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Why have only humans and social insects evolved a complex division of labor

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Abstract

Social species, those that have a complex division of labor, comprise about two thirds of the earth's biomass. These social species – humans and social insects – are located at extreme points of the set of possible evolutionary paths. The queens of small social insects produce thousands of small larvae, whereas human females invest heavily in their children, who are born already with a very large brain. In spite of these and many other evident differences, social insects and humans have conquered the earth because they share two characteristics: a highly developed system of social cooperation, and a complex division of labor. These observations prompt two questions: If there are evident evolutionary advantages of cooperation and specialization, why have only few species been able to increase their fitness in this way? Why have these characteristics emerged as such extremely different forms of life? In order to answer these two questions, we will focus on possible "transition societies" in the evolutionary paths towards social species. We will argue that, in both the human and social insect cases, sexual selection had a crucial role in the development of the division of labor and entailed that the division of labor required either minimum or maximum unitary investments in the offspring. The species located in between these two extremes could not exploit the advantages of specialization.

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1. Introduction.

In his book “The Social Conquest of the Earth” the famous sociobiologist O. E. Wilson (2012) pointed out that social species, including only humans and social insects, have colonized a very large share of the earth’s biomass. The reproductive success of humans and social insects is due to their particular social nature, which entails a sophisticated division of labor. The features shared by human and social insect organizations have attracted the attention of social scientists for a long time. Perhaps, the most famous case is Mandeville’s (1806) fable of bees, celebrated by Keynes (1936) for its early understanding of the importance of conspicuous consumption and of the principle of effective demand. Even if social insect societies do not seem to provide an appropriate example of the virtues of conspicuous consumption, Mandeville could not find a better analogy than the life existing in an imaginary beehive. Only social insects, displaying a division of labor could make this analogy credible.

The analogy between human and social insect organizations is puzzling. Cooperative divisions of labor happen to be located at the two very distant points of the spectrum of living species. Humans and social insects share very little in their size, in their morphologies and in their genotypes. One wonders why so many species, located in between these two distant forms of life, have failed to evolve such favorable selection characteristics. More importantly, the reproduction systems of humans and social insects lie at opposite poles. Social insect queens invest very little in each of the many small larvae that they deliver. By contrast, human females invest heavily in one of their few children, who, being born with little legs and an exceptionally large head, depend on their parents’ care for a very long time.

Thus, the emergence of a cooperative division of labor in such different species raises two questions:

1) If there are evident evolutionary advantages of cooperation and specialization why have only a few species been able to increase their fitness in this way?
2) Why have these characteristics emerged in such extremely different forms of life?

In this paper we will try to suggest a possible solution to this puzzle by focusing on possible transition paths from non-social related species to humans and social insects. We will argue that, in both the human and social insect cases, sexual selection had a crucial role in the development of a cooperative division of labor. We will also maintain that the two paths had contrasting features. In the case of social insects it was related to a massive deprivation of sexual reproductive attributes. In the case of humans it came together with a great increase in resources devoted to sexual activities.

In the following section we will review the principles of the division of labor. We will point out that there are two fundamentally different ways in which specialization is explained in economics. One explanation, famously put forward by Adam Smith (1776), is founded on human capabilities to communicate and exchange and stresses the learning-by-doing benefits of specialization. The other one, propounded later by Charles Babbage (1832), relies on the minimization of training cost and on the exploitation of comparative advantage. Section 3 considers the division of labor in insect societies. We argue that in the world of insects the Smithian principles are irrelevant. By contrast, insect queens apply some sort of adapted Babbage principle. They minimize the production costs of the capabilities of their mostly unfertile subjects and exploit the principle of comparative advantage. The transition to this society is achieved by centralization of the reproduction activities and by exploiting benefits that could not be obtained by each individual insect without the cooperation of the others. Within the centralized reproduction facility there is a conflict between the queen struggling to exercise monopoly on reproduction and her subjects, who may smuggle their eggs into the common nest. This arrangement, typical of wasps, has the potential to evolve into full-blown super-organisms where the queen can use her reproductive monopoly to organize the entire society. This evolutionary path is not feasible for organisms where females generate a limited amount of offspring of large size. In this case the division can only be based on sophisticated learning and communication systems. In section 4 we argue that there are transition primates with a potential to evolve these systems, which requires a huge investment in each single infant. In section 5 we describe how the human route towards the division of labor proceeded on Smithian lines. The dynamics of sexual selection favored the development of a large brain, communication and exchange which eventually paved the way to the learning-by-doing advantages achieved by an appropriate level of specialization. In the concluding section we argue that the division of labor required either minimum or maximum parental investment. Only few species located at these extremes of the life reproduction spectrum could evolve such a sophisticated form of cooperation. This may explain why, in spite of its great advantages, so few species evolved a complex division of labor.

2. Principles of the division of labor.

In a well-known passage, Adam Smith used pin-making to illustrate what he claims to be the three advantages of the division of labour: improved dexterity, saving of time otherwise spent in changing occupations, and application of machinery invented by workmen thanks to their specialization in a particular field. *'One man draws the wire, another straightens it, a third cuts it' is the famous beginning of Adam Smith's example* (1976, p. 8). In Adam Smith, the division of labor attributed the "Wealth of Nations" to the division of labor, which was, in turn, determined by the extent of the market economy. Smith's analysis rested on the assumption that the division of labor would favor learning by doing: the workers could improve their job-specific skills if they specialized in one single activity. If Nations wanted to enjoy the full advantages of the division of labor, they should eliminate all the obstacles to trade.

List (1909, p. 121) pointed out that the principle of the *division* of labor also required "*a confederations or union of various energies, intelligences, and powers on behalf of common production*. The cause of productiveness of these operations is not merely that *division,* but essentially this union". According to List, Adam Smith was well aware of this when he stated that

“The necessaries of life of the lowest members of society are a product of joint labour and of co-operation of a number of individuals. “

The stream of literature stemming from Adam Smith emphasizes that humans are capable of a large-scale cooperative division of labor and that the advantages of the latter derive from their positive learning-by-doing effects. Communication, reciprocity and tendency to trade are seen as the human-specific characteristics that make such a sophisticated division of labor possible.

Charles Babbage (1832) analyzed the division of labor from a different viewpoint. Whereas Smith saw skills differences as a result of the division of labor, Babbage assumed that individuals were endowed with different skills and had different comparative advantages in various activities. According to Babbage, specialization was advantageous because it entailed the exploitation of the comparative advantages of individuals. Thus, according to Babbage, the Master Manufacturer will apply the following principle of the division of labor:

That the master manufacturer, by dividing the work to be executed into different processes, each requiring different degrees of skills or force, can purchase exactly that precise quantity of both which is necessary for each process; whereas, if the whole work were executed by one workman, that person must possess sufficient skill to perform the most difficult, and sufficient strength to execute the most laborious, of the operations in which that art is divided.

(Babbage, 1832 pp.137-8).

In some respects, the "Babbage principle" is analogous to Ricardo's theory of comparative advantage explaining the division of labor among Nations and the benefits of free trade. According to Babbage (and Ricardo), the differences in skills (and other factors affecting productivity) are more a cause than a result of the division of labor. However, this is not the only difference between Babbage and Smith. Smith argued that the division of labor maximized the learning that is acquired by doing. By contrast, Babbage maintained that the great advantage of the division of labor lies in the minimization of the learning that it is necessary to acquire before doing. Narrowing the content of a job decreases what is necessary to learn before production.

According to the arguments of Smith and Babbage, different degrees of specialization are optimal. Smith's principles imply that specialization should not be too narrow; otherwise it could prevent, rather than favor, learning by doing. By contrast, Babbage's principles imply that extreme specialization and job de-skilling may be convenient because they always decrease the learning required before the doing and allow better exploitation of given comparative advantages. Moreover, the Smithian principles point to the advantages of a horizontal division of labor where everyone enjoys the learning-by-doing advantage. The "Babbage principle" has instead strong hierarchical implications. We can obtain the greatest savings on training when the most skilled tasks are separated from unskilled ones, and only the people with the greatest comparative advantage are trained for the skilled tasks.[1]

Even if Babbage's and Smith's principles are different, their joint application is, at least in principle, certainly possible. Their arguments can be integrated to some extent by observing that, within certain limits, the division of labor can decrease the learning that is required before doing, increase the learning that is acquired by doing, and exploit innate skills and comparative advantages. However, natural and social constraints can entail that only one of the two principles may be applied or that one of them has a dominant role in the organization of human and non-human societies.

3. The evolution of a cooperative division of labor in insect societies.

In the case of social insects, the prevailing theory of the cooperative division of labor derives from Hamilton (1964), who explained the fitness of altruism with the sharing of genes. If each selfish gene maximizes its fitness, some degree of altruism towards close relatives is compatible with this rule, extending the effects of the selfishness of the genes to more individuals. Social insects share the same mother queen and have a degree of relatedness greater than that existing in the other species. Thus, Hamilton's rule would explain their altruism and their cooperative behavior leading to a sophisticated division of labor.

O. E. Wilson (2012)[2] has challenged this argument by observing that in bees' or ants' societies only queens transmit their genes. The altruism, or the selfishness, of the other social insects is therefore irrelevant to explaining their behavior. We can add to Wilson's criticism that altruism

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[1] On the analysis of the principles of the division of labour see Pagano (1985) and (1991)

[2] Wilson's challenge has given rise to a fierce dispute within the field of evolutionary biology. Dawkins (2012) has reacted very harshly to Wilson's claim that some altruism of the selfish gene is not the cause of cooperation. For balanced accounts of the debate see Gadagkar (2010) and Gintis (2012).

cannot by itself explain the division of labor. The division of labor is a sophisticated type of cooperation in which different members of the population specialize in different and interdependent tasks. Some degree of cooperation can be found in several species. What is distinctive of social insects (and humans) is that cooperation takes the form of a complex division of labor. The world of insects is full of species, such as mosquitoes, which have not developed any type of sophisticated cooperation or centralized the reproduction function. A plausible evolutionary account should explain how some species have been able to centralize the reproductive function and how they have also been able to develop sophisticated modes of social interaction including a division of labor.

In order to study the development of specialization in insect societies, Raghavendra Gadagkar (2011) has used a clever strategy by focusing on possible "transition societies" such as that of wasps. In wasps' societies the fertilization system has mixed characteristics. Whilst some wasps have an individual reproduction system similar to that of non-social insects, others cooperate in a common nest ruled by a queen specialized in the production of larvae. In the queen's nest, workers are still potentially fertile. They can do better than isolated wasps, which are not granted the common facilities (for instance, defense) existing in the nest. The workers may hide their own offspring in the queen's nest. Sometimes, they may even organize a *coup d'état* and, if successful, become queens.

The survival and reproduction strategies carried out in the queen's nest involve both cooperation and conflict. For instance, while all cooperate in raising the larvae, the wasp-workers try to smuggle their eggs into the nest, undermining the fitness of the queen. In this case, a possible strategy of the queen is to produce largely unfertile offspring that specialize in different functions and transmit their genes only to very few fertile potential queens. This mutation, genetically transmitted and reinforced from queen to queen, can easily spread to the entire population. The nests where this queen's strategy is adopted can outcompete the other nests by decreasing the cost of conflicts and by capturing the gains of specialization.

It is not surprising that this type of sophisticated specialization has occurred in a world where each larva requires a minimum reproductive investment and where an inseminated queen can fly away, carrying with her thousands of eggs and found her own colony where they discontinue and outsource many functions of their bodies to their unfertile offspring. Because mammals are characterized by very high investments in their offspring, they could not follow a similar path for the evolution of a sophisticated division of labor. In the case of mammals, a “mega-mother” cannot specialize in a massive reproductive function and have other tasks performed by a large unfertile progeny.

The relation between the organization of insect societies and the economic principles of the division of labor is not obvious. The Smithian advantages of the division of labor do not have an important role. No, or very little, learning by doing characterizes the working lives of insects. Capabilities, including the organizational rules, are genetically transmitted. Moreover, no exchange among insects takes place. By contrast, some principles analogous to those indicated by Babbage seem to operate in insect societies. Similarly to Babbage’s Master Manufacturer, the queen minimizes her total reproductive effort by generating many relatively small ant-workers only able to carry small amounts of food, and a limited number of much bigger fighting ants endowed with powerful offensive weapons. In other words, like Babbage’s Master Manufacturer, the queen minimizes the cost of producing the capabilities of her subjects and organizes the division of labor on the basis of comparative advantage. The big ants have an absolute advantage in both fighting and carrying food but they have no comparative advantage in the second activity. Hence they specialize in fighting. Because the small ants have a comparative advantage in carrying food, they specialize in that activity.

4. The organization of primate societies.

There are many obvious differences between the fertilization systems of primates (and in general mammals) and social insects. Some of them are particularly relevant:

1) In primate societies sex consumes a great deal energy and involves many fights (among males). By contrast, social insects are characterized by little energy devoted to sex. Males are in subordinate positions. Most fights are among females.

2) Female insects can produce a large number of offspring. Primates (including humans) can produce only a few.

3) In the case of mammals (including primates), great individual care is required for each offspring. Insects can rely on large numbers of larvae requiring comparatively little individual initial investment and care.

The pre-condition of the insects' division of labor is that one female (the queen) can specialize in the reproductive function, outsourcing the remaining tasks to others. This specialization is impossible in the case of mammals. In their case, the division of labor must take a different, and indeed opposite, route. We will consider an evolutionary path where a particular species has a status analogous to wasps' transition society described in Gadagkar's work. The puzzle to be explained is why, in spite of many common characteristics with other primates, only humans, similarly to social insects, have developed a sophisticated division of labor. For this purpose gorilla's societies seem to offer a fairly convincing possible evolutionary dynamic because, similarly to wasps, the dynamic of sexual selection have some potential to move towards different types of arrangements.

Unlike chimps, gorillas help the females (of their harems) to protect their offspring. This behavior is related to a security of paternity that promiscuous male chimps cannot have. Like many other species, female chimps advertise their fertility period as much as possible. Since what matters is not simply to advertise but also to signal with greater efficacy than other females, fertility signals are often very strong. Female enhanced receptivity during the fertility period and other fertility signals (smell, visual signals etc.), as well as the length of the receptivity period, undergo a process of positional competition[3]. As a result, the increase in the intensity of the fertility signals is likely to cease only at the point where the energy invested in the positional advantage equals the fitness sacrifice due to forgone alternative investments. Given this type of female investment, males have little incentive to invest in exclusive access and in the defense of their unrecognizable offspring. They invest more in insemination capabilities, such as powerful reproductive organs than in fighting capabilities, such as body size. Fighting for exclusive access to females is made too costly by the strong and prolonged fertility signal and by the missing of opportunities offered by the many other females simultaneously signaling their receptivity.

[3] For each female what matters is not simply a strong signal but a signal stronger than that trasmitted by other females. Relative positions and positional competition determine reproductive success. On positional goods and positional competition see Pagano and Vatiero (2017).

When a high fertility signal has made exclusive access become too costly, the only way in which the females can increase their mating fitness is to advertise their fertility more than their competitors. This increases the quantity and enhances the quality of their offspring. For instance, in the case of chimps, strong fertility signals can increase the competition of males and favor generation of an offspring with higher insemination capabilities, which will, in turn, help spread the genes of the mothers. Because of these positional dynamics, there is a widespread tendency among mammals to have very evident female fertility signals.

However, there are alternative, even if less frequent, evolutionary paths. If the female fertility signal is fairly low and short, it may be convenient to make it even lower and shorter. In this way males incur a lower cost of monitoring the entire fertility period and they can invest in exclusive access to females and in protection of their offspring. Gorillas are characterized by one of these less frequent reproductive systems. High sexual dimorphism is an evident sign of the male investment in body size useful for fighting other males and gaining exclusive access to females. The strongest males are able to control a territory where some females may choose to live and reproduce. The short and weak fertility female signal can be perceived only within the territory controlled by the dominant male. If a male gorilla is strong enough, the harem can be easily controlled. In such a monopolistic setting, chimp-like competition in insemination capacities would be a useless waste of energy. The small size of a gorilla's sexual attributes can be explained as an adaptation to this situation (Battistini, Pagano 2008).

Similarly to the wasps' nest analyzed by Gadagkar, the territory controlled by the male gorilla is a locus of conflict and cooperation. Like wasps, female gorillas can increase their fitness by joining the harem of a silverback. In the same way as the individual female wasp can also reproduce outside the queen's nest, a female gorilla can reproduce outside the territory of a dominant male. Similarly to a female chimp, she can try to be inseminated by the numerous gorilla males who have failed to monopolize a valuable area of the territory. However, for the female gorilla, the benefit of multiple inseminations would be negligible in comparison to a very relevant fitness loss. She misses the opportunity to acquire the good genes of a dominant male gorilla and his parental co-operation. Even more than female wasps, the female gorilla has strong incentives to opt for a common place with shared reproduction facilities.

However, similarly to wasps' nests, the gorilla territory is not only a place of cooperation but also a locus of conflict. Each female of the harem may gain fitness by receiving more attention from the silverback. The latter has a relatively easy task in distributing his attentions and monitoring effort only if the signals are so weak and short as to be unperceivable to the gorillas outside the territory but still sufficiently evident for the male gorilla monopolizing that space. Roughly speaking, this seems to be the case of gorilla society.

However, conflicts involving some deviation from this situation are well possible. The two signals of fertility (female receptivity and "mechanical" signals such as color and smell) may be manipulated and disentangled by adaptive mutations. A female who can extend and reinforce her behavioral receptivity signals and hide her mechanical signals may attract more attention than the other females. A dynamic of extended receptivity signals and decreased mechanical signals is likely to take place. In this case the monitoring costs of the silverback become much higher. The silverback no longer has a useful criterion with which to concentrate his attention on a particular female. In the end, the sexual conflict may involve a disintegration of the harem system. In this respect, similarly to wasps, the gorilla arrangements may characterize a possible transition society.

5. The possible emergence of a complex primate society.

The gorilla society can be viewed as an elementary primate society analogous to the wasp primitive insect society considered by Gadagkar. In both settings there are cooperation and an elementary division of labor. In the same way in which the queen wasp specializes in reproduction, the silverback specializes in defense and protection. However, if the wasp society is distant from the complex division of labor characterizing bees and ants, the gap between the gorilla society and the complex division of labor that characterizes humans is even wider.

The conflicts existing in the wasp nests can generate the conditions for a transition to the sophisticated arrangements of ants' and bees' societies. We have seen that the wasp workers can try to increase their fertility by smuggling eggs into the queen's nest and by plotting *coup d'état*.

Queens can counter this strategy by producing infertile offspring. Eventually, the phenotypic differentiation within the nest can become more sophisticated. Infertile wasps can assume alternative shapes better suited to becoming workers or warriors. The queen, having outsourced most of the functions of her organs to the infertile offspring, can take a shape fitting her specialization in her increasingly sophisticated reproductive activity. If these changes take place in few nests, the mutations are likely to spread among the entire wasp population. The classic advantages of the division of labor involve a greater fitness of the new social arrangements.

The insects' route to a complex division of labor, however, is blocked for mammals. No female mammal can afford to centralize the reproductive function in her body and generate much infertile specialized offspring. As Adam Smith convincingly argued, the human route towards a sophisticated division of labor must rely on reciprocity and communication. However, similarly to the wasps' nest, the seeds of this possible development can already be seen in the conflicts existing in the gorilla's harem.

We have seen that there is a "latent" possible tendency of females to decrease the already weak mechanical signs of fertility and attract the silverback's attentions with other seductive techniques.[4] This development makes control of the harem difficult. The silverback may react by developing improved capabilities to understand the fertility signals. Suppose that, in a hypothetical new species, females win this battle and males are unable to understand which female is fertile. This mutation favors smaller harems and eventually even widespread monogamy. More importantly, the techniques of control have to change. The absence of short and weak fertility signals makes male physical strength a much weaker means to secure exclusive access to a female. Females' self-monitoring and their assessment by males become very important. Communicating trust and reciprocity stimulates paternal investment. In this situation, a language much more sophisticated than birds' melodies or gibbons' love songs[5] can become an adaptation that can greatly increase fitness. A brain-intensive understanding of potential

[4] The idea that the origin of the sophisticated human and intellectual capabilities is associated with the weakening of mechanical fertility signals and the development of seductive techniques is considered in detail in Battistini Pagano (2008), Pagano (2013, 2014). Alternative theories are considered by Bowles (2006, 2013), Gintis (2013) and Hodgson (2013).

[5] With reference to the evolution of human language, Darwin observed how "some early progenitor of man, probably first used his voice in producing truemusical cadences, that is singing, as do some of the gibbon-apes at the present day; and we may conclude from a widely-spread analogy, that this power would have been especially exerted during the courtship of the sexes – would have expressed various emotions, such as love, jealousy, triumph - and would have served as a challenge to rivals. It is, therefore, probable that the imitation of musical cries by articulate sounds may have given rise to words expressive of various complex emotions" (Darwin 1879, p. 109).

partners and rivals becomes necessary to make convenient cooperation deals, and sometimes break them. Females can gain by developing the ability to estimate the future parental help of potential male partners correctly and by skillfully directing their non-mechanical signals of sexual availability. Males can enhance their fitness by understanding which females are trustworthy. Both genders can gain by making deals with their potential competitors. A costly large brain and other costly mutations of the human body may be required to develop these capabilities. However because of their advantages in terms of sexual selection, these mutations may spread in the population. A new smart and communication-intensive society may emerge from the disintegration of the gorillas' harems.

Once a sophisticated communication system has evolved, specialization can go well beyond the simple division of tasks existing between the silverback and the female members of his harem. Because of the evolution of language, our species was able to become by far the most powerful and aggressive predator that has ever existed in natural history. Small human hunters could coordinate different actions and kill large prey.

Another important effect of a sophisticated language is well illustrated by Adam Smith when he explains how specialization could evolve in primitive societies. According to Smith,

"*the division of labour, from which so many advantages are derived, is not originally the effect of any human wisdom, which foresees and intends that general opulence to which it gives occasion. It is the necessary, though very slow and gradual consequence of a certain propensity in human nature which has in view no such extensive utility; the propensity to truck, barter, and exchange one thing for another. Whether this propensity be one of those original principles in human nature of which no further account can be given; or whether, as seems more probable, it be the necessary consequence of the faculties of reason and speech, it belongs not to our present subject to inquire. It is common to all men, and to be found in no other race of animals, which seem to know neither this nor any other species of contracts".* (Smith 1776 p. 17)

According to Smith, the faculties of reason and speech were likely to allow a particular person in a tribe of hunters or shepherds to specialize in producing bows and arrows and agree to trade with other members of the tribe specialized in the production of different goods. In this way a person specializing in the production of bows and arrows could improve the skills necessary for this activity and get “*more cattle and venison than if he himself went to the fields to catch them”* (Smith 1776, p. 19).

Unlike the case of insect societies, humans can also rely on the Smithian advantages of the division of labor. The division of labor evolves more from reciprocal exchanges and specialized learning-by-doing than from a centralized effort to decrease the cost of production and to use efficiently different inborn capabilities.

The case of the tribe of hunters offers a possible evolutionary account of the emergence the division of labor. Humans used the communication and exchange capabilities, developed under the pressure of sexual selection, to divide their work within hunting, and later between hunting and the construction of weapons. Both hunters and weapon-makers could learn their trades better by specializing in these activities. By contrast, Adam Smith's more famous example of the pin-making factory seems to have much less to do with the typical features of the human division of labor. The pin-making factory was intended to show how the division of labor is organized by a market economy. However, in this example the man who draws the wire does not *sell* it to the man who straightens it, and the latter does not *sell* the straightened wire to the man who cuts it.

Smith does not seem to perceive the difference between this example and the tribe of hunters or shepherds, in which the person specialized in the production of bows and arrows trades with other members of the tribe. In the tribe, exchanges and learning by doing are the engines of specialization. By contrast, in the pin-making factory a master-manufacturer organizes the production process, and the restricted nature of each task seems to be inconsistent with the learning-by-doing advantages pointed out by Adam Smith.

Indeed Babbage’s principle[6] provides a better explanation for the division of labor of the Smithian pin-making factory. Jobs are already too narrow to favour any substantial learning–by-doing process. By contrast, much training costs have been saved when one individual is engaged only in straightening the wire or only in cutting it. The capabilities of the workers do not grow with their production activities. Not only the mind but also the body of the worker suffers. To quote Marx: “the better formed his product, the more deformed becomes the worker ” (Marx,

[6] Charles Babbage (1832, p. 138) pointed out that, although he would have selected the art of making needles, “including a very large number of processes all remarkably different in their nature”, as an example of the division of labour, the art of pin making was to be preferred because of its popularity due to the influence of the work Adam Smith.

1844 p. 38). The master manufacturer is here applying principles of the division of labor similar to those of an insect society where some extreme form of application of the Babbage principle makes the queen shape the bodies of her subjects according to her (re-)productive needs. There is some truth in the criticism that the division of labor of the modern factory system is de-humanizing. The typical human path towards the division of labor consisted of reciprocity and learning, while the factory system is based on principles that too closely resemble the hierarchical insect societies where no learning (other than that transmitted by genetic heritage) takes place.

6. Conclusion: *in medio non stat virtus?*

Humans and social insects are the only species that have evolved a complex division of labor. As a result, having so far been more successful than other species, they account for large part of the total biomass. A feature shared by their two evolutionary paths is the importance of sexual selection. However the two paths are dramatically different and are indeed located at two opposite poles of the reproductive spectrum: the greatest unitary investment of female mammals in the generation of their offspring and the lowest unitary investments of female insects in their larvae.

The departure of humans from elementary primate societies has been linked to a disproportionate attention of our species to emotional and intellectual activities related to the search for a sexual partner. In this respect, the contrast with social insects could not be greater. The evolution of social insects has been related to the sterility of the greatest part of the population. The transition to a complex division of labor has not only happened at two opposite poles of the reproductive spectrum. The transition to complex societies has also been related to a further reinforcement of these differences. Social insect queens decreased even further the negligible unitary cost of reproduction of the insect world. Human females greatly increased the costs of production of offspring, which were already high among mammals.

While located at two opposite poles, humans and social insects have shared the fate of becoming successful exceptions in natural history. Evolution has allowed a complex division of labor only in two extreme cases on the spectrum of reproductive systems. By contrast, the many species falling in between these two extreme cases could not benefit from the advantages of the division of labor. On the one hand, their insufficient individual investment in each newborn individual has prevented them from exploiting the Smithian advantages of the division of labor requiring reciprocity, social intelligence and sophisticated communication. On the other hand, their relative high cost of reproduction has prevented them from developing a system of centralized reproduction and a genetic division of labor analogous to that advocated in the Babbage principle.

Evolution refuted the Aristotelian principle "*In medio stat virtus*", meaning that successful behavior is to be found in the middle. Only at the extremes of the evolutionary possible paths did a complex division of labor become possible and allow some species to prosper and to colonize our planet. The many species in between these two extremes failed to evolve what was going to become such an amazingly successful evolutionary trait.

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