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Why only humans and social insects have a division of labour

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Humans and social insects are located at extreme points of the set of possible evolutionary paths. However, they share a complex division of labour and comprise a large proportion of the earth's biomass. These observations prompt two questions: If there are evident evolutionary advantages of cooperation and specialisation, 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 labour and entailed that the division of labour required either minimum or maximum unitary investments in the offspring. The species located in between these two extremes could not exploit the advantages of specialisation.

Key words: Division of labour, Parental investment, Evolution, Social insects, Human capabilities
JEL classifications: B00, D83, D87, N10, Z13

1. Introduction

In his book, *The Social Conquest of the Earth*, O. E. Wilson (2012) pointed out that social species, including only humans and social insects, have colonised a very large share of the earth's biomass.[1] The reproductive success of humans and social insects is due to their particular social nature, which entails a sophisticated division of labour. The features shared by human and social insect organisations have attracted the attention of social scientists for a long time. Perhaps, the most famous case is Mandeville's (1714)

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[1] 'An odd parity exists between social insects and humanity. About 6.6 billion individuals compose *Homo Sapiens*, the most social and ecologically successful species in vertebrate history. And the number of ants alive at any given time has been estimated conservatively at 1 million billion to 10 million billion. If this latter estimate is correct, and given that each human weighs on average very roughly 1 or 2 million times as much as a typical ant, then ants and people have (again very roughly) the same global biomass.' (Holldobler and Wilson, 2009, p. 5). Social insects organise the division of labour in very different ways (see, for instance, Landa and Tullock, 2003). However, the present article deals only with the emergence and some common characteristics of the division of labour existing in insect societies.

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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 labour, could make this analogy credible.

The analogy between human and social insect organisations is puzzling. Cooperative divisions of labour 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 favourable 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 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 labour in such different species raises two questions:

1) If there are evident evolutionary advantages of cooperation and specialisation, 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.[2] 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 labour. 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 labour. We will point out that there are two fundamentally different ways in which specialisation 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 specialisation. The other one, propounded later by Charles Babbage (1832), relies on the minimisation of training cost and on the exploitation of comparative advantage. Section 3 considers the division of labour 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 minimise the production costs of the capabilities of their mostly infertile subjects and exploit the principle of comparative advantage. The transition to this society is achieved by centralisation 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 centralised reproduction facility, there is a conflict between the queen struggling to

[2] We will only try to explain how given species could evolve the division of labour among their members. We do not consider how different species could cooperate and specialise and we will not deal with the division of labour existing among different organs of a single body or the 'economics of the body' analyzed by Ghiselin (1978).

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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 organise 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 sophisticated systems, which requires a huge investment in each single infant. In Section 5, we describe how the human route towards the division of labour proceeded on Smithian lines. The dynamics of sexual selection favoured 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 specialisation.[3] In the concluding section, we argue that the division of labour 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 labour. The analogy between human and social insects paradoxically emerges from the fact that they are located at extreme modes of reproduction of life—a paradox that should be taken into account when humans are forced to adopt a division of labour based on some of the principles organising insect societies.

2. Principles of the division of labour

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 specialisation 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 labour is attributed the 'Wealth of Nations' to the division of labour, which was, in turn, determined by the extent of the market economy. Smith's analysis rested on the assumption that the division of labour would favour learning by doing: the workers could improve their job-specific skills if they specialised in one single activity. If Nations wanted to enjoy the full advantages of the division of labour, they should eliminate all the obstacles to trade.

List (1841, p. 121) pointed out that the principle of the *division* of labour 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

[3] The forms of the human division of labour which we could observe in recorded history are mainly a result of cultural evolution. Darwinian processes of random mutation, selection and retention were relevant at the beginning of the specialisation processes but their relative importance has greatly decreased in human history. As Witt (2008, p. 550) points out the 'mechanisms by which the species have evolved in nature under natural selection pressure, and are still evolving, have shaped the ground for, and still influence the constraints of, man-made, cultural forms of evolution, including the evolution of the human economy. But the mechanisms of man-made evolution that emerged *on* that ground differ substantially from those of natural selection and descent.'

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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.

An important stream of the literature stemming from Adam Smith emphasises that humans are capable of a large-scale cooperative division of labour 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 labour possible.

Charles Babbage (1832) analyzed the division of labour from a different viewpoint. Whereas Smith saw skills differences as a result of the division of labour, Babbage assumed that individuals were endowed with different skills and had different comparative advantages in various activities. According to Babbage, specialisation 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 labour:

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 labourious, of the operations in which that art is divided. (Babbage, 1832, pp. 137–38)

In some respects, the 'Babbage principle' is analogous to Ricardo's theory of comparative advantage explaining the division of labour 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 labour. However, this is not the only difference between Babbage and Smith. Smith argued that the division of labour maximised the learning that is acquired by doing. By contrast, Babbage maintained that the great advantage of the division of labour lies in the minimisation 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 specialisation are optimal. Smith's principles imply that specialisation should not be too narrow; otherwise it could prevent, rather than favour, learning by doing. By contrast, Babbage's principles imply that extreme specialisation 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 labour 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.[4]

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 labour can decrease the learning that is required before doing, increase the learning that is acquired by doing,

[4] On the analysis of the principles of the division of labour, see Braverman (1974) and Pagano (1985, 1991) pointing out how the characteristics of the division of labour do not only influence productivity but also directly human welfare.

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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 organisation of human and non-human societies (Pagano, 1991).

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

In the case of social insects, the prevailing theory of the cooperative division of labour derives from Hamilton (1964), who explained the fitness of altruism with the sharing of genes. If each selfish gene maximises 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 behaviour leading to a sophisticated division of labour.

O. E. Wilson (2012)[5] 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 behaviour. We can add to Wilson's criticism that altruism cannot by itself explain the division of labour. The division of labour is a sophisticated type of cooperation in which different members of the population specialise 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 labour. The world of insects is full of species, such as mosquitoes, which have not developed any type of sophisticated cooperation or centralised the reproduction function. A plausible evolutionary account should explain how some species have been able to centralise the reproductive function and how they have also been able to develop sophisticated modes of social interaction including a division of labour.

In order to study the development of specialisation 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 fertilisation system has mixed characteristics. While some wasps have an individual reproduction system similar to that of non-social insects, others cooperate in a common nest ruled by a queen specialised 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, defence) existing in the nest. The workers may hide their own offspring in the queen's nest. Sometimes, they may even organise 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 infertile offspring that specialise in different functions and transmit their genes only to very few fertile potential queens. This mutation, genetically transmitted and reinforced

[5] 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).

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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 specialisation.

It is not surprising that this type of sophisticated specialisation 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 infertile offspring. Because mammals are characterised by very high investments in their offspring, they could not follow a similar path for the evolution of a sophisticated division of labour. In the case of mammals, a 'mega-mother' cannot specialise in a massive reproductive function and have other tasks performed by a large infertile progeny.

The relation between the organisation of insect societies and the economic principles of the division of labour is not obvious. The Smithian advantages of the division of labour do not have an important role. No, or very little, learning-by-doing characterises the working lives of insects. Capabilities, including the organisational 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 minimises 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 minimises the cost of producing the capabilities of her subjects and organises the division of labour 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 specialise in fighting. Because the small ants have a comparative advantage in carrying food, they specialise in that activity.

4. The organisation of primate societies

There are many obvious differences between the fertilisation 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 characterised 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 labour is that one female (the queen) can specialise in the reproductive function, outsourcing the remaining tasks to others. This specialisation is very difficult in the case of mammals.[6] In their case, the division of labour must take a different, and indeed opposite, route. We will consider an

[6] The only exception are the Naked Mole-Rats which, however, live and reproduce under very special environmental conditions (Jarvis, 1981). Moreover, their specialisation is very elementary and is not comparable with the complex division of labour existing among social insects.

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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 labour. For this purpose, gorilla's societies seem to offer a fairly convincing possible evolutionary dynamics because, similarly to wasps, their sexual selection processes have some potential to move towards different types of arrangements.

Unlike chimps, gorillas help the females (of their harems) to protect their offspring. This behaviour 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.[7] 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 defence of their unrecognisable 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 signalling their receptivity.[8]

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 favour 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 (Battistini and Pagano, 2008). Gorillas are characterised by one of these less frequent reproductive systems (Stewart and Harcourt, 1987). 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

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

[8] The longer and more pronounced receptivity of bonobos (otherwise very similar and strictly related to ordinary chimps) can offer an explanation for the more peaceful and matriarchal nature of their society (Furuichi, 2011). Both chimps and bonobos share more genes with us than gorillas. We concentrate on the 'gorilla society' because, before the advent of (almost) concealed ovulation, humans females must have necessarily gone through a weakening of fertility signals.

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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.[9]

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 monopolise 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.[10] She misses the opportunity to acquire the good genes of a dominant male gorilla and his parental cooperation. 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 monopolising 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 colour and smell) may be manipulated and disentangled by adaptive mutations. A female who can extend and reinforce her behavioural 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 characterise a possible transition society.

5. The emergence of the human division of labour

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

[9] The weight of a gorilla male is about twice that of a female. By contrast, the difference between male and female chimpanzee body sizes is even smaller than in the case of humans. As for testis size, the chimpanzee average is 120 g against the 35 g of gorillas. Note that when they are compared to the weight of the body, they are ten times bigger (0.3% in the case of chimpanzees and 0.03% in the case of gorillas). See Gribbin and Cherfas (2001, p. 170).

[10] Maynard Smith (1982) pointed out how some long-run outcomes of evolutionary process could be modelled as if genes were maximising their fitness—an analogy which, in some cases, we follow with the necessary caution in this article. The analogy between maximisation and evolutionary processes can be often misleading. One should always take into account the epistatic interactions existing among the different genes. These interactions may imply that the genes cannot adapt to the environment (Kauffman, 1993; Feldman, 2001) or that they can adapt only in path-dependent ways as in the famous case of the Panda's thumb (Gould, 1992).

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cooperation and an elementary division of labour. In the same way in which the queen wasp specialises in reproduction, the silverback specialises in defence and protection. However, if the wasp society is distant from the complex division of labour characterising bees and ants, the gap between the gorilla society and the complex division of labour that characterises 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 specialisation 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 labour involve a greater fitness of the new social arrangements.

The insects' route to a complex division of labour, however, is blocked for mammals. No female mammal can afford to centralise the reproductive function in her body and generate much infertile specialised offspring. As Adam Smith convincingly argued, the human route towards a sophisticated division of labour 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.[11] 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 favours 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 less effective 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[12]

[11] 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) and in Pagano (2013). A *sexual selection subsidy* allowed humans to overcome the high initial cost of developing a large brain and the other requirements necessary for the evolution of their sophisticated intellectual capabilities. Alternative (but somehow complementary) theories are considered by Bowles (2006), Battistini (2013), Bowles (2013), Gintis (2013), Hodgson (2013) and Pansini (2013), all commenting on Pagano (2013). In the reply to my commentators (Pagano, 2014a), I argue that plausible explanations of the 'human singularity' should satisfy two conditions: (i) The explanation should rely on circumstances peculiar, or better unique, to human evolution and (ii) the explanation should not rely on factors that require the pre-existence of human intellectual capabilities. Unlike some alternative explanations, the *sexual selection subsidy* hypothesis satisfies both conditions.

[12] 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,

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can become an adaptation that can greatly increase fitness. A brain-intensive understanding of potential partners and rivals becomes necessary to make convenient co-operation 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 developing empathy for the potential partners[13] and 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 linguistic and social 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. Cultural differences among different groups are going to arise. They do not only involve different (proto-) languages but also different beliefs, ornaments and rites. A process of group selection may take place to a degree, which is far stronger than in other species where, in absence of cultural differentiation, the boundaries among different groups cannot be easily identified. The warfare among different groups will favour groups characterised by stronger internal solidarity[14] and by better systems of organising the division of labour.

Once a sophisticated communication system has evolved, specialisation 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.[15]

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

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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). Sexual selection is as important to understanding the economy of nature as the adaptation to the natural environment (Ghiselin, 1974).

[13] In *The Theory of Moral Sentiments*, Adam Smith was already aware of the neurological basis of the feeling of sympathy towards other human beings and clearly grasped the adaptive significance of moral sentiments (Ghiselin, 1974, p. 257). For instance, he observed how 'Men of the most robust make, observe that in looking upon sore eyes they often feel a very sensible soreness in their own. . .' (Smith, 1759 [1790 edition, p. 5]).

[14] Tough group selection and strong group solidarity are an outcome of human cultural evolution. They cannot explain how a human (proto-) culture, differentiating us from other species, could evolve (Pagano, 2013, 2014a).

[15] 'There must be very powerful reasons why time and chance have never brought speech to any other species. Surely lions would be better hunters if they could talk among themselves and develop more promising plan.' (Blair Bolles, 2011, p. 11). Human communication relies on joint attentional frames within which each individual can understand and can emotionally share the interests of the others. This common ground involves that a simple gesture, such as pointing at something, can take complex meanings which cannot have in other species. The latter are unable to share intentionality and to point at what may interest other individuals (Tomasello, 2003). However, under the exceptional conditions of the human fertilisation system, both romantic melodies and meaningful gestures were not enough for successful reproductive deals. The individuals, who developed more sophisticated communication capabilities, had remarkable evolutionary advantages.

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> 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 specialise in producing bows and arrows and agree to trade with other members of the tribe specialised in the production of different goods. In this way, a person specialising 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 labour. The division of labour evolves more from reciprocal exchanges and specialised learning-by-doing than from a centralised 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 labour. 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 specialising 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 labour. The pin-making factory was intended to show how the division of labour is organised 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 specialised 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 specialisation. By contrast, in the pin-making factory, a master manufacturer organises 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[16] provides a better explanation for the division of labour of the Smithian pin-making factory.[17] Jobs are already too narrow to favour any

[16] 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.

[17] In book V of the Wealth of Nations, Smith considered also the deleterious effects of the division labour on the capabilities of the workers. 'Smith's apparent afterthoughts of Book V, where he refers to the deleterious effects of the division of labour upon the work force, constitute a major source of inspiration for the socialist critique of capitalist institutions, as Marx himself acknowledged' (Rosenberg, 1965, p. 127). Smith's analysis is not inconsistent. As Rosenberg (1965, p. 139) maintains the main thrust of his analysis 'is that, as a direct result of increasing division of labour, the creativity of society as a whole grows while that of the labouring poor (". . . that is, the great body of the people") declines'. However, the implications of his principles did not entail the dramatic deskilling involved by the application of the Babbage principle.

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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, 1844, p. 38). The master manufacturer is here applying principles of the division of labour 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.[18]

Our division of labour evolved at one extreme of the life spectrum, far away from the other extreme, which characterised insect societies. It was associated to the development of empathy and communication and to a desire to share experiences and knowledge, favouring a cumulative process of learning by doing. However, the shift from hunting and gathering to agriculture,[19] and later to industry, was often marked by the adoption of principles of the division of labour that were not far from those prevailing in insect societies. Experience and knowledge have often not been shared by many but they have been rather monopolised by few. Limited instructions have been hierarchically transmitted to many and worker's skilling costs have been minimised, as if they were the infertile offspring of an insects' queen. Unsurprisingly, this development has often been perceived as doing violence to human nature. There is some truth in this perception. For many millennia, we evolved our system of division of labour at the other extreme of life.

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

Humans and social insects are the only species that have evolved a complex division of labour. 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

[18] Braverman (1974) maintained that the application of the Babbage principle was the main cause of the degradation of work in the twentieth century. This process, which is evident in the Tayloristic firm (Braverman, 1974), is even stronger in present world of intellectual monopoly capitalism (Pagano, 2014b). Thanks to the privatisation of intellectual assets, production workers have been often expelled from knowledge-intensive firms and production activities are often located in different regions and countries. The global division of labour of contemporary intellectual monopoly capitalism has eliminated most remains of empathy and communication that had even survived the Tayloristic firm.

[19] In agriculture, slavery and hierarchy were possible at monitoring costs lower than in hunting and gathering where individuals had to be necessarily mobile. Thus, even when its overall productivity was inferior to the productivity of hunting and gathering, the transition to agriculture could be convenient for the dominant groups (Bowles and Choi, 2013; Scott, 2017). If, because of the frequent warfare among human tribes, cheap slave or serf labour was available, then agriculture could make the winners better off. What mattered for the winners was the cost to be paid for the forced labour of the losers. The transition to agriculture may have lowered monitoring costs and decreased the products' share of the workers. In this way, in spite of decreasing productivity, it may have increased the welfare of the dominant groups (Pagano, 2013).

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greatest part of the population. The transition to a complex division of labour 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 labour 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 labour. On the one hand, their insufficient individual investment in each newborn individual has prevented them from exploiting the Smithian advantages of the division of labour 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 centralised reproduction and a genetic division of labour analogous to that advocated in the Babbage principle.

If one plots a measure of the complexity of the division of labour as a function of the amount of parental investment in offspring, one obtains some sort of U-shaped curve, such as the one drawn in Figure 1, where a high level of complexity was achieved by social insects with a minimum investment and by humans with a maximum investment.[20]

Evolution refuted the Aristotelian principle '*In medio stat virtus*', meaning that successful behaviour is to be found in the middle. Only at the extremes of the evolutionary possible paths did a complex division of labour become possible, allowing some species to prosper and to colonise our planet. The many species in between these two extremes failed to evolve what was going to become such an amazingly successful evolutionary trait. This argument allows us to understand why only human and social insects have evolved a division of labour and also why Mandeville's fable referred to bees, not to

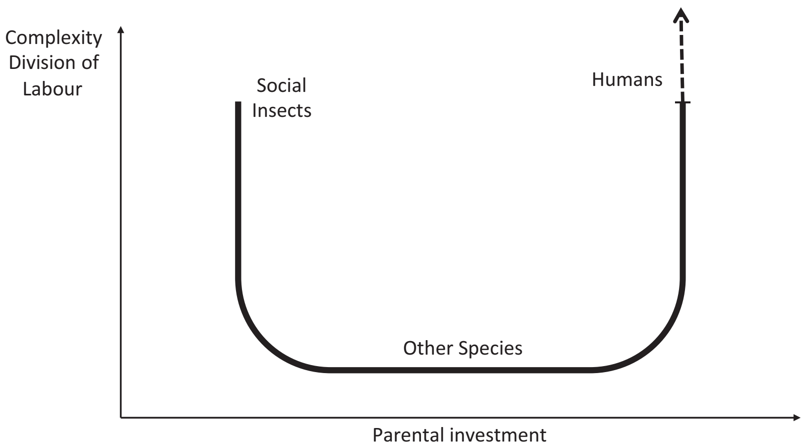

Fig. 1. *The U-shaped relationship between the complexity of the division of labour and parental investment.*

[20] The two extreme cases of Figure 1 are not symmetrical because at certain point humans started a process of knowledge accumulation and of cultural selection (dotted line). This entailed a much greater complexity of the division of labour.

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chimps, to gorillas or to some other of our close relatives. Paradoxically, minimum and maximum parental investments made the analogy possible.

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