a number of theoretical and terminological disagreements among primatologists as the source of this disorder. He attempted to remedy the disarray by defining a number of vital concepts in primate locomotor and postural study, including the term "positional behavior." Field study of primate positional behavior has since benefitted from many such readjustments and refinements. We believe our field can now profit from a further standardization of positional mode definitions.

Anatomists, particularly those who use biomechanical approaches, have long recognized, often explicitly, that the most complete understanding of the primate musculoskeletal system must rely on quantitative primate positional behavior data. Such a perspective assumes that the primate body is adapted to routine and/or critical forces that act on it.

Only by understanding these forces can a behavior/anatomy connection be made (TUTTLE, 1969; STERN & OXNARD, 1973; JENKINS & FLEAGLE, 1975; FLEAGLE, 1979; RODMAN, 1979). It is vital, however, that positional data be detailed, explicit and quantitative. It must be gathered on primates behaving naturally in their natural habitat. The quality of these data is critical because even small differences between two species in the frequency of a particular behavior may be expressed in anatomical differences, if the differences have sufficient time-depth.

It is only in the last 25 years that such quantitative positional data have become available, but in that time information has appeared steadily, even spectacularly[1]. A concomitant increase in our understanding of the morphological correlates of some positional behaviors has resulted. Further advance, however, is hampered by lack of comparability between field studies. There are two principal ways data from different studies lose comparability, (1) through uncorrected observational biases, and (2) because non-comparable positional classifications are used.

Case 1, observational bias, can occur for a number of reasons that primatologists should take account of before beginning positional data collection. Incompletely habituated study subjects do not behave normally. Very poorly habituated animals may hurry activities, even taking abnormal risks. Partly habituated individuals may be quite tolerant of observers during arboreal behavior, but may avoid observers when they come to the ground. In such cases data are biased toward arboreal bouts, even though terrestrial behavior may be an important or even vital part of the species' adaptation. Conversely (and perhaps more commonly), in exclusively arboreal animals behaviors high in the canopy may not be sampled as often as behaviors lower in the canopy. This bias can be corrected by recording canopy location during intervals when animals are not adequately observed, and adjusting the proportions of the results (standardizing).

Some animals are more sensitive to observers when resting than when feeding, so that food-gathering postures may be oversampled. Poorly habituated individuals may be less likely to flee when feeding on a particularly desired food resource, but may flee when feeding on less selected items, introducing bias toward positional modes associated with certain food items. More rarely, one sex may be more easily habituated or more easily observed than another (e.g. males among chimpanzees), which can introduce significant bias when the sexes differ in behavior and diet. Among chimpanzees, estrous females are less fearful of researchers than non-estrous females, a concern because the positional behaviors and activity budgets of estrous and non-estrous females are differ dramatically (HUNT, 1989).

Case 1 biases can also occur because many primates are more noticeable and/or noisier during locomotion, which means that locomotor behaviors disproportionally represent first-observations. If primates are followed for short time-periods, locomotor modes are oversampled. Locomotor bouts can be *under*sampled because they are frequently of shorter

1) For example, RICHARD, 1970; CHIVERS, 1972; GRAND, 1972, 1984; ROSE, 1974, 1977, 1978; SUSSMAN, 1974; WALKER, 1974, 1979; FLEAGLE, 1976, 1978; KINZEY, 1976; MITTERMEIER & FLEAGLE, 1976; MENDEL, 1976; MORBECK, 1977a, b; MITTERMEIER, 1978; SABATER PI, 1979; FLEAGLE & MITTERMEIER, 1980; GARBER, 1980, 1984, 1991; SUSMAN et al., 1980; SUGARDJITO, 1982; GITTINS, 1983; CROMPTON, 1984; KANO & MULAVWA, 1984; NIEMETZ, 1984; SRIKOSAMATARA, 1984; SUSMAN, 1984; TUTTLE & WATTS, 1985; CANT, 1986, 1987a, b, 1988; CROMPTON & ANDAU, 1986; SUGARDJITO & VAN HOOFF, 1986; SCHÖN YBARRA & SCHÖN, 1987; FLEAGLE & MELDRUM, 1988; BOINSKI, 1989; FONTAINE, 1990; HUNT, 1991, 1992; GEBO, 1992; DORAN, 1992, 1993a, b; DAGOSTO, 1994; CANNON & LEIGHTON, 1994; WALKER, 1994, in press; REMIS, 1995; GEBO & CHAPMAN, 1995a, b.

duration than postural bouts, and may be overlooked or left unrecorded, especially during continuous sampling.

Time-of-day biases may occur when subjects are observed over the same time-period consistently (e.g. mornings). Chimpanzees eat more fruits in the morning, and arm-hang more when harvesting fruits than most other foods. They eat more foliage in the late afternoon and evening, during which time they typically sit. Morning only sampling will oversample forelimb-suspension, afternoon only sampling will oversample sitting.

Most Case 1 biases become less profound as the level of habituation at a study site increases thereby allowing observation across all hours of the day, in all contexts, in all habitats, in all seasons, and on both sexes. Most other Case 1 biases can be solved by judicious standardizing.

Case 2 biases are a different matter. They will require a coordinated effort to resolve. In Case 2, important behavioral information is lost in a categorical system wherein a critical positional mode may be conflated with one set of behaviors in one study and a different set in another. This problem was anticipated rather early by RIPLEY (1967), and a solution offered: define positional modes before study begins. Unfortunately, primatologists are generally unable to anticipate the breadth of a primate's positional repertoire before actually observing the species in the wild. Some locomotor modes come as a complete surprise, and even in hindsight appear as nothing less than bizarre (e.g. transaxial bounding in *Leontopithecus*, ROSENBERGER & STAFFORD, 1994). Despite such surprises, we judge that enough field studies have been completed that an attempt at standardizing positional modes seems warranted.

One difficulty faced by the prospective standardizer is choosing the best level of resolution, that is, how finely to differentiate between positional modes. The problem can never be completely resolved because some sampling methods permit more detailed note-taking than others, yet high-resolution methods are not appropriate for every problem (DORAN, 1992). Instantaneous sampling (especially, e.g. every minute or every 2 min) permits an observer more time to record data than continuous sampling, making it possible to score and record variables on such diverse areas as the proximity and identity of conspecifics, grip types for each hand or foot, support orientation, and so on. Instantaneous sampling, however, cannot provide information on the average length of a positional bout, nor distance traveled (DORAN, 1992). It decreases the total number of observations, since behavior between time-points is not recorded. Continuous sampling is therefore preferred when fine-grained distinctions between modes are less important or when few observations are anticipated, even though it allows fewer variables to be observed and results in lower-resolution distinctions between positional modes. The level of detail and discrimination among positional modes we offer here is appropriate for rather fine-grained study, while we are well aware that it will be insufficient for studies that address very specific or localized morphology (e.g. carpal joints). Focused kinematic studies are necessary for the latter sort of comparison. Such detailed study, moreover, will help to refine and correct the details implicit in the categories provided here, especially in comparisons of phyletically diverse taxa. We work from the explicit assumption that the more modes recognized in advance of research, the less chance a researcher has of significantly miscasting a behavior by conflating it with a kinematically different mode.

Continuity between different positional modes provides a challenge to every observer, and ultimately makes categorization limiting (PROST, 1965; RIPLEY, 1967). For some problems, categorization is simply inappropriate (ibid; CANT, 1992). Although descriptions of particular modes can be extremely complicated, we argue that there is still enough consistency in positional behavior that categorization is profitable. With current field methods it is impossible to differentiate every movement, nor is it desired, since we cannot possibly analyze the anatomical implications of each of a near-infinite roster of positional modes. Instead, modes that have kinematically and mechanically similar attributes can be grouped under a convenient nomen that has some anatomical meaning.

Below we present descriptions of 32 major positional modes, comprised of 126 sub-modes. Mode descriptions are complete enough to be used with instantaneous sampling, and written to allow an informed pooling of modes for continuous sampling. Our intention is that these modes will help to allow comparisons across all primate (and some non-primate) taxa.

METHODS

In devising positional mode descriptions we made every attempt to use terms that are substantially similar or identical to those in common use. Where practical and helpful, we provide a species exemplar for each mode. Where terms differ only slightly from study to study, we have used our judgement in deleting certain aspects of the definition so as to make standardization possible.

Several positional mode terms that have proven confusing, but are nevertheless in common use, have been excluded here, or have been recast with restricted meanings. Perhaps the most significant is the term climbing (also quadrumanous climbing, or cautious climbing). The unqualified term "climbing" is often used to describe any arboreal movement, walking on horizontal supports and brachiation the modes most likely to be distinguished from "climbing." Using a single behavioral category for such diverse behaviors gives the mistaken impression that, for example, animals which most frequently move pronograde across horizontal supports and those that more often vertically climb are subject to similar selective pressure on their anatomy. We suggest reserving the term "climb" for ascent and descent of supports angled at $\geq 45°$ (i.e. synonymously with "vertical climb," see below for more detail). That is, we recommend *that the term "climb" not be used for ANY horizontal movement.*

We have used FONTAINE's (1990) method of categorizing leaping and dropping modes with takeoff and landing behaviors kept separate. It seems advisable during instantaneous sampling to record "leap" with a note on both takeoff and landing.

We have used colloquial terms for some scientific terms where there is little possibility of confusion. The manus (plural: manus) is referred to as the hand(s). We use foot for the pes (plural: pedes), or hindfoot. Other terms that are in less common use are occasionally unavoidable. We have tried to avoid the term cheiridium (plural: cheiridia), a label that can refer to either the manus, the pes, or both. "Substrate" is commonly used to refer to a weight bearing structure on top of which a study subject stands or locomotes. Likewise, "superstrate" is a structure from which an animal suspends itself. We use "support" to mean both or either.

We have given the terms "subhorizontal" and "subvertical" their most common meanings, i.e. horizontal/near-horizontal and vertical/near-vertical, respectively. It is our impression that this is typically operationalized as within approximately 20° of vertical, but that horizontal may be more strictly defined. We suggest the term "vertical" for within 10° of true vertical, and "sub-vertical" $>10-20°$ of vertical. Similarly, horizontal for within 10° of true horizontal, and "sub-horizontal" for within $>10-20°$ of horizontal. "Angled" may be a convenient term for any other orientation if a more accurate measure of angle cannot be provided.

Hand or foot contact and orientation is an integral part of the primate positional strategy, yet distinguishing two modes simply on the basis of differing grips provides only marginally more information. We have tried to pool positional behaviors that are substantially similar except for hand and foot positions, and have provided separate notes on hand and food contact.

For postures, the area of the base of support is an important determinant of a mode's stability, especially on small supports. We have avoided conflating postures (e.g. flexed-sit and exended-sit) where the area of the base is different.

Throughout the descriptions below, weight-bearing is held as the critical datum when determining into which of two modes a particular behavior falls. The authors agree that during data collection in the field it is possible to estimate the portion of weight borne by various body parts. Clues can be obtained about weight-bearing by observing the degree of deformity of supports, the location of the torso in relation to hands, feet, and support, how strongly a support rebounds when weight is shifted, and the appearances of hands, feet, and limbs. While we are aware that further study is desirable to confirm or disprove the assumptions we make about weight-bearing, we also suggest that estimates of this datum are useful at present. As a rule of thumb, we suggest that a body part which does not appear to bear more than its own weight should not be considered in determining positional mode. If important to the research topic of interest, a tally of the body parts touching supports can be taken as a separate datum.

Among prehensile-tailed New World monkeys many positional modes are stabilized by tail grips. When the tail is bearing little body weight, positional modes appropriate for Old World primates are adequate. When substantial body weight is borne by the tail, independent mode labels are suggested.

Often the orientation of the trunk has important effects on other body segments. We have attempted to pay particular attention to this datum. Further, we have provided a schematic indication of the orientation of the torso [i.e. (–) for pronograde and (|) for orthograde] with some mode descriptions to facilitate a quick scanning of the modes during field observation.

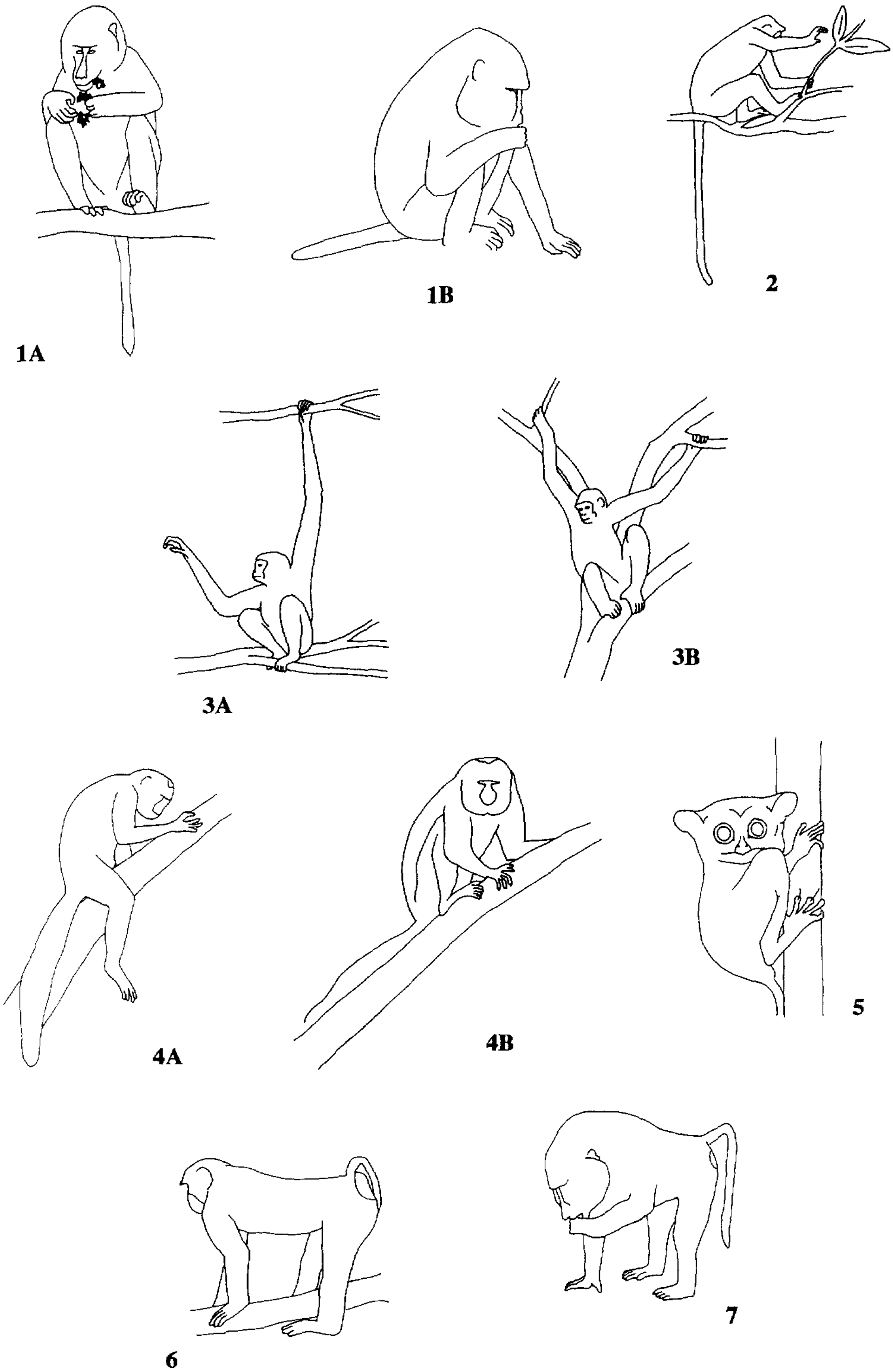
In practice, the field observer is confronted with any number of "hybrid" positional behaviors in the course of even short observations. In these cases, e.g. sit/forelimb-suspend, we have placed the mode that the weight bearing pattern most closely conforms first, and the less critical mode second. Forelimb-suspend/sit therefore is a mode where most weight is borne by the forelimb, whereas in sit/forelimb-suspend most weight is borne by the ischia.

POSITIONAL MODE DESCRIPTIONS

Postural Modes

P1. Sit: A posture in which the ischia bear substantial portion (usually more than half) of the body weight; the torso is relatively orthograde (|).

a. *Sit-in*: Weight is supported by the ischia and the feet with the hip and knee tightly flexed so that the heel(s) are very near the ischia, often touching the dorsal aspect of the thigh.


1A
1B
2
3A
3B
4A
4B
5
6
7

The feet bear an amount of the weight roughly proportional to that borne by the ischia. The trunk is orthograde (|), though the spine may be strongly bowed (cf. FLEAGLE, 1978, Fig. 10F), especially its cranial portion (Fig. 1A & B).
b. *Sit-out*: Sitting with the hindlimbs extended; that is, the feet "out" so that the ischia bear most of the body weight. The feet are used mainly for balance, and do not bear significantly more than their own weight (Fig. 2).
c. *Foot-prop sit*: Similar to sit-out, but the hindlimbs are flexed at the hips and extended at the knees, with the feet propped against a vertical support. The trunk may also flex at the hips, so that it rests against the hindlimbs. Common sleeping posture in its exemplar, *Papio.*
d. *Sit-in/out*: One hindlimb is extended while the other is flexed.
e. *Ischium-sit*: Neither the hindlimbs, forelimbs nor other body parts bear significant body weight; only the ischia (or ischium; including callosities) bear body weight.
f. *Chair-sit*: A torso-orthograde sitting posture in which the ischia and dorsal thigh(s) bear most of the body weight, but the elbow, back, stomach, side, or some part of the forelimbs contact a supporting stratum, often with the back supported by a stratum nearly perpendicular to that supporting the ischia; the pattern is reminiscent of a person sitting in a chair.
g. *Sit/forelimb-suspend*: More than half of the weight depends on the ischia (and the feet, if in contact with the support), but one or both abducted forelimbs grasp an overhead branch to stabilize the body and support some body weight (Fig. 3A & B).
h. *Angled sit*: This category is described with reference to support use, since on highly angled supports, the distribution of forces on the body differ from those on a horizontal support, due to friction. Other descriptors follow P1a, b, etc. (i.e. angled sit-in, angled sit-out, and so on) (Fig. 4).

P2. Squat: The body weight is borne solely by the feet/foot, both hip and knee are strongly flexed. Neither forelimbs nor ischia bear substantial body weight. The trunk is orthograde or suborthograde (|) and the back is typically flexed. The animal often facing at right angle to the length of the support. Sit-in (P1a) is different than squat in that the ischia bear body weight in sitting.

P3. Cling: Flexed limb posture most common on vertical-subvertical supports.
a. *Bimanual cling* (=vertical cling): Both hands grasp a support with the elbows flexed; the forelimbs are adducted and the torso is orthograde or suborthograde. Hindlimbs are

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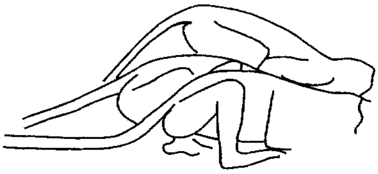
Fig. 1. Sit-in, or flexed-hindlimb sitting. A: Arboreal sit-in; B: terrestrial sit-in, redrawn from ROSE (1977) Figure 2A & 2C.
Fig. 2. Sit-out, or extended-hindlimb sitting. Note that the hindlimbs may be very important for balance, but at the same time may bear very little of the body weight, redrawn from FLEAGLE (1978) Figure 10A.
Fig. 3. Sit/forelimb-suspend. A: Gibbon, redrawn from FLEAGLE (1976) Figure 10F; B: spider monkey, redrawn from MITTERMEIER & FLEAGLE (1976) Figure 2C. Note that the ischia appear to bear most of the body weight; a forelimb provides significant stabilization without bearing proportional body weight.
Fig. 4. A & B: Angled sit.
Fig. 5. Bimanual cling, redrawn from RICHARD (1985) Figure 5.3, after a photo by D. HARING, Duke Primate Center.
Fig. 6. Quadrupedal stand. Note that the limbs are not flexed, redrawn from FLEAGLE (1980) Figure 7.3E.
Fig. 7. Tripedal stand, redrawn from ROSE (1977) Figure 3B.



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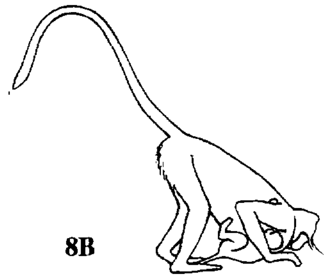

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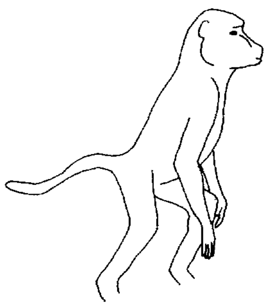

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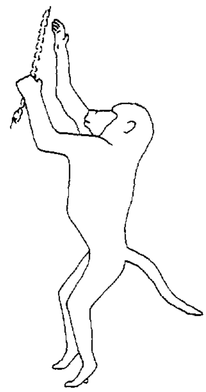

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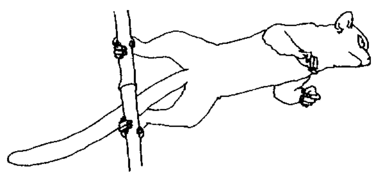

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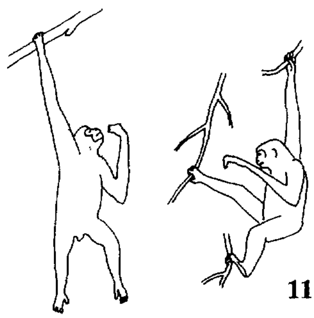

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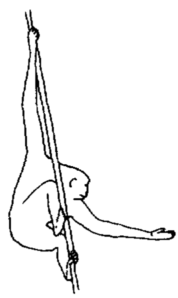

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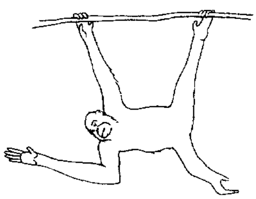

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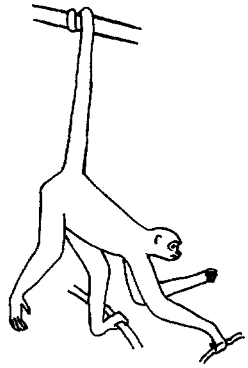

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flexed at hip and knee. The foot/feet may or may not grasp the support with a power grip, but support at least a proportional amount of the body weight (usually > half). The ischia bear none of the body weight. The forelimb supports may be more horizontal, but in all cases the elbow, knee, and hip are flexed and the hindlimbs bear at least half the body weight (Fig. 5).
b. *Unimanual cling*: As above except only one hand grasps the support with a flexed forelimb.
c. *Cling/forelimb-suspend*: As in unimanual cling, except one forelimb is extended in an arm-hanging fashion. More than half of the weight is borne by the hindlimbs and flexed forelimb in a clinging gestalt.
d. *Ladder cling*: As with bimanual cling, except that weight depends on two or more separate, horizontal branches, often necessitating a more pronated hand or foot position and requires less powerful gripping.

P4. Stand:
a. *Quadrupedal stand*: Four-limbed standing on horizontal or subhorizontal supports; the elbow and knee are (relatively) extended and the trunk is near horizontal (Fig. 6).
b. *Tripedal stand*: As above except with two hindlimbs and one forelimb bearing weight (exemplar: *Papio*, Fig. 7).
c. *Crouch*: Quadrupedal flexed elbow and/or flexed knee posture. (1) Full-crouch, where both elbows and hindlimbs are flexed (Fig. 8A); (2) Forelimb-crouch, wherein the elbows are flexed, but the knees are not (Fig. 8B); and (3) Hindlimb crouch, wherein the hindlimbs but not the elbows are flexed.

P5. Bipedal stand:
a. *Flexed bipedal stand*: Standing on the hindlimbs with no significant support from any other body part. The torso is typically held at an approximately 45° angle. The hip and knees are flexed (Fig. 9A & B).
b. *Extended bipedal stand*: Hip and knee are completely extended, but there is no significant support from the forelimb(s). The trunk is near orthograde. This mode best describes human-like bipedal standing. If one foot does not contact a support this term is still recommended.
c. *Stand/forelimb-suspend*: More than half of the body weight supported by the hindlimbs, but there is significant support from a forelimb oriented in an forelimb-suspend pattern, either (1) extended-stand/forelimb-suspend; or (2) flexed-stand/forelimb-suspend.

Fig. 8. Crouch. A: Three langurs, the two nearer in a full crouch, the most distant in a forelimb crouch, redrawn from RIPLEY (1967) Figure 8; B: forelimb-crouch with elbows flexed, redrawn from RIPLEY (1967) Figure 8.
Fig. 9. Flexed bipedal stand. A: A typical scanning stance, redrawn from ROSE (1976) Figure 2A; B: bipedalism during feeding, if the left arm bore more weight this would be a flexed stand/forelimb-suspend, P4c, redrawn from ROSE (1976) Figure 1C.
Fig. 10. Cantilever. Note the rigidity of the spine, redrawn from GEBO (1987).
Fig. 11. A: Unimanual forelimb-suspend; B: a more typical forelimb-suspend wherein the hindlimbs provide stabilization, though little support, redrawn from FLEAGLE (1976) Figure 10.
Fig. 12. Forelimb-hindlimb/stand, redrawn from FLEAGLE (1976) Figure 10.
Fig. 13. Forelimb-hindlimb-suspend (=arm-foot hang), redrawn from CANT (1987a) Figure 5.
Fig. 14. Tail-suspend, redrawn from FLEAGLE (1988) Figure 5.16.

P6. Tripod:
a. *Horizontal tripod*: "A combination of tail-hang and bipedal standing in which the animal is partly supported by its tail, anchored to a support above the base of the tail, and also partly by weight transmitted downward or rearward through the feet." The torso is pronograde or subpronograde (CANT, 1986: 3; perhaps identical to "inverted bipedalism," FONTAINE, 1990).
b. *Vertical tripod*: A flexed bipedal stand in which additional stability is provided by contact between the stiffened tail and the ground.

P7. Cantilever: The feet anchor the lower body to a stable near-vertical support. The trunk is held rigid and near horizontal as the individual reaches out to snatch insects with the forelimbs (Fig. 10). This behavior is quite different from bridging (P14) and should not be conflated with it. When the tail is recruited it becomes indistinguishable from P5a.
a. *Extended cantilever*: Knees and body are extended, often fully so in lorisids and cheirogaleids.
b. *Lean out cantilever*: Knees are flexed (exemplar: tarsiers).

P8. Forelimb-suspend (=arm-hang): Posture wherein more than half of the body weight is borne by the forelimb(s) grasping a support above the animal's center of mass.
a. *Unimanual forelimb-suspend*: Suspension by one hand with insignificant support from other parts of the body. The humerus is abducted and the elbow is usually completely extended. The trunk is orthograde (|). Other body parts may touch a support, but bear no more or little more than their own weight (Fig. 11A & B).
b. *Bimanual forelimb-suspend*: Suspension from both abducted forelimbs (substantially similar to P11b, but without support from the tail).
c. *Forelimb-suspend/sit*: Suspension with approximately half the body weight estimated to be suspended from one or both forelimbs, and the remainder supported by the ischia and/or feet (with hindlimbs flexed). One forelimb may be completely abducted and supporting the body weight in tension, while the other forelimb is oriented in a manner similar to that seen in clinging (humerus adducted and elbow flexed). An individual may be scored as arm-hanging or clinging depending on which forelimb appears to be bearing the most weight. Similar to sit/forelimb-suspend, except that more than half of the weight is borne by the forelimb(s).
d. *Forelimb-suspend/squat*: Suspension as above with the lower body supported in a squatting gestalt.
e. *Forelimb-suspend/stand*: More than half of the body weight suspended from one or both forelimbs, the other half supported with a bipedal standing pattern (Fig. 12). The knee and hip may or may not be extended. The trunk is held at least 45° above the horizontal.
f. *Forelimb-suspend/cling*: Hindlimbs flexed, grasping a support and bearing approximately half the body weight; one or both forelimbs under tension similar to forelimb-suspend (apparently quite similar to "orthograde lay back," FONTAINE, 1990).
g. *Forelimb-suspend/lie*: Suspension as above with the lower body supported in a lying (side or back) posture. The spine cannot be vertical. Somebody weight may be borne by an elbow (i.e. the olecranon process of the ulna).
h. *Trunk-vertical-suspend*: Suspension involving one or both forelimbs and one or both hindlimbs bearing weight in tension, foot/feet above the level of the hip, the trunk orthograde (|). Differs from other suspensory modes in that all the four limbs are in tension and the torso is orthograde (exemplar: orang).

i. *Unimanual flexed-elbow-suspend*: Suspension with the humerus relatively adducted and retracted and the elbow not completely extended. No other part of the body significantly supports the body weight.
j. *Bimanual flexed-elbow-suspend*: Similar to "i" except that suspension is from two hands.

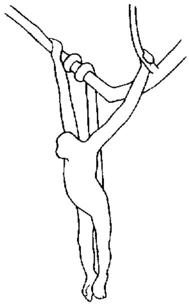
P9. Forelimb-hindlimb-suspend (=arm-foot hang): Suspension by a forelimb and a foot with the trunk in a subhorizontal orientation. Limbs are typically extended. Differs from forelimb-suspend in the more pronograde orientation of the torso, and in that the forelimb need not be completely abducted (see Fig. 13) (exemplar: orang).
a. *Ipsilateral forelimb-hindlimb-suspend*: Suspension with the torso pronograde by a forelimb and hindlimb on the same side of the body (Fig. 13).
b. *Contralateral forelimb-hindlimb-suspend*: Suspension with the torso pronograde by a forelimb on one side of the body, a hindlimb on the other.

P10. Quadrumanous-suspend: Suspension with the torso pronograde (–), with all the four limbs providing approximately equal support. Orientation of the trunk distinguishes this behavior from trunk-vertical-suspend (P8h).

P11. Tail-suspend:
a. *Tail-suspend*: Suspension from the tail with little or no support from the limbs (Fig. 14).
b. *Tail/forelimb-suspend*: Where at least an half the body weight is borne by the tail with significant weight borne by the forelimb(s). The humerus is abducted and the elbow is completely extended. The trunk is probably never completely orthograde (|) (Fig. 15).
c. *Tail/hindlimb-suspend*: Suspension with substantial support from the extended hindlimb(s) and the tail (Fig. 16).
d. *Pronograde tail/quadrumanous-suspend*: All the five extremities provide support. The trunk is pronograde (–).
e. *Orthograde tail/quadrumanous-suspend*: All the five extremities provide support, but the trunk is orthograde (|).

P12. Hindlimb-suspend: Suspension from the foot/feet. Differs from P8 and P9 in lacking support from the forelimb and from P11 in lacking support from the tail.
a. *Flexed-hindlimb-suspend*: Knee and/or hip flexed.
b. *Extended-hindlimb-suspend*: Both knee and hip extended.

P13. Lie: Torso orthograde posture on a relatively horizontal supporting stratum, body weight borne principally by the torso. When an individual grasps a support, the extremity bears little more than its own weight. When lying on a side an individual may support the upper body with an elbow.
a. *Supine lie*: Limbs may be flexed under the body, or not, and may bear some weight, but the belly and the hands/feet are on approximately the same level (="flexed resting" sensu FONTAINE, 1990).
b. *Sprawl*: Limbs dangled down while resting on belly, usually on a branch; sometimes used to aid cooling (Fig. 17; sensu FONTAINE, 1990).
c. *Lateral lie*: Weight rests principally on the lateral aspect of the torso.
d. *Back lie*: Weight rests principally on the dorsum (back).
e. *Sit/lie*: Sitting with the upper body supported partly by an elbow resting on the same support (or one at a similar elevation) as the ischia and feet.



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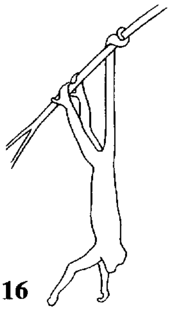

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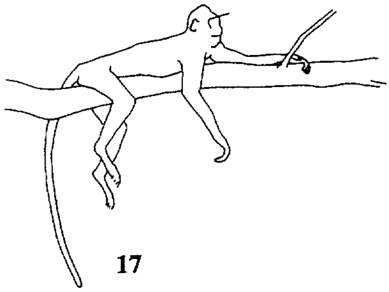

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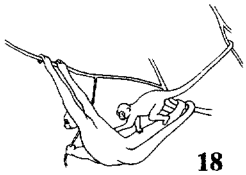

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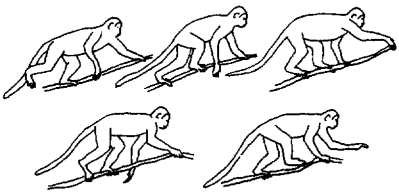

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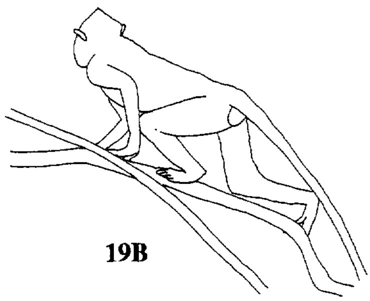

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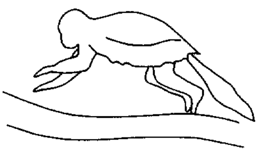

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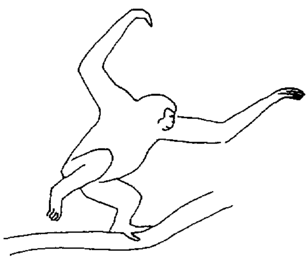

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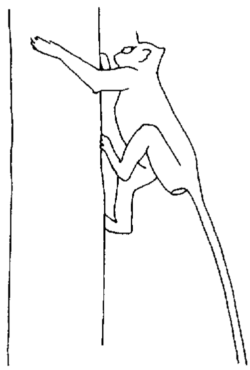

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P14. Postural bridge: The feet grasp a support on one side of a gap, the hands grasp support on the other side, with the body spanning the gap, in tension. Mothers may use their body as a "bridge" for infants (Fig. 18).

LOCOMOTOR MODES

L1. Quadrupedal walk: Locomotion on top of supports angled at <45°; typically all the four limbs contact the support in a particular sequence. The torso is pronograde (−) or roughly parallel to the support. Walking is distinguished from running principally by its slow or medium speed. Gaits are not treated in detail here; refer to HILDEBRAND (1967, 1977) for a complete categorization and discussion of gaits and their importance.
a. *Symmetrical gait walk*: (1) Walk: usually a diagonal sequence, diagonal couplets gait (HILDEBRAND, 1967). Limbs are extended. Symmetrical gaits are characteristic of most primate walking (Fig. 19); (2) Crouch walk: as for "walk" except that the elbows and knees are flexed, so that the body is held closer to the support for greater stability (SCHMITT, 1994).
b. *Asymmetrical gait walk*: (1) Bound: "the forelimbs move forward simultaneously and the hindlimbs move forward simultaneously, with both limbs of each pair contacting the substratum simultaneously." (MITTERMEIER & FLEAGLE, 1976: 242 and Fig. 20). Supports are typically large in relation to body size; (2) Tripedal bound: as in (1), with only one forelimb; (3) Slow bound: as in (1), at a slow pace, often for a single cycle, or with substantial pauses. Lateral movements with a similar gestalt are included in bounding (sensu FONTAINE, 1990); (4) Crutch walk: terrestrial quadrupedal torso-orthograde (|) slow-speed variation of bounding in which (unlike bounding) much of the torso passed between the forelimbs as the feet move forward. The adducted forelimbs move forward in concert; the elbow is completely or almost completely extended. After planting the forelimbs the body and hindlimbs are swung though the forelimbs. More precisely, this mode is a reversed bound without a free-floating phase. Crutching is seen almost exclusively during steep descents (exemplar: chimpanzee); (5) Transaxial bound: fore- and hindlimbs contact the support in equal proportions, with unusually long step lengths and a relatively unflexed back. The hindlimbs typically overstride the forelimbs. The axis of the hands are oriented in the same direction. The result is an "irregular cadence...marked by elevations and swaying of the hindquarters. Thus the animal progresses along a branch with all the four cheiridia oriented to one side or another of the substrate during movement, occasionally

Fig. 15. Tail/forelimb-suspend, redrawn from MITTERMEIER & FLEAGLE (1976) Figure 2G.
Fig. 16. Tail/hindlimb-suspend, redrawn from JOLLY (1985) Figure 5.9, from a photo by K. GLANDER.
Fig. 17. Sprawl, redrawn from RIPLEY (1967) Figure 7.
Fig. 18. P14, Postural bridge. Note that the body is in net tension, and the spine is not held rigid, redrawn from MITTERMEIER & FLEAGLE (1976) Figure 2F, as in CHIVERS (1968) p. 357.
Fig. 19. A: Palmigrade walking, redrawn from FLEAGLE (1980) Figure 7.2; B: on smaller or less stable supports individuals lower their center of gravity (SCHMITT, 1994), redrawn from RIPLEY, 1976, Figure 4.
Fig. 20. Bound, both limbs of each pair contact the support simultaneously, redrawn from MORBECK, 1974, Figure 1.
Fig. 21. Flexed bipedal walk, redrawn from FLEAGLE (1976) Figure 7A.
Fig. 22. Flexed-elbow vertical climb, redrawn from RIPLEY (1976) Figure 1A.
Fig. 23. Extended-elbow vertical climbing, redrawn from RIPLEY (1967) Figure 11.

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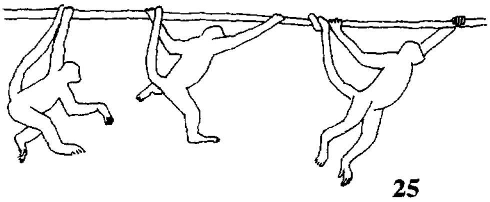

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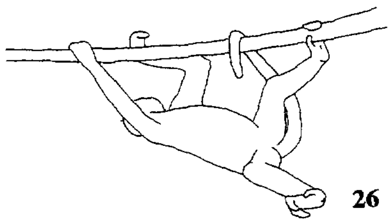

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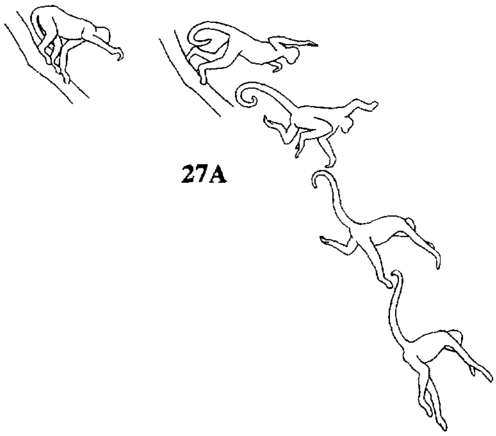

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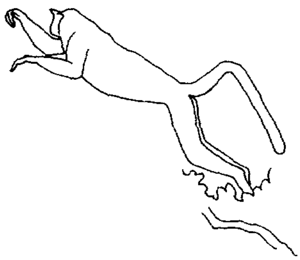

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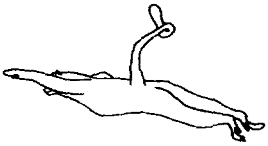

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switching sides between strides'' (ROSENBERGER & STAFFORD, 1994: 387; exemplar: *Leontopithecus*); and (6) Half bound: only one set of limbs moves in unison, i.e. either fore- or hindlimbs. Note: HILDEBRAND (1977) refers to L1b(1) and (5) as slow speed galloping.
c. *Irregular gait walking*: (1) Scramble (=pronograde clamber): torso-pronograde (−), non-suspensory quadrupedal progression lacking a regular gait. Typically supports are small, irregularly placed and variously angled. A locomoting individual may appear quite unstable. Pronograde clamber is most often seen among the terminal branches of trees. Progression is within 45° of horizontal. Speed may be slow to medium-fast. This mode is sometimes labelled ''climbing,'' a practice we discourage; and (2) Tardigrady: lorisoid, extremely slow, quadrumanous, torso-pronograde (−) progression that typically involves movement of only one limb at a time. In many ways a low velocity, sure-grasp pronograde clamber, this behavior typically involves more erratic limb excursions. *The use of the term ''slow climbing'' for this behavior is confusing and should be discontinued.* Ascent on support angled ≥45° by lorises can be described by the term ''vertical climbing'' with little loss of resolution.

L2. Tripedal walk: Same as quadrupedal walking in its various expressions, except one limb is not used in locomotion, the other often being used to grasp a carried object.
a. *Forelimb tripedal walk*: Both forelimbs used in walking, hindlimb may be reserved for carrying.
b. *Hindlimb tripedal walk*: Both hindlimbs used for locomotion, a forelimb may be used for carrying.

L3. Bipedal walk:
a. *Extended bipedal walk*: The hindlimbs provide support and propulsion, with only insignificant contributions from other body parts. The hip and knee are relatively extended, in a manner similar to human walking. This mode is extremely rare in chimpanzees and probably even more so in other nonhuman primates.
b. *Flexed bipedal walk*: As above, except the hip and knee are relatively more flexed (Fig. 21).

L4. Bipedal hop: Torso-orthograde (|) bipedal progression wherein the hindlimbs push off and land roughly simultaneously; there is a period of free flight (i.e. period of time in which no body part touches a support). Different from leaping in its repetitive, stereotyped progression and orthograde (|) torso.

L5. Quadrupedal run: Fast locomotion using asymmetrical or irregular gaits and with a period of free flight.

Fig. 24. Rump first descent. A: In a baboon, redrawn from ROSE (1977) Figure 7A; B: in a langur, redrawn from RIPLEY (1967) Figure 11.
Fig. 25. Brachiate, redrawn from MITTERMEIER & FLEAGLE (1976) Figure 1C.
Fig. 26. Inverted quadrupedal running, redrawn from MITTERMEIER & FLEAGLE (1976) Figure 1B.
Fig. 27. Leap. A: In *Ateles*, with redrawn from MITTERMEIER & FLEAGLE (1976) Figure 3; B: in the langur, redrawn from RIPLEY (1976) Figure 5A.
Fig. 28. Vertical clinging leaps. A: Stretched-out vertical cling leap; B: curled-up vertical cling leap; C: limbs-down vertical cling leap, redrawn from OXNARD et al. (1990) Figure 2.4.
Fig. 29. Unimanual suspensory drop, redrawn from FLEAGLE (1980) Figure 7.1.7.

a. *Asymmetrical gait run*: Galloping, including fast bounding and half-bounding.
b. *Irregular gait run*: Fast locomotion wherein footfall pattern follows no regular sequence.

L6. Tripedal run: Gallop with only three limbs contacting the support.

L7. Bipedal run: As in L3, but with a period of free flight. Particular attention should be paid to determining whether there is a period of free flight or not; most primate "running" is actually fast walking, without free flight. Note: Some species differ in locomotor modes principally in GRIP or CONTACT CATEGORIES. The following contact categories encompass much of this variation. (1) *Palmigrady*: the feet contact an arboreal support via the digits and the midfoot region, and may or may not grasp the substrate. The hands contact supports via the volar area of the digits and palm, but do not grasp the support. The wrist is supinated so that the long axis of the hand is near-perpendicular to the support (i.e. long axis makes an angle of >45° with the support). Foot heel-strike may be semiplantigrade, wherein only some portion of the plantar surface contacts the support, or plantigrade, wherein there is a true heel-strike at touch-down (SCHMITT & LARSON, 1995); (2) *Digitigrady*: the forelimb contacts the support via volar skin over the metacarpal heads and the digits are flattened along the support; the palm does not contact the support. The hindfoot may also contact the support via volar skin over the metatarsal heads, rather than the plantar surface (e.g. *Erythrocebus*); (3) *Knucklewalk*: similar to palmigrade quadrupedal walking, but the forelimb contacts the support via the dorsal skin over the intermediate phalanges of digits II-V (V least often), while the hindlimb contacts the support with heel-strike plantigrady (i.e. "the heel contacts the substrate at touch-down at the end of swing phase," SCHMITT & LARSON, 1995). The hindlimb is protracted prior to heel contact. Progression may be at a diagonal to the axis of the torso; (4) *Fistwalk*: an orangutan (rarely: chimpanzee) variant of (3), wherein the forelimbs contact the support via the knuckles of a closed fist, most often on the dorsal skin over the proximal phalanges of digits II-V; (5) *Graspwalk*: quadrupedal walking in which the pollex in addition to the hallux grasps the support, and digits are aligned on the sides rather than the tops of supports. The heel may contact the support first (e.g. in Great Apes), not at all (*Erythrocebus*), or it may contact after the midfoot (e.g. atelines); (6) *Serpentine graspwalk*: grasping by the non-hallucial and/or non-pollicial digits alone. In lorises the hands and feet have been modified into a pincer-like grasp where hands and feet are aligned more mediolaterally relative the long axis of the support. Long stride lengths and low stride frequencies are the rule; the back is mobile; (7) *Schizodactyl graspwalk*: similar to grasp walking, but with manual grasping occurring between the second and third digits (e.g. *Alouatta*); and (8) *Clawed quadrupedalism*: traction mostly provided by means of claws on the fingers and toes. Confined to callitrichids (as described in ROSE, 1973).

L8. Vertical climb:
a. *Flexed-elbow vertical climb*: Ascent on supports angled at ≥45°. Typically a hindlimb and its contralateral forelimb provide propulsion. The forelimbs help to elevate the body by the retraction (=extension) of the humerus and flexion of the elbow. Limb kinematics follow a diagonal sequence (hand-over-hand, foot-over-foot). The humerus is typically protracted in the process of reaching upward, not abducted. The torso is held pronograde (|) and nearly parallel to the support being climbed. Grasping hands are palmigrade in their contact with the support, and feet are semiplantigrade (Fig. 22). Identical to the "flexed-arm vertical climbing" of HUNT (1992).

b. *Ladder climb*: Similar to flexed-elbow climbing except supports are often relatively horizontal, and are never a single vertical support. Limb kinematics follow a diagonal sequence. This mode is similar to the movement of a person climbing a ladder with a diagonal gait.
c. *Vertical scramble*: Upward (≥45°) progression on multiple often oddly angled supports, typically without a discernible gait pattern.
d. *Extended-elbow vertical climbing*: Ascent on larger supports (e.g. >20 cm in chimpanzees and baboons) angled ≥45° in which the elbow is extended. The gait is a diagonal couplet, i.e. hand-over-hand, foot-over-foot climbing similar to vertical or ladder climb, except the elbow is extended. The support is gripped by the entire volar surface of the hand, including palm and fingers. Foot contact is principally semiplantigrade. Retraction of the humerus and extension of the hip provide most of the propulsive power; elbow flexion provides little propulsive force (Fig. 23, see also MITTERMEIER & FLEAGLE, 1976: Fig. 2A; identical to extended-arm vertical climbing: HUNT, 1992) (exemplar: *Pan*).
e. *Pulse climb* (=vertical bound): Ascent of supports angled at ≥45°. The forelimbs grasp a support as the hindlimbs are gathered underneath the body by flexion of the knee, hip, and spine; extension of the hindlimbs and back push the body upward. While the back and hindlimbs propel the body upward, the forelimbs release the support and are protracted in unison to reach a higher handhold. The motion has a pulsing appearance. This mode has also been labeled variously "hop" (EISENBERG & KUEHN, 1966), "trunk climb" (RIPLEY, 1967), "shinny" (RIPLEY, 1967; FONTAINE, 1990), "bear climb" (MACKINNON, 1974), and more typically "vertical bound."
f. *Bimanual pull-up* (=hauling or hoisting): A typically horizontal support is grasped by both hands and the body is lifted by retracting the humerus and flexing the elbow; the spine may be flexed to aid bringing the hindlimb on top of the support.
g. *Rump-first descent*: (1) Symmetrical rump-first descent: vertical quadrupedal descent of a support angled at ≥45°; rather the kinematic reverse of ascent, but often with more abduction of the forelimb (Fig. 24A & B); and (2) rump-first scramble descent: as with rump-first descent, exception multiple supports with odd orientations and diameters.
h. *Head-first descent*: (1) Symmetrical head-first descent: similar to quadrupedal walking, except the limbs served a braking function on these steep descents (≥45°); some skidding may occur (cf. FONTAINE, 1990); (2) head-first scramble descent: as with symmetrical head-first descent, except on multiple supports with odd orientation and sizes, and a less symmetrical gait; and (3) cascade: as with head-first scramble descent, except supports are still smaller, and radically angled. Limbs and tail grasp briefly and in rapid succession to brake descent.
i. *Sideways vertical descent*: the body is held at right angles to the long axis of the support. The downside fore- and hindlimbs provide most of the braking support.
j. *Head-first bounding descent*: both forelimbs move together, followed by both hindlimbs. Hands and feet act as brakes. May grade into a pronograde slide.
k. *Pronograde slide*: Head-first, quadrupedal, relatively passive descent of smooth oblique branches and boughs wherein the hindlimbs and forelimbs are held steady and the body moves by sliding the hands, feet, and other body contacts against the support (sensu FONTAINE, 1990). Torso is typically pronograde (−), and/or held parallel to the support.
l. *Fire-pole slide*: Rump-first, largely passive quadrupedal orthograde (|) sliding on vertical or subvertical support, usually very large (>20 cm). The support is circumducted by the forelimbs and hindlimbs, after which the animal allows its body to descend by sliding with little other movement. Not infrequently the forelimbs regulate the velocity of the descent with a hand over hand movement.

L9. Torso-orthograde suspensory locomotion:

a. *Brachiate*: Classic hand over hand orthograde suspensory locomotion in which the forelimbs bear more than half of the body weight, but in which some support from the hindlimbs or tail may occur. There is extensive trunk rotation, approaching 180°. The humerus is completely abducted and the elbow is extended, not infrequently completely extended (Fig. 25). Brachiation is virtually always assisted by the tail in those New World monkeys that brachiate.

b. *Ricochetal brachiation*: Hand over hand suspensory locomotion in which there is a period of free flight; it is faster than brachiation. As with brachiation, ricochetal brachiation is virtually always assisted by the tail in atelines.

c. *Brachiating leap*: Inertia from a rapid bout of brachiation, often followed by an especially powerful one-armed swing, propels the body forward.

d. *Forelimb swing* (=armswing): Similar to brachiate (L9a) but with little trunk rotation; typically assisted by tail in prehensile-tailed New World monkeys.

e. *Flexed-elbow forelimb swing*: As in forelimb swing (L9d) but with elbows bent; may be assisted by tail in prehensile-tailed New World monkeys.

f. *Transfer*: This mode often begins with bimanual forelimb-suspension, and may contain a brachiation-like gap-closing motion (a "lunge"), wherein a hand grasps a small support in an adjacent tree, after which a branch is pulled toward the animal with a hand over hand or hand over foot motion. Weight is gradually transferred to the adjacent tree. The torso remains more or less orthograde (|) throughout; more weight is born by the forelimbs than hindlimbs; usually assisted by tail in New World monkeys with prehensile tails.

g. *Orthograde clamber* (=cautious climbing=amoebic suspensory locomotion): Horizontal progression in a forelimb-suspensory torso-orthograde mode, but with the hindlimbs assisting. All the four limbs act as propulsors, with most body weight borne by the abducted forelimbs. Kinematically this mode most resembles brachiation, but it differs in that the hindlimbs provide support from virtually any orientation, including completely abducted. CANT (1987a, 1992) defined the mode as follows: "the body is orthograde with the head superior, and various combinations of all the four appendages attach to substrates in different ways, including suspension by the forelimbs from above."

h. *Arrested drop*: Swinging from on top to underneath a support. A bout begins either from sitting or with the body behind a single horizontal substrate supported by adducted forelimbs, elbows extended; the hands are near the hips and bearing most of the weight. From this pose the torso descends while remaining orthograde, so that the individual swings under the branch that had been near or touching the belly or hips.

L10. Torso pronograde suspensory locomotion:

a. *Inverted quadrupedal walk*: All the four hands/feet are used in some combination; the torso is pronograde (−), and limbs are in tension. Regular gaits are common (MITTERMEIER & FLEAGLE, 1976; CANT, 1986). This mode is often accompanied by the grasp of a prehensile tail in atelines and *Cebus* (exemplar: lorises).

b. *Inverted quadrupedal run*: As above, but more rapidly (Fig. 26).

c. *Inverted scramble*: As above, except on irregularly angled and sized supports.

L11. Bridge:

a. *Cautious pronograde bridge*: A torso-pronograde (−) gap-closing movement where the hands reach out to grasp a support on one side of a gap and cautiously pull the body across

the open space with the feet (and tail in atelines and *Cebus*) retaining their grips until a secure position is established on the other side (YOULATOS, 1993) (exemplar: lorises).
b. *Lunging bridge*: feet and/or tail grasps a support and a lunge ("incomplete leap" FONTAINE, 1990) closes the gap, allowing the hands grasp a distant support. The forelimbs pull the distant support closer with all four limbs in tension. May be followed by a postural bridge.
c. *Upward vertical bridge*: As with lunging bridge, but progression is at ≥45°.
d. *Supinograde bridge*: As with lunging bridge, except suspensory.
e. *Descending bridge*: "An incomplete leap yielding hindlimb suspension" that spans a discontinuous gap, followed by grasping a support with the forelimbs, followed by quadrupedal locomotion (FONTAINE, 1990). Progression is downward at ≥45°.

L12. Leap: Leaping is a gap-crossing movement in which the hindlimbs principally are used as propulsors. The flexed hindlimbs and flexed back are forcefully extended, often aided by the forelimbs. There is an extended period of free flight, distinguishing this mode from bounding.
a. *Pronograde leap*: The torso is primarily pronograde at take-off, and the leap may be initiated from either a postural or locomotor position. This type of leap is characteristic of most anthropoids. Longer leaps tend to have a downward component, which increases the horizontal distance covered (OXNARD, 1984; GEBO, 1989). Anthropoid leaps effecting ascent are typically over short spaces, with a series of such leaps used to ascend the tree. This mode grades into bounding (Figs. 27A & B).
b. *Pumping leap*: Similar to pronograde leap, with the addition of several forceful extensions of the limbs used to initiate a sway in the branch, the force of which is used to add length to the leap.
c. *Vertical clinging leap*: This leap begins with a torso-orthograde clinging posture on a relatively vertical supports, with pushoff predominantly hindlimb-powered (NAPIER & WALKER, 1967; NIEMETZ, 1984); differs from pronograde leap (L12a) in that it starts from a cling (exemplar: tarsier). This is characteristic primarily of some prosimians; among the anthropoids, only *Pithecia*'s leaps can be classified in this category (WALKER, in press). OXNARD et al. (1990) divide this mode into three categories (Figs. 28A, B, & C): (1) stretched-out vertical cling leap: femur extended during mid-flight posture (OXNARD et al., 1990) (exemplar: *Indri*); (2) curled-up vertical cling leap: torso sub-orthograde, limbs in front of body during mid-flight posture (OXNARD et al., 1990) (exemplar: *Galago* spp.); and (3) limbs-down vertical cling leap: torso-pronograde, limbs hang down during mid-flight posture (OXNARD et al., 1990) (exemplar: dwarf lemurs spp.).
d. *Hindlimb-forelimb suspensory leap*: "Takeoffs that involve suspension by any hindlimb-forelimb combination in which simultaneous swaying motions of forelimbs and hindlimbs (generate) propulsive force" (FONTAINE, 1990).
e. *Hindlimb suspensory leap*: Flinging the trunk and forelimbs forward from suspension by one or both hindlimbs (and possibly tail) (sensu FONTAINE, 1990).

L13. Drop: This mode differs from leaping in that takeoffs are initiated not by substantial muscle propulsion, but by falling after releasing a support. It is categorized by the semi-posture ("semi" because there is little pause before dropping) assumed before the drop. Visualizing the mode may be easier if illustrations of the postures that precede the drops are consulted.
a. *Bipedal drop*: Above branch bipedal balanced posture before drop.

b. *Quadrupedal drop*: Posture indistinguishable from quadrupedal or tripedal standing before drop.
c. *Unimanual suspensory drop*: Forelimb suspension assumed before drop (Fig. 29).
d. *Bimanual suspensory drop*: Suspension from both forelimbs; not unusually preceded by bimanual armswing. Often both hand grasp another support nearly simultaneously on landing. This mode has been referred to as "dropping" or "lowering" (e.g. HOLLIHN, 1984).
e. *Flexed-elbow suspensory drop*: As above, but with the elbows flexed.
f. *Tail-suspend drop*: Including tail-suspend with minor hindlimb support, including "tail swinging drop" (FONTAINE, 1990).
g. *Hindlimb suspensory drop*: Hindlimbs support body weight before the drop; there is little or no support by the tail.
h. *Forelimb-hindlimb suspend drop*: Suspension from a combination of forelimb and hindlimb, including involvement of tail, followed by release.

L14. Tail swing: Pendular movement during tail suspension propels the animal forward to cross a gap (FONTAINE, 1990).

L15. Landings for leap, drop, and tail swing:
a. *Suspensory forelimb landing*: Catching action with the forelimbs, after which a period of forelimb-suspensory locomotion or posture is common.
b. *Bipedal landing*: Hindlimbs land first, flexing to absorb most or all of the energy of impact; used primarily after leaps with vertical cling take-offs.
c. *Quadrupedal landing*: Both forelimbs and hindlimbs decelerate the body by flexion, with only a slight difference between the time of contact of fore- and hindlimbs, usually the forelimbs contact first. Not followed by a suspensory bout.
d. *Forelimb landing*: The forelimbs do most of the work of decelerating the body, after which the hindlimbs contact a substrate. The torso remains relatively pronograde (−) throughout.
e. *Hindlimb-forelimb suspensory*: More than half the body weight is decelerated by any combination of hindlimb and forelimb in tension (FONTAINE, 1990). Typically suspension is from the forelimbs.
TAIL ASSISTED LOCOMOTION: In prehensile-tailed New World monkeys any of these landing modes may be aided by tail grips.

L16. Tree sway: A gap crossing movement used between trees; "swaying a tree to and for in oscillations of increasing amplitude, or bending a tree by using the body weight until the animal can reach the next tree" (SUGARDJITO & VAN HOOFF, 1986: 15). Tree sway differs from transfer (L9f) in that body weight or oscillation are used to deform branches rather than lunging, and often the pre-gap-closing posture resembles clinging more than suspension (exemplar: orangutan).

L17. Ride: Similar to tree sway, but used from tree to ground. A vertical, small diameter support is grasped in a clinging posture and a (sometimes violent) movement or oscillation overbalances the support (typically a small tree). The weight of the individual's body pulls the tree from a vertical orientation toward horizontal. As the tree approaches horizontal a suspensory posture may result, after or during which the grip with the hindlimb is released and the feet contact the ground.

L18. Scoot: The body is propelled by sliding while the ischia support a substantial proportion of the body weight; knee and thigh remain flexed while propelling the body.

CONCLUSION

Categorization necessarily discards information about kinematics, and can hinder functional interpretations of anatomy (Prost, 1965; Ripley, 1967). Yet most functional morphologists recognize that categorization is a necessary evil. The scheme presented here aims at minimizing the evil. Still, there are pitfalls. At present we have quantitative positional data for few primates, which means the modes presented here are incomplete. Furthermore, there is continuity between many modes, a continuity that can be obscured by categorization. We do not mean to discourage new terms for newly discovered behaviors, nor do we wish to imply that continuity between positional modes does not exist. Rather, our aim is to regularize the use of terms in the context of current knowledge of primate positional behavior, and to discourage the pooling of behaviors that place dramatically different stresses on the body. This latter issue is one that deserves emphasis.

In order to draw inferences about function, different behavioral modes must be distinguished when they have distinct anatomical requirements. When positional modes are by necessity pooled during data collection or analysis, the best anatomical discrimination can be retained only when anatomical requirements are more similar within modes than between them. For example, suspensory behaviors that stress musculoskeletal elements in net tension (e.g. inverted quadrupedal walk) should not be pooled with modes that stress elements in net compression (e.g. quadrupedal palmigrade walk). The ability of apes and atelines to completely abduct their forelimb during forelimb-suspension has musculoskeletal implications that require that this mode be distinguished from, e.g. quadrupedal grasp-walking or flexed-elbow vertical climbing. In situations where assignment of a positional mode is equivocal, we believe that joint orientation and relative stresses on specific anatomical elements are the variables which should be considered in assigning a positional mode.

Two issues in particular are of current importance, though both are easily resolved. The first concerns orthograde suspension. Complete abduction of the humerus requires a degree of shoulder mobility that many other modes do not require. Behaviors in which the humerus is abducted should be distinguished from those in which it remains adducted. If relatively few positional modes are to be distinguished, it is best that forelimb-abducted suspensory modes be pooled with one another, rather than with adducted modes.

The second issue concerns ascents. "Climbing" or "quadrumanous climbing" are terms that have come to be particularly troublesome. Frequently "climbing" conflates vertical ascent, vertical descent, a variety of forelimb suspensory horizontal movements, orthograde clambering, scrambling and even arboreal walking. In other words, in the past climbing has been used to describe nearly any arboreal movement except leaping. The principal problem with such conflation lies in the fact that ascents, descents and above-branch and below-branch horizontal movements are likely to make quite different demands on the musculoskeletal system. Using a single behavioral category for these diverse behaviors gives the mistaken impression that, for example, animals which most frequently move pronograde across horizontal supports and those that more often vertical climb are under similar selective pressures. Ascent of $\geq 45°$ requires more powerful and persistent muscle action than walking, since it requires that the body weight be lifted. It should not be pooled with walking in most cases. In short, the widespread use of the term "climbing" to describe horizontal movement is confusing, and we strongly discourage its use in this context. We recommend reserving "climbing" for ascent of support angled at ≥45°.

To the extent that positional modes are an expression of capabilities limited by anatomy, a "good" mode should be one that has unique kinematic, kinetic and gait components. Distinctions without (significant) differences are fruitless. For most positional modes, this type of analysis is still in its infancy. If and when such analyses are made, it will become evident that some of the modes here are biomechanically equivalent, and that others have improperly conflated, biomechanically disjunct modes. Descriptions given here represent a working categorization subject to change and refinement as the "by-eye" assessment of modes that pervades positional study currently is replaced by proper mechanical analyses.

Standardization requires sacrifice. Each of the authors of this article has found terms in his or her published articles made obsolete. Each has compromised and reconsidered. We anticipate similar and more profound sacrifices among other primatologists. We believe, however, that the benefits of advancing closer to a common terminology in our field are well worth the effort.

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